PHENOTYPIC AND GENOTYPIC CHARACTERIZATION OF WHITE MAIZE INBREDS, HYBRIDS AND SYNTHETICS UNDER STRESS AND NON-STRESS ENVIRONMENTS

A Dissertation

by

DAN MAKUMBI

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

August 2005

Major Subject: Plant Breeding

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Approved by:

Chair of Committee,	Javier F. Betrán
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ABSTRACT

Phenotypic and Genotypic Characterization of White Maize Inbreds, Hybrids and Synthetics under Stress and Non-Stress Environments.

(August 2005)

Dan Makumbi, B.Sc., Makerere University, Kampala, Uganda;

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Maize is susceptible to biotic and abiotic stresses. The most important abiotic stresses in Africa are drought and low soil fertility. Aflatoxin contamination is a potential problem in areas facing drought and low soil fertility. Three studies were conducted to evaluate maize germplasm for tolerance to stress. In the first study, fifteen maize inbred lines crossed in a diallel were evaluated under drought, low N stress, and well-watered conditions at six locations in three countries to estimate general (GCA) and specific combining ability (SCA), investigate genotype x environment interaction, and estimate genetic diversity and its relationship with grain yield and heterosis. GCA effects were not significant for grain yield across environments. Lines with good GCA effect for grain yield were P501 and CML258 across stresses. Lines CML339, CML341, and SPLC7-F had good GCA effects for anthesis silking interval across stresses. Additive genetic effects were more important for grain yield under drought and well-watered conditions. Heterosis estimates were highest in stress environments. Clustering based on genetic distance calculated using marker data from AFLP, RFLP, and SSRs grouped lines according to origin. Genetic distance was positively correlated with grain yield and specific combining ability. In the second study, synthetic hybrids were evaluated at seven locations in three countries to estimate GCA and SCA effects under low N stress and optimal conditions and investigate genotype x environment interaction. GCA effects were significant for all traits across low N stress and optimal conditions. The highest yielding synthetic hybrids involved synthetics developed from stress tolerant lines. Synthetics 99SADVIA-# and SYNA00F2 had good GCA for grain yield across low N stress conditions. Heterosis was highly correlated with grain yield. Optimal environments explained more variation than stress environments. The third study evaluated the agronomic performance and aflatoxin accumulation of single and three-way cross white maize hybrids at five locations in Texas. Inbreds CML343, Tx601W, and Tx110 showed positive GCA

effects for grain yield. Significant GCA effects for reduced aflatoxin concentration were observed in lines CML269, CML270, and CML78 across locations. Differences in performance between single and three-way crosses hybrids were dependent mostly on the inbred lines.

DEDICATION

This dissertation is dedicated to the memories of my father Kosai, brothers Robert and Kefa, and sisters Margaret and Beatrice who did not live to see me get this far. Your support was always great.

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In closing, I thank God. For only through God's grace and blessings has this pursuit been possible.

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CHAPTER I

INTRODUCTION

Maize (*Zea mays* L.) is one of the three most important cereal crops in the world together with wheat and rice. Global production of maize reached 622 million metric tons in 2003-2004 (USDA-FAS, 2005). It is estimated that about 68% of the global maize area is in the developing world, but the developing world accounts for only 46% of the world's maize production (Pingali and Pandey, 2001). The United States is the world's largest producer and exporter of maize. In 2003-2004, maize production in the U.S. was 256 million metric tons (USDA-FAS, 2005). Maize produced in the United States is primarily used as livestock feed, with about 60% of the production being for that purpose. Maize is also used in a number of food and industrial products. The grain type of maize grown in the United States is the yellow dent type. Maize production in Africa in 2004 was estimated to be 41.6 million metric tons of which 27.4 million metric tons was produced in sub-Saharan Africa (FAOSTAT, 2005). In eastern and southern Africa, maize is by far the dominant staple crop grown by the vast majority of rural households. Consumption of maize is high throughout most of the region, reflecting its role as the primary food staple. Maize accounts for over 50% and 30% of the total calories consumed in eastern and southern Africa respectively (Hassan et al., 2001). In southern Africa, per capita annual consumption of maize averages more than 100 kg in several countries (Lesotho, 149 kg; Malawi, 181 kg; South Africa, 195 kg; Swaziland, 138 kg; Zambia, 168 kg; and Zimbabwe, 153 kg (CIMMYT, 1999). In eastern Africa, per capita annual consumption ranges from 40 kg in Burundi to 105 kg in Kenya (Hassan et al., 2001). The predominant grain color of maize grown in eastern and southern Africa is white since white maize is the dominant food staple in the region. Yellow-grained varieties are grown in some countries in southern Africa especially South Africa and Zimbabwe (Hassan et al, 2001).

Maize in Africa is grown by small- and medium-scale farmers who cultivate 10 ha or less (DeVries and Toenniessen, 2001) under extremely low-input/low risk systems where average maize yields are 1.3 Mg ha^{-1} (Bänziger and Diallo, 2004). Less than 50% of tropical maize is sown to hybrid seed with the rest sown to low yielding landraces (Hassan et al., 2001;

This dissertation follows the style and format of Crop Science.

Bellon, 2001). A number of maize production constraints both biotic and abiotic are present in the region. Biotic factors limiting maize production in the region include insect pests, diseases, and parasitic weeds. The most important insect pests in Africa include the spotted stem borer (*Chilo partellus*), African stem borer (*Sesamia calamistis*), stalk borer (*Busseola fusca*), and the pink stem borer (*Sesamia cretica*). Important storage pests are the grain weevil (*Sitopholus zeamais*) and the larger grain borer (*Prostephanus truncates*). The most important diseases of maize in eastern and southern Africa include turcicum leaf blight (*Exserohilum turcicum*), common rust (*Puccinia sorghi*), gray leaf spot (*Cercospora zeae-maydis*), and the maize streak virus transmitted by *Cicadulina* leaf hoppers.

The most important abiotic stresses limiting maize production in eastern and southern Africa are drought and low soil fertility, and these two are among the most important stresses threatening maize production, food security and economic growth in eastern and southern Africa (Bänziger and Diallo, 2004). Maize production in sub-Saharan Africa shows variability through time (Hassan et al., 2001; Bänziger and Diallo, 2004) and this is attributed to abiotic stress (Bolaños and Edmeades, 1993a; DeVries and Toenniessen, 2001). Most tropical maize is produced under rain-fed conditions and many of the maize-growing environments in eastern and southern Africa are susceptible to drought. Drought at any stage of crop development affects production, but maximum damage is inflicted when it occurs around flowering. Edmeades et al. (1992) estimated that in the developing world, annual yield losses due to drought may approach 24 million tons, equivalent to 17% of a normal year's production. The incidence of stress may increase, due partly to global climate changes, displacement of maize to marginal environments by high value crops, and to declines in soil organic matter, reducing soil fertility and water holding capacity (Bänziger et al., 2000). Tropical soils also vary greatly, giving rise to differences in moisture and N at a single site within a single year (Beck et al., 1996). Tropical soils are renowned for their low soil fertility, particularly low nitrogen, and this ranks as the second most important abiotic constraint to maize production in tropical ecologies (Bellon, 2001). Intensified land use and the rapid decline in fallow periods, coupled with the extension of agriculture into marginal lands, have contributed to a rapid decline in soil fertility, particularly in sub-Saharan Africa (Bellon, 2001). In the tropics, drought and low soil fertility frequently occur in association (Bänziger et al., 1997). Maize in sub-Saharan Africa is produced in a wide range of environments that can be grouped into lowland tropical zones (0-1,000 meters above sea level

(masl)), wet subtropical zones (900-1500 masl), dry subtropical zones (900-1500 masl), and highland zones (>1800 masl), with varying amounts of rainfall (Hassan et al., 2001). In seasons when rainfall is high, maize crops are often severely N deficient (Bänziger et al., 2000). The International Maize and Wheat Improvement Center (CIMMYT) initiated programs to improve tropical maize for stress tolerance under both low N and drought conditions (Edmeades et al., 1992).

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

Drought and low soil fertility conditions are related to aflatoxin problems in maize (Widstrom, et al., 1990; Payne, 1992; Moreno and Kang, 1999). Aflatoxin contamination of maize is of great interest because of its potential impact on the health of all species using maize and its by-products as food. Aflatoxins are secondary metabolites produced by the fungus *Aspergillus flavus* Link and are potent liver toxins and carcinogens (Castegnaro, and McGregor, 1998; Scott and Zummo, 1988; Duvick, 2001; Cleveland et al., 2003). Aflatoxin contamination occurs worldwide. In the U.S., aflatoxin contamination of maize is chronic in the southeastern states and occurs, at least to a limited extent, each year (Scott and Zummo, 1988; Widstrom, et al., 1990; Payne, 1992). Several reports have been made on aflatoxin in maize in Africa (Setamou, et al., 1997; Cardwell et al., 2000; Bankole and Adebanjo, 2003). In the USA, grain with more than 20 ng g^{-1} of aflatoxin B1 is banned for interstate commerce and grain with more

than 300 ng g^{-1} of aflatoxin B1 cannot be used as livestock feed. Factors leading to increased aflatoxin accumulation in maize include poor husk coverage and insect damage. Some resistant germplasm has been reported but has not been incorporated into commercial hybrids. Maize germplasm from outside the U.S. is a possible source of resistance that can be introgressed into temperate germplasm.

This dissertation comprises three studies presented in chapters II, III, and IV. In Chapter I, a diallel study involving 15 tropical and sub-tropical white inbred lines was conducted under stress and nonstress conditions to estimate general and specific combining abilities of the inbred lines, investigate genotype x environment interaction across stress conditions and testing locations, and estimate genetic diversity in the inbred lines. In chapter III, synthetic hybrids were evaluated under low N stress and optimal conditions to estimate the general and specific combining abilities among synthetics, investigate genotype x environment interaction across stress conditions and testing locations for synthetics and their hybrids, and evaluate the performance of synthetic hybrids. In chapter IV, a study was carried out to compare the performance of white single crosses (SC) and three-way crosses (TWC) between exotic (tropical and subtropical) and temperate white lines, evaluate the SC and TWC hybrids for aflatoxin accumulation, and estimate combining abilities of the inbred lines for aflatoxin accumulation.

CHAPTER II

COMBINING ABILITY, HETEROSIS, AND GENETIC DIVERSITY IN TROPICAL MAIZE INBREDS UNDER STRESS AND NON-STRESS CONDITIONS

INTRODUCTION

Maize (*Zea mays* L.) crops in the tropics are continually exposed to drought. Drought at any stage of crop development affects production, but maximum damage is inflicted when it occurs around flowering. Edmeades et al. (1992) estimated that in the developing world, annual yield losses due to drought may approach 24 million tons, equivalent to 17% of a normal year's production. The incidence of stress may increase, due partly to global climate changes, displacement of maize to marginal environments by high value crops, and to declines in soil organic matter, reducing soil fertility and water holding capacity (Bänziger et al., 2000). In the tropics, drought and low soil fertility, mainly nitrogen deficiency, frequently occur in association. Nitrogen is the nutrient that most often limits maize yields in the lowland tropics (Lafitte and Edmeades, 1994a) yet a considerable proportion of maize in the tropics is grown under low nitrogen conditions (Bänziger et al., 1997).

Nitrogen deficiency is common where nitrogen (N) is applied at below-optimal levels because of high cost relative to economic returns, or where there are significant risks of drought and frost or of excessive leaching of nitrate (Lafitte and Edmeades, 1994a). Nitrogen is an essential component of all enzymes and therefore necessary for plant growth and development. There is a positive correlation among nitrogen uptake, biomass production, and grain yield. The application of N fertilizers and organic amendments can generally correct nitrogen deficiency, though these are often not available (Lafitte and Edmeades, 1994a) or are beyond the farmer's capability (Paterniani, 1990). It has been estimated that the average fertilizer application in sub-Saharan Africa is only 7 kg ha^{-1} (Bellon, 2001). One approach to reducing the impact of N deficiency on maize production may be to select cultivars that are superior in the utilization of available N, either due to enhanced uptake capacity or because of more efficient use of absorbed N in grain production (Lafitte and Edmeades, 1994a). Selection for yield in the target environment has been suggested as an effective method rather than selection for yield potential alone (Blum, 1988). However, such environments are not favored by maize breeders due to increased environmental variability as soil fertility declines resulting in a decline in heritability

for grain yield (Lafitte and Edmeades, 1994a). 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 and Hamblin, 1981).

Maize productivity in maize-based cropping systems could be greatly improved by using cultivars that utilize nitrogen more efficiently as well as tolerating the periodic droughts which befall the region. The development of cultivars that either escape or tolerate the stress is one way of reducing the effects of drought. Through conventional breeding, the International Maize and Wheat Improvement Center (CIMMYT) has made significant progress in developing maize germplasm tolerant to drought and low nitrogen (Edmeades et al., 1992; Lafitte and Edmeades, 1994a, b; Bänziger and Lafitte, 1997; Bänziger et al., 1997; Bänziger et al. 2000; Beck et al., 1996). This germplasm includes inbred lines and populations developed through different breeding programs within CIMMYT. With several regional breeding programs at CIMMYT, it is important to know the relationship between elite lines from different programs used as testers to produce experimental hybrids, and to gain an understanding of how this facilitates flow of materials and strategies for hybrid production. Furthermore, the germplasm available as inbred lines can be used to develop maize hybrids, either single-crosses or three-way crosses. Knowledge of the combining ability of this germplasm would be very beneficial to the breeders in deciding how to best develop single-cross hybrids, three-way cross hybrids, or synthetic varieties from these lines. Many countries in sub-Saharan Africa stand to gain from this germplasm by developing hybrids in their respective breeding programs through use of this improved germplasm in a bid to attain increased maize production. This will eventually lead to self sufficiency in food production. In addition to inbreds with some degree of stress tolerance, other elite inbreds have been developed in breeding programs with evaluation under optimal conditions in target environments. Several of these inbreds, which show good combining ability and yield potential, are used as testers to differentiate heterotic response of experimental lines.

Objectives of the study

(i) Estimate the general and specific combining abilities among tropical and sub-tropical inbred lines used as testers in different breeding programs for grain yield and other agronomic traits.

(ii) Investigate genotype x environment interaction across stress conditions and testing locations among inbred lines and their hybrids.

(iii) Estimate genetic diversity among this set of inbred lines and its relationship with grain yield and heterosis.

REVIEW OF LITERATURE

Breeding for abiotic stress environments has been done for a number of crops like oat (Atlin and Frey, 1989), barley (Ceccarelli, 1987), alfalfa (Rumbaugh et al., 1984), wheat (Fischer and Maurer, 1978; Kingsbury and Epstein, 1984; Ud-Din et al., 1992), and maize (Fischer et al., 1989; Edmeades et al., 1992; Bolaños and Edmeades, 1993a, b). Such abiotic stresses that affect crops include drought, low N, and low phosphorus. Drought, or more generally, limited water availability is the main factor limiting crop production and is a main constraint to agricultural production in many developing countries. Breeding maize for tolerance to drought and low nitrogen conditions has been ongoing at CIMMYT, and germplasm with tolerance to both stresses has been developed and progress documented (Edmeades et al., 1992; Bolaños and Edmeades, 1993a,b; Bolaños et al., 1993; Lafitte and Edmeades, 1994a, b, c; Bänziger et al., 1997; Bänziger and Lafitte, 1997; Beck et al., 1996).

Bolaños and Edmeades (1993a) evaluated eight cycles of selection for drought tolerance in lowland tropical maize and reported that selection under drought increased yield at the rate of 8.9% (30 kg ha^{-1}) per cycle. They also reported a significant gain of 9.4% for ears per plant and an increase in kernel number per fertile ear in early cycles of selection under drought conditions. Bolaños and Edmeades (1993a) further reported that about 25% of the gains that were recorded in those trials could be attributed to improved adaptation to the selection site. Bolaños and Edmeades (1993b) reported a reduction in time to 50% anthesis under well-watered and severe drought stress but a decrease of -3.4 days per cycle under severe stress. They also reported that the mean anthesis silking interval (ASI) increased to 18.8 days under severe stress conditions, but selection significantly reduced ASI from 34.2 days in C_0 to 9.8 days for cycle C_8. Bolaños and Edmeades (1993b, 1996) reported a strong dependence of grain yield on ASI. Bolaños and Edmeades (1996) reported an average genetic correlation of -0.48 between grain yield and ASI and noted that grain yield decreased to less than 20% of its well-watered levels as ASI increased from 0 to 5 days, and then declined asymptotically to almost zero yields as ASI increased.

Bolaños et al. (1993) reported no significant increase in relative leaf and stem extension rate, and reduced rates of leaf senescence under moisture stress after eight cycles of selection for drought tolerance. Yield under mild and severe water stress was negatively correlated with ASI, with correlation under severe stress being highly significant (Fischer et al., 1989). Betrán et al. (2003c) also reported high negative correlation between ASI and grain yield in hybrids and inbred lines.

Edmeades et al. (1999) evaluated changes in grain yield, biomass, and harvest index in three maize populations (La Posta Sequía, Pool 26 Sequía, and Tuxpeño Sequía) that had undergone recurrent selection for drought tolerance. Advanced cycles of the three populations significantly outyielded their original cycles of selection and the checks under drought stress conditions. Yield ranged from 1.0 to 4.5 Mg ha^{-1} and 5.8 to 10.4 Mg ha^{-1} under water stressed and well-watered conditions, respectively. Yield gains from selection across drought environments ranged from 0.08 to 0.29 Mg ha^{-1} (3.8 to 12.7%) per cycle while that across well-watered environments ranged from 0.04 to 0.18 Mg ha^{-1} (0.5 to 2.3%) per cycle. In the same population, Chapman and Edmeades (1999) obtained gain in selection that ranged from -1.18 to 0.44 days (-26.8 to -6.9%) per cycle for ASI and 0.025 to 0.075 (3.4 to 8.9%) per cycle for ears per plant (EPP) across drought environments. Across well-watered environments, gain in selection was -28.2 to -7.7% per cycle for ASI and 1.1 to 5.9% per cycle for EPP. Water deficits increased the average ASI to 4.5 days from an average of 1.0 days under well-watered conditions.

Lafitte and Edmeades (1994a) evaluated different cycles of full-sib recurrent selection under low and high N conditions. They reported that realized heritability was generally larger for yield under low N than for yield under high N, and that all traits evaluated had larger values of heritability when measured in cycle 2 versus cycle 0 of recurrent selection. Lafitte and Edmeades (1994b) evaluated four cycles of full-sib (FS) recurrent selection under low and high N levels for four seasons. They observed significant differences among FS families at both N levels for days to anthesis and silking, plant height, grain yield, ear-leaf area at low N, green leaf area below the ear for low N, and ear-leaf chlorophyll concentration for low N. Lafitte and Edmeades (1994b) noted that the observed variance among FS families was adequate to identify significantly different best and worst fractions of the population for most traits studied.

Presterl et al. (2003) reported a reduction of 37% in grain yield at low N compared to high N conditions. Genotypic correlation for grain yield between performance at high N and low N averaged 0.74. Genotypic correlation between grain yield at high N and low N decreased significantly with increasing levels of N deficiency stress. Heritability for grain yield averaged 65% both under high N and low N environments (Presterl et al., 2003). In a study to evaluate hybrid progenies of drought-tolerant populations and high-yielding lowland tropical single-cross hybrids in stress and nonstress environments, Zaidi et al. (2004) reported that ASI in the drought tolerant topcrosses averaged 2.0 and 4.5 days under low N and drought respectively, in the drought tolerant topcrosses. Anthesis silking interval averaged 17 and 4 days for single-cross hybrids under drought and low N stress environments, respectively. Ears per plant averaged 0.94 under drought and 1.08 under low N environments for the drought tolerant topcross hybrids.

Bänziger and Lafitte (1997) evaluated the relative value of secondary traits for improving the identification of high yielding maize genotypes in low N selection environments. They reported genetic correlations between grain yield and secondary traits which indicated that high grain yields were associated with a short anthesis-silking interval, increased number of ears per plant, larger leaf chlorophyll concentrations, and delayed leaf senescence. Pollmer et al. (1979) in a study of N uptake and N translocation among hybrids involving inbred lines highly diverse for percent grain protein found that additive and non-additive gene actions were important in the inheritance of N uptake and translocation. They observed that G x E interactions influenced the inheritances of N uptake and translocation. Similar results were reported by Beauchamp et al. (1976).

Four advanced populations selected for drought tolerance and their original cycles were evaluated in low and high N environments (Bänziger et al., 2002). Original and drought-tolerant cycles did not differ consistently in plant and ear biomass, N accumulation, ear N content or ear N concentration at silking. ASI was reduced in drought-tolerant selection cycles in comparison to the original cycles. Bänziger et al. (2002) reported that selection for tolerance to mid-season drought stress reduced ASI in severe N stress and changes in ASI explained changes in ears per plant that occurred with selection for tolerance to mid-season drought stress. Betrán et al. (2003c) reported a positive and significant correlation between EPP and grain yield in hybrids and inbred lines under both stress and non-stress environments, but stronger correlation under stress. Betrán et al. (2003b) evaluated seventeen maize inbred lines crossed in a diallel design under 12 stress and nonstress environments. They reported significant genotype and genotype x

environment interaction effects for grain yield of hybrids and inbred lines. Grain yield ranged from 1.14 Mg ha^{-1} to 9.18 Mg ha^{-1} under severe stress and well-watered conditions, respectively, with an average of 6.01 Mg ha^{-1} across environments for the hybrids. Grain yield for the inbreds ranged from 0.15 Mg ha^{-1} to 3.95 Mg ha^{-1} under severe stress and well-watered conditions respectively. Correlation between midparent and hybrid were significant at ten environments (0.20-0.61) and non-significant for two environments (0.04-0.14).

Considerable genetic variation for performance under stress conditions has been reported by Lafitte and Edmeades (1994a) and Bänziger et al. (1997) in maize, Atlin and Frey (1989) in oat, and Ud-Din et al. (1992) in wheat. Bänziger et al. (1997) evaluated maize germplasm adapted to lowland tropics under high and low N conditions. They found that genotypic variance for grain yield under low N was about one third of the average genotypic variance for grain yield under high N, but the average error variance was similar at both low and high N levels. They found that among low N experiments, genotypic variance and error variance for grain yield tended to decrease with increasing relative yield reduction under low N while heritability did not change. Bänziger et al. (1997) further reported that broad sense heritabilities of grain yield under low N were smaller than under high N. They reported positive genetic correlation between grain yield under low and high N. Ceccarelli et al. (1992) reported variable genetic correlations between grain yield in low-yielding sites and grain yield in high yielding sites. Bänziger et al. (1999) evaluated populations of maize improved for tolerance to drought under both well-fertilized and N stress. Selection for tolerance to midseason drought stress led to an increase in grain yield of 86 kg ha^{-1} yr^{-1} across populations, and N levels increases in biomass were larger under severe N stress. In a study involving 270 full-sib families derived from drought-tolerant-population Pool 16DT, Badu-Apraku et al. (2004) estimated heritability for drought adaptive traits and genetic correlations among them. Narrow sense heritability for ASI was 23% in nonstress and ranged between 22 to 51% in stress environments, respectively, while heritability for days to anthesis (AD) was 30% in nonstress environments and ranged between 34 to 52% in stress environments. Genetic correlation between grain yield and AD was negative at each of the two sites and across sites while that between grain yield and ASI was positive across sites. Dow et al. (1984) reported that the date of mid anthesis and anthesis silking interval were highly correlated to drought resistance (-0.61 and -0.71 respectively).

Atlin and Frey (1989) estimated genotypic correlation between yields in non-stress environments and yields in low N, low P, and later planted oat. They found that N stress reduced the grain yield of oat by more than 50%. They suggested that an identical complement of alleles controlled yield at both N levels. They found the heritability of grain yield to be slightly greater in high N than in low N environments. From their study, they noted that genotype by stress-level interaction was common. Ud-Din et al. (1992) estimated genetic parameters for grain production in drought stress and irrigated environments in a winter wheat population. They found that genetic variance for grain yield was greater in the irrigated environments than in the stress environments. They reported that the error variances were higher than genetic variances in drought-stressed and irrigated environments. Ud-Din et al. (1992) also reported low genetic correlation between grain yields in drought-stresses and irrigated environments. The heritability estimates for grain yield in the irrigated environments was slightly higher than that in the dryland environment. Ceccarelli (1987) evaluated F_3 families of barley in two environments with differing rainfall amounts. A high and negative correlation was found between the drought susceptibility index and grain yield at the driest site indicating that larger yields are associated with higher levels of drought tolerance or with higher stability. The highest yielding families under moisture stress had grain yield below average under more favorable conditions. Fischer and Maurer (1978) reported significant reduction in yield of wheat cultivars subjected to drought stress. Mild drought stress led to a greater reduction in kernel weight than in grain number, but grain number was reduced more as drought severity increased.

Heterosis and genetic diversity

The term heterosis was coined by Shull (1952). Heterosis is defined as the difference between the hybrid value for one trait and the mean value of the two parents for the same trait (Falconer and Mackay, 1996). Heterosis is important in maize breeding and is dependent on level of dominance and differences in gene frequency. The manifestation of heterosis depends on genetic divergence of the two parental varieties (Hallauer and Miranda, 1988). Genetic divergence of the parental varieties is inferred from the heterotic patterns manifested in a series of variety crosses. Heterosis in maize has been investigated extensively. Hallauer and Miranda (1988) summarized results from studies on heterosis for grain yield in maize up to 1979. Mid-parent heterosis ranged from -3.6% to 72.0% while high-parent heterosis ranged from -9.9% to 43.0%. Crossa et al. (1987) reported estimates of heterosis as percentage of high yielding parent

ranging from 0 to 47.7 in maize population crosses. In a study by Vasal et al. (1992a), high-parent heterosis ranged from -3.1% to 12.7% for grain yield, -7.7% to 4.5% for plant height, -4.7% to -0.1 for days to silk in pools and populations.

Genetic distance (GD) based on molecular markers has been suggested as a tool for grouping of similar germplasm as a first step in identifying promising heterotic patterns (Melchinger, 1999). The development of molecular marker techniques has provided new tools for heterosis prediction and DNA markers have been used extensively in investigating correlations between parental GD and F_1 performance or mid-parent heterosis (MPH). If well-established heterotic groups are not available, marker-based GD estimates can be used to avoid producing and testing of crosses between related lines. Furthermore, crosses with inferior MPH could be discarded prior to field testing based on prediction. Genetic distance could also be used in the choice of an appropriate tester for evaluating the combining ability of lines in testcrosses (Melchinger, 1999).

Melchinger et al. (1990b) evaluated diversity for restriction fragment length polymorphisms and heterosis in two sets of maize inbreds. Genetic distance (Roger's Distance, RD) ranged from 0.57 to 0.69 and 0.31 to 0.68 in the older and newer inbred lines, respectively. Positive correlations were found between RD and F_1 performance for grain yield, specific combining ability (SCA) effects, and heterosis, and it was noted that the RDs of the parental lines were of no predictive value for the yield of single crosses. A significant correlation was found between RD and heterosis for grain yield. Melchinger et al. (1992) reported positive correlations of GD with F_1 performance, MPH, and SCA that ranged between 0.09 and 0.60 among flint and dent maize inbred lines. Senior et al. (1998), in a study to assess genetic similarities among 94 maize inbred lines, used 70 simple sequence repeat (SSR) marker loci. Their analysis revealed that the SSR loci used in the study had average polymorphism information content (PIC) of 0.59 with a range of 0.17 to 0.92. Senior et al. (1998) found genetic similarities among the 94 maize inbred lines that ranged from 0.21 to 0.90 and clustering using the Unweighted Pair Group Method using Arithmetic Averages (UPGMA) grouped the inbred lines into nine clusters. Senior et al. (1998) reported that principal component analysis also revealed the same clustering as UPGMA and this agreed with the pedigree of the inbred lines and that the clusters were representative of heterotic groups.

Melchinger et al. (1991) assessed genetic diversity among thirty-two U.S. maize inbred lines belonging to the Iowa Stiff Stalk Synthetic (BSSS), Reid Yellow Dent (RYD), and Lancaster Sure Crop (LSC) groups using restriction fragment length polymorphism (RFLP). Genetic distance (Roger's Distance, RD) averaged 0.54, 0.57, 0.60, 0.58, and 0.60 for line combinations BSSS x BSSS, LSC x LSC, BSSS x LSC, RYD x BSSS, and RYD x LSC, respectively. Principal component analysis of the RFLP data revealed that the first three principal components accounted for 18.5% of the total variation and the lines grouped according to their known phylogenetic relationships, with BSSS and LSC lines forming two clearly separate groups. Thirty three U.S. maize inbred lines were studied for genetic similarity and also used to compare the informativeness of restriction fragment length polymorphism (RFLP), random amplified polymorphic DNA (RAPD), simple sequence repeat (SSR), and amplified fragment length polymorphism (AFLP) for genetic diversity analysis (Pejic et al., 1998). Their results showed that SSRs revealed the lowest similarity values and AFLPs the highest values. Pejic et al. (1998) reported that in genetic similarity trees generated from the four different markers, the inbred lines were grouped according to the major groups of BSSS and LSC with a few exceptions. They further noted that SSR data provided the highest level of discrimination between any pair of inbreds and that, in general, the grouping agreed with pedigree information of the lines. Pejic et al. (1998) also reported that genetic similarities based on AFLP data had the highest correlation with pedigree data, while those based on RAPDs had the lowest correlation.

Reif et al. (2003b) using 85 SSR markers studied the relationship between genetic distance and heterosis in seven tropical maize populations. Genetic distance (modified Roger's distance, MRD) between pairs of populations averaged 0.26 with a range of 0.20 to 0.32. Their results showed that in the analysis of molecular variance (AMOVA), 89.8% of the molecular genetic variance was found within populations and 10.2% between populations. Principal coordinate analysis based on modified Roger's distance revealed that the first three principal coordinates explained 65.2% of the total variation. Squared modified Roger's distance was significantly correlated with panmictic mid-parent heterosis (PMPH) for grain yield (r = 0.63) and negatively correlated for days to silking (r = -0.44) and plant height (r = -0.13). Reif et al. (2003b) concluded that the low correlations between squared modified Roger's distance (MRD^2) and PMPH for plant height and days to silking were mostly due to small PMPH estimates for the two traits. Reif et al. (2003b) noted that the classification of the seven populations based on SSR data mostly confirmed the results of the diallel data set except for one population. A similar

result was reported by Reif et al. (2004) using SSRs and Parentoni et al. (2001) using RAPDs among tropical maize populations. In another study involving 20 pools and populations in three separate experiments, MRD between pairs of populations based on SSR data ranged from 0.21 to 0.30, 0.21 to 0.31, and 0.27 to 0.33 for experiment 1, 2, and 3, respectively (Reif et al., 2003a). Polymorphism information content ranged from 0.10 to 0.85 for the SSR loci and analysis of molecular variance revealed that about 12% of the molecular variance was among and the rest within populations. Specific combining ability was found to be highly correlated to the specific MRD^2 in tropical and sub-tropical environments while PMPH was highly correlated to MRD^2 (Reif et al., 2003a).

Reif et al. (2004) reported that principal coordinate analysis based on MRD estimates of tropical, subtropical, and temperate maize populations revealed a total of 34.2% of the molecular variance to be explained by the first two principal coordinates (PC), with PC1 separating the tropical populations from the others. They also reported that most of the variation was within the populations and very little between populations. Xia et al. (2004) studied genetic diversity among eighty six and sixty nine yellow lowland tropical maize inbred lines using SSR markers. Polymorphism information content of the SSR markers ranged from 0.13 to 0.87. Genetic distance for yellow x yellow and white x white line combinations ranged from 0.44 to 0.88 and 0.37 to 0.89, respectively, with an average of 0.76. The average genetic distance for white x yellow line combinations was 0.77. Cluster analysis showed that among the white inbreds, lines derived from the Tuxpeño synthetic Pop43 formed one group while lines derived from quality protein maize (QPM) populations also clustered together. Xia et al. (2004) reported that few clear groups could be identified through cluster analysis of the yellow tropical maize inbred lines. In a study to characterize maize inbred lines and open pollinated populations using SSR markers, the open pollinated populations clustered as predicted based on pedigree and known heterotic groups (Warburton, et al., 2002). Warburton et al. (2002) reported further that among the inbred lines, the dendrogram generated did not show good association based on heterotic grouping as assigned by field evaluations and testers. Melchinger et al. (1990a) and Smith et al. (1997) reported that cluster analysis using data from RFLP and SSR revealed associations of inbreds similar to that expected based on pedigree data.

Benchimol et al. (2000) calculated genetic distance among eighteen tropical maize inbred lines derived from a synthetic population and a composite population using RFLP markers. Modified Roger's Distance ranged from 0.39 to 0.83 with a mean of 0.74, with the

Brazilian composite population showing a greater range (0.39 to 0.80) compared to the Thai synthetic population (0.57 to 0.76). Cluster analysis led to grouping of the populations into two according to their heterotic patterns. Benchimol et al. (2000) reported that simple correlations of genetic distance and with F1 performance and heterosis were highly significant (0.60 and 0.57, respectively). Barbosa et al. (2003) also reported highly significant correlation between genetic distance and F_1 performance (0.71) and genetic distance and heterosis (0.67) in a study using AFLP markers on inbred lines derived from the same populations used by Benchimol et al. (2000).

Parentoni et al. (2001) in a study involving twenty eight open pollinated varieties reported a low but significant correlation ($r = 0.16$) between marker genetic distance and specific combining ability. Lubberstedt et al. (2000) evaluated genetic diversity among fifty one early European maize inbreds and reported that genetic similarity estimates for unrelated line combinations of flint x flint ranged from 0.47 to 0.77 while those of dent x dent ranged from 0.45 to 0.69 with a mean of 0.57 and 0.55, respectively. Principal coordinate analysis calculated from AFLP genetic similarity estimates clearly separated the dent from the flint lines. Lubberstedt et al. (2000) noted that correlation between genetic similarity estimates based on AFLP, RAPD, and RFLPs were highly significant and ranged from 0.43 to 0.67 for flint and dent lines, with the highest correlation being between genetic similarity estimate based on AFLP and RFLP data. Betrán et al. (2003a) evaluated tropical maize inbreds under stress and nonstress conditions and estimated genetic diversity for RFLPs, genetic distance, and heterosis. Polymorphism information content ranged from 0.28 to 0.82 for the RFLP probes. Average genetic distance among the inbred lines ranged from 0.20 to 0.84 with an average of 0.72, with sister lines having a low GD (<0.25). Principal component analysis using the calculated GD classified the inbred lines according to their origin and pedigree. Genetic distance was positively correlated with F_1 performance, MPH and high-parent heterosis (HPH) in all environments. Betrán et al. (2003a) indicated that correlations of GD with MPH and HPH increased when the drought-stress levels decreased.

A study of genetic diversity among sixty eight wheat lines targeted for different megaenvironments analyzed with 99 SSRs revealed that genetic similarity for all pairs of lines ranged from 0.39 to 0.91 with a mean of 0.59 for all genotypes (Dreisigacker et al., 2004). Dreisigacker et al. (2004) also reported that principal coordinate analysis based on modified Roger's distances did not separate the genotypes according to their targeted megaenvironments.

In another study on wheat landraces, genetic distances ranging between 0.16 and 0.82 were reported and principal coordinate analysis based on MRD did not separate the accessions according to their countries of origin (Dreisigacker et al., 2005). Bohn et al. (1999) reported that genetic similarity ranged from 0.40 to 0.83, 0.52 to 0.89, and 0.16 to 0.91 based on AFLP, RFLP, and SSR markers, respectively among winter wheat crosses. Genetic similarity across all marker systems ranged from 0.53 to 0.87, with an average of 0.63. Cluster analysis using UPGMA based on genetic similarity estimates did not show distinct separation of cultivars.

Combining ability

The concepts of general and specific combining ability were introduced by Sprague and Tatum (1942). General combining ability (GCA) is the average performance of a line in hybrid combination and specific combining ability (SCA) is the deviation of crosses on the basis of average performance of the lines involved. Diallel analysis is used to estimated GCA and SCA effects and their implications in breeding (Griffing, 1956; Gardner and Eberhart, 1966; Baker, 1978). Griffing (1956) proposed an analysis for diallel mating systems that estimate the general and specific combining abilities of lines and hybrids. Combining ability analysis is important in identifying the best parents or parental combinations for a hybridization program. General combining ability is associated to additive genetic effects while specific combining ability is associated to non-additive genetic effects (Falconer and Mackay, 1996). Combining ability has been investigated by several authors in maize (Beck et al., 1990; Crossa et al., 1990; Vasal et al., 1992a,b; Kang et al., 1995; Kim and Ajala, 1996; Wang et al., 1999; Mickelson, et al., 2001; Betrán et al., 2002; Revilla et al., 2002; Betrán et al., 2003a,b; Bhatnagar et al., 2004; Long et al, 2004; Menkir and Ayodele, 2005) and in other crops (Boye-Goni and Marcarian, 1985; Nienhuis and Singh, 1986; Borges, 1987; Tenkouano et al., 1998; Hartman and St. Clair, 1999) for different traits.

Vasal et al. (1992a) evaluated 7 tropical white maize populations crossed in a diallel mating design for grain yield, plant height, and days to silking at seven locations. They reported GCA to account for 67%, 85%, and 78% of the sums of squares among crosses for grain yield, days to silk, and plant height, respectively. Vasal et al. (1992a) reported that GCA x E interaction for grain yield was not significant while that for days to silk and plant height were significant. Positive and significant GCA effects for grain yield for three of the populations and negative significant GCA effects for two populations were reported but no significant SCA

effects were found for grain yield. Vasal et al. (1992b) and Hede et al. (1999) also reported positive GCA effects for grain yield for some tropical maize inbred lines. Hede et al. (1999) evaluated twenty three inbred lines test crossed to synthetic lines and reported that crosses with significant positive SCA effects for yield were inter-population crosses. Kang et al. (1995) reported that GCA was more important than SCA in inheritance of maize weevil preference or non-preference and proposed a recurrent selection procedure to improve inbred lines with positive GCA effects. Kim and Ajala (1996) reported positive GCA effects for grain yield in tropical maize inbreds grown in two forest environments and noted that SCA effects were a major factor for inbred lines from tropical x temperate crosses. Betrán et al. (2003b) evaluated seventeen maize inbred lines crossed in a diallel design under stress and nonstress environments and reported significant GCA and GCA x environment interaction effects for grain yield. Betrán et al. (2003a) reported significant SCA effects ranging from -3.78 Mg ha^{-1} to 1.12 Mg ha^{-1} for grain yield but non-significant SCA x environment interaction effects for grain yield.

MATERIALS AND METHODS

Germplasm

Fifteen inbred lines of tropical origin with a range of response to abiotic stresses that were developed by breeding programs at CIMMYT-México and CIMMYT-Zimbabwe were used in this study (Table 2.1). The inbred lines included five from the sub-tropical program at CIMMYT México (P502, P501, CML78, CML311, CML321), four from the stress breeding program at CIMMYT México (CML339, CML341, SPLC7-F, CML343), three from the tropical program at CIMMYT México (CML247, CML254, CML258), and three from the maize breeding program at CIMMYT Zimbabwe (CML202, CML206, CML216). These inbreds are or have been used as testers by the different programs to evaluate new experimental lines and classify them in potential heterotic groups. Diallel crosses were made among the fifteen inbred lines in 1996-7 at CIMMYT México. Seeds from reciprocal crosses were bulked to form a set of 105 F_1 hybrids.

Table 2.1. Maize inbred lines used in a diallel study evaluated under stress and non-stress conditions in Africa and America, their pedigree, and classification.

Line	Pedigree	Classification
CML78	P.32 C19MH32-1-#2-B-###-3-B	Sub-tropical
CML311	S89500 F2-2-2-2-B*5	Sub-tropical
CML321	P502C0F1-1-3-1-B*4	Sub-tropical
CML247	P24F119*P24F54)-6-4-1-1-BB-f	Tropical
CML254	TUXSEQ-149-2-BBB-##-1-BB-f	Tropical
CML258	21C5HC218-2-3-B-###-B-1-BBB-f	Tropical
CML202	ZSR 923 S4BULK-5-1-B-B	Mid-altitude
CML206	[EV7992#/EVPOP44-SRBC3]#BF37SR-2-3SR-2-4-3-B-B	Mid-altitude
CML216	[MSR:131]-3-3-3-5-B-B	Mid-altitude
CML339	LPSC3-H297-2-1-1-1-3-#-#-B-B-B	Tropical
CML341	LPSC3-H1-2-2-2-1-1-##-B-B-B	Tropical
CML343	LPSC3-H17-1-2-3-2-1-##-B-B-B	Tropical
P501 (CML379)	P501c1#-303-1-1-1-2-B	Sub-tropical
P502 (CML384)	P502c1#-771-2-2-1-3-B	Sub-tropical
SPLC-F	SPLC7-F254-1-2-3-2-1-B-B	Sub-tropical

Environments and stress management

The F_1 hybrids were evaluated at Tlaltizapán and Poza Rica in México, College Station and Weslaco in Texas, USA, and Harare and Chiredzi in Zimbabwe (Table 2.2). The following growing conditions were used:

(i) drought stress

(ii) low nitrogen stress conditions

(iii) well-watered and optimal fertilization.

Water stress was achieved by withholding water from 2 weeks before silking to the end of the flowering period. Low nitrogen stress conditions were achieved at the sites by continuous cropping of maize without N fertilizer application. In the well-watered experiment, irrigation water was supplied to avoid moisture stress. There were four well-watered, two drought stress, and two low-N stress environments (Table 2.2). The 15 parental inbred lines were also evaluated under well-watered, drought stress, and low N stress at Harare, Chiredzi, and Poza Rica in separate experiments adjacent to the hybrid trials. Standard cultural and agronomic practices were followed in trial management.

Experimental design and field measurements

The experiments were planted in 1999 at all locations. All experiments were planted in an alpha-lattice design (Patterson and Williams, 1976) with two replicates and two row plots at each environment. Plot sizes varied by location (Table 2.2). Measurements on plot basis were recorded on the following agronomic traits: anthesis date (days from planting to 50% pollen shed), silking date (days from planting to 50% silking), plant height (distance in cm from the ground to the top of tassel), ear height (distance in cm from the ground level to the node bearing the main ear), and ears per plant (ratio of number of ears to number of plants harvested). An ear was counted if it had at least one fully developed grain. Anthesis silking interval was calculated as the difference between silking and anthesis dates (ASI = SD – AD). Grain weight was measured and used to calculate grain yield (expressed in Mg ha^{-1} and adjusted to 87.5% moisture content). Grain moisture (g kg^{-1} moisture) of grain at harvest was measured using a moisture meter or provided by combine mounted equipment. Leaf senescence was scored on a scale from 0 to 10 by dividing the percentage of estimated total leaf area that is dead by 10. A score of 1 = 10%; 2 = 20%; 3 = 30%, 4 = 40%; 5 = 50%; 6 = 60%; 7 = 70%; 8 = 80%; 9 = 90%, and 10 = 100% dead leaf area (Bänziger et al, 2000).

DNA finger printing

Maize genomic DNA was extracted from the 15 inbred lines according to CIMMYT's Applied Biotechnology Center Manual of Laboratory Protocols (CIMMYT, 2001). For RFLP analyses, DNA was purified, quantified, digested with the restriction enzyme (*Eco*RI), separated in agarose gels (0.7%, w/v) and transferred to nylon membranes by Southern blotting. Labeled probes (digoxigenin-dUTP) were used to detect polymorphism with antidigoxigenin-alkaline phosphatase-AMPPD chemiluminescent reaction. A set of 80 restriction fragment length polymorphism probes spread across the genome were used to screen the plant material. RFLP patterns were binary coded by 1 for presence or 0 for absence of bands in each inbred line.

AFLP marker analyses were performed as described by Vos et al. (1995). Genomic DNA of the maize inbred lines was digested with enzymes *Eco*RI and *Mse*I in a buffer. Double-stranded adapter sequences were ligated to the restricted DNA fragment ends. Six primer combinations used for amplification were ACA-CAT, ACA-CAC, ACA-CAG, ACA-CGA, ACA-CGG, and ACA-CGT. The polymerase chain reaction (PCR) products were separated by electrophoresis on a denaturing polyacrylamide gel. After drying, the gels were exposed to phosphor-imager plates for 16 hours. The imager plates were scanned with a phosphor-imager and polymorphic bands were binary scored by 1 or 0 for presence or absence in each inbred line respectively.

For SSR analyses, the procedure and PCR conditions described in detail by Warburton et al. (2002) were followed. Thirty two SSR markers were chosen from the MaizeDB database to genotype the 15 maize inbred lines. Fragments were separated using acrylamide gels run on an ABI377 automatic DNA sequencer. Fragment sizes were calculated with GeneScan 3.1 (Perkin Elmer/Applied Biosystems) using the Local Southern sizing method. Allele identity was assigned using Genotyper 2.1 (Perkin Elmer/Applied Biosystems). Simple sequence repeat bands were binary coded by 1 or 0 for their presence or absence in each inbred line.

Statistical analyses

Analysis of variance per environment was conducted with the PROC MIXED procedure (SAS, 1997) considering genotypes as fixed effects and reps and blocks within reps as random. Adjusted means were used to estimate general combining ability (GCA) effects of the parents and specific combining ability (SCA) effects for the crosses following Griffing's Method IV

Table 2.2. Locations and environments used to evaluate F_1 hybrids and inbred lines and their characteristics and codes.

Location	Country	Latitude	Longitude	Altitude	Type of environment	Code	Plot Size
				masl†			**m**
Chiredzi	Zimbabwe	21°03' S	31°57' E	395	Drought stress	ZBSS	4.0 x 0.75
Harare	Zimbabwe	17°48' S	31°02' E	1506	Well-watered	ZBWW	4.5 x 0.75
Harare	Zimbabwe	17°48' S	31°03' E	1506	Low N stress	ZBLN	4.0 x 0.75
College Station, TX	USA	30°37' N	96°29' W	96	Well-watered	CSWW	6.4 x 0.75
Weslaco, TX	USA	26°09' N	97°99' W	22	Well-watered	WEWW	6.4 x 0.75
Tlaltizapán	México	18°41' N	99°07' W	940	Well-watered	TLWW	5.0 x 0.75
Tlaltizapán	México	18°41' N	99°07' W	940	Drought stress	TLSS	5.0 x 0.75
Poza Rica	México	21°55' N	97°48' W	60	Low N stress	PRLN	5.0 x 0.75

†masl, meters above sea level.

(crosses only) and Model I (fixed) of diallel analysis (Griffing, 1956) using a modification of the DIALLEL-SAS program (Zhang and Kang, 1997). Combined analyses of variance across locations were computed using PROC GLM in SAS (SAS, 1997). The significance of GCA and SCA sources of variation was determined using the corresponding interaction with the environments as the error terms. The significance of GCA x environment and SCA x environment interactions was determined using the pooled error. GCA and SCA variance components of mean squares were calculated assuming a fixed model for the diallel. The relative importance of GCA and SCA was estimated according to Baker (1978) as the ratio $\frac{2\hat{\sigma}^2_{GCA}}{(2\hat{\sigma}^2_{GCA}+\hat{\sigma}^2_{SCA})}$ where $\hat{\sigma}^2_{GCA}$ and $\hat{\sigma}^2_{SCA}$ are the variance components for GCA and SCA, respectively.

Genotypic and phenotypic correlations were calculated between traits for each environment and across environments considering genotypes (hybrids and inbreds) as random effects. Repeatability was estimated for each trait per environment and across environments for hybrids and inbred lines considering genotypes random. Repeatability was calculated as $R=\frac{\sigma^2_g}{\sigma^2_g+\frac{\sigma^2_e}{r}}$ where σ^2_g is the genotypic variance, σ^2_e is the error variance and r is the number of replications for a single environment. Across environments, repeatability was calculated as $R=\frac{\sigma^2_g}{\sigma^2_g+\frac{\sigma^2_{ge}}{e}+\frac{\sigma^2_e}{re}}$ where σ^2_g is the genotypic variance, σ^2_{ge} is the genotype x environment variance, σ^2_e is the error variance, *e* is the number of environments, and *r* is the number of replications for a single environment. Genotypic and phenotypic correlations and repeatability were calculated using SAS (Holland et al, 2003; and SAS codes available at www4.ncsu.edu/~jholland/correlation).

Adjusted means for hybrids and inbred lines across locations were estimated using of PROC MIXED procedure in SAS (SAS, 1997). Additive Main Effects and Multiplicative Interaction (AMMI) analysis of grain yield and ASI of lines in hybrid combination and inbred lines *per se* was carried out to assess the relationship among inbreds and environments and also to assess SCA among inbred lines. This analysis was carried out using IRRISTAT (IRRI, 1998) and Biplot v1.1 (Dr. E.P. Smith, Virginia Tech; http://www.stat.vt.edu/facstaff/epsmith.html).

Stability analysis of hybrids and parental inbreds across locations and stresses was conducted with joint linear regression method (Eberhart and Russell, 1966) using IRRISTAT (IRRI, 1998) and SAS.

Mid-parent and high-parent heterosis were calculated using the adjusted means of the hybrids and inbred lines. Mid-parent heterosis was calculated as $\text{MPH} = \frac{(F_1 - \text{MP})}{\text{MP}} \text{x}100$ where, F_1 is the mean of the F_1 hybrid performance and MP = $(P_1 + P_2)/2$ where P_1 and P_2 are the means of the two inbred parents. High-parent heterosis was calculated as $\text{HPH} = \frac{(F_1 - \text{HP})}{\text{HP}} \text{x}100$ where HP is mean of the best parent. Simple linear regression was computed to determine the relationship between grain yield, specific combining ability, and mid-parent heterosis.

Polymorphism information content (PIC) for the SSR and RFLP markers in the sample DNA was calculated as PIC = 1- Σp^2_i where p_i is the frequency of the i^{th} allele in a locus for individual p. Genetic similarity (GS) between any pair of inbred lines and marker type was calculated from the matrix of 0 and 1 based on the Dice coefficient (Dice, 1945) using NTSYSpc (Rohlf, 1998). Genetic distance (GD) between a pair of lines based on AFLP data was calculated using the method of Nei and Li (1979) as $GD = 1 - \frac{2N_{ij}}{N_i + N_j}$ where N_{ij} is the number of bands common to lines *i* and *j*, and N_i and N_j are the total number of bands for lines *i* and *j*, respectively. Genetic distance based on RFLP and SSR markers was estimated between any pair of lines using both the method of Nei and Li (1979) and Modified Roger's Distance (Wright, 1978). Modified Roger's Distance, $MRD = \sqrt{\frac{1}{2m}\sum_{i=1}^{m}\sum_{j=1}^{ai}(pij - qij)^2}$ where p_{ij} and q_{ij} are the allele frequencies of the j^{th} allele at the i^{th} marker in the two lines under consideration, a_i is number of alleles at the ith marker, and *m* is the number of markers.

Cluster analysis of genetic distances using the Unweighted Pair-Group Method using Arithmetic Averages (UPGMA) method was carried out to identify relationships among the inbred lines using NTSYSpc software (Rohlf, 1998). This was done using GD estimates between all pairs of inbred lines calculated from each of the AFLP, RFLP, and SSR data and also using GD estimates calculated when the data from the three marker types was combined. Simple linear regression was carried out to investigate the relationship between GD and grain yield, specific combining ability, and mid-parent heterosis.

RESULTS AND DISCUSSION

Well-watered environments

Highly significant differences ($P<0.01$) were observed among the hybrids for all traits except grain yield across well-watered environments (Table 2.3). Mean days to silking was 88.63 d (range 82.80 – 93.19 d). Days to anthesis ranged from 83.46 to 92.91 d with a mean of 88.04. Mean anthesis silking interval was 0.73 d (range -1.17 to 1.54) while mean number of ears per plant was 1.09 (range 0.83 to 1.54). Mean grain yield ranged from 3.18 to 5.35 Mg ha^{-1}, with a mean of 4.26 Mg ha^{-1}. The highest yielding hybrid across well-watered environments was CML216 x CML341 (5.35 Mg ha^{-1}). Combining ability analysis revealed significant GCA for all traits except grain yield and significant SCA mean squares ($P<0.05$) for all traits except grain yield and ears per plant (Table 2.3). Ears per plant showed significant GCA but not significant SCA mean square. Specific combining ability mean squares were consistently smaller than GCA mean squares, suggesting that non-additive effects are less important than additive effects for these traits.

Hybrid x environment interaction was highly significant for all traits ($P<0.001$). This suggested that the hybrids did not perform consistently across locations. There was highly significant ($P<0.001$) GCA x environment (E) interaction for all traits. SCA x environment interaction was significant ($P<0.05$) for grain yield and highly significant for anthesis date, silking date, plant and ear height, ASI and ears per plant but not significant for grain moisture. Significant GCA x environment for all traits indicates that GCA effects associated with parents were not consistent over locations. The larger magnitude of GCA mean squares compared to GCA x E mean squares for plant and ear height, anthesis and silking date suggests that interaction effects may be of relatively minor importance for these traits.

Table 2.3. Combined analysis of variance and means for grain yield and agronomic traits across well-watered environments.

Source of variation	Mean squares									
	df	GY†	SD	PH	EH	GM	df	AD	ASI	EPP
		Mg ha^{-1}	**d**	**cm**		**g kg^{-1}**		**d**		**no.**
Environment (E)	3	1027.83***	24581.56***	58903.02***	140993.93***	4956.74***	2	35693.30***	57.99***	1.93***
Reps(E)	4	5.47**	2.78	333.39*	157.63	30.08***	3	4.57**	1.47	0.01
Hybrids	104	2.60	36.68***	846.25***	627.85***	22.75***	104	20.84***	3.24**	0.10***
GCA	14	7.39	229.21***	4345.16***	3562.93***	114.08***	14	123.45***	12.76*	0.51**
SCA	90	1.85	6.73***	301.97***	171.28*	8.53**	90	4.88***	1.76*	0.03
Hybrids x E	312	2.27***	5.62***	203.05***	163.94***	8.36***	208	3.91***	1.99***	0.04***
GCA x E‡	42	7.13***	18.70***	538.40***	427.63***	25.62***	28	14.22***	5.77***	0.14***
SCA x E§	270	1.52*	3.59***	150.88***	122.92***	5.67	180	2.31***	1.40***	0.03***
Error	414	1.22	1.60	107.36	71.47	4.86	312	1.26	0.94	0.02
Mean		**4.26**	**88.63**	**247.03**	**121.51**	**16.25**		**88.04**	**0.73**	**1.09**
Min.		**3.18**	**82.80**	**225.55**	**102.66**	**13.19**		**83.46**	**-1.17**	**0.83**
Max.		**5.35**	**93.19**	**271.00**	**146.05**	**22.97**		**92.91**	**3.99**	**1.54**
LSD (0.05)		**0.85**	**1.24**	**10.18**	**8.31**	**3.60**		**1.28**	**1.10**	**0.15**

*, **, *** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.

† AD, anthesis date; ASI, anthesis silking interval; EH, ear height; EPP, ears per plant GCA, general combining ability; GM, grain moisture; GY, grain yield; PH, plant height; SCA, specific combining ability; SD, silking date.

‡ GCA x E was used to test the significance of MS for GCA.

§ SCA x E was used to test the significance of MS for SCA.

Low N stress environments

Highly significant differences (P<0.01) were observed among the hybrids for all traits except anthesis silking interval, ears per plant and grain yield across low N environments (Table 2.4). Mean days to anthesis was 87.08 d (range 81.31 to 91.63 d) while days to silking ranged from 85.94 to 94.72 d with a mean of 90.34. Mean anthesis silking interval was 3.26 d (range 0.61 to 6.71) while mean number of ears per plant was 0.90 (range 0.61 to 1.10). Mean grain yield ranged from 0.91 to 3.85 Mg ha^{-1}. The highest yielding hybrid across low N stress environments was P501c x CML247 (3.85 Mg ha^{-1}). Combining ability analysis revealed highly significant (P<0.01) GCA mean squares for anthesis date, silking date and ears per plant (Table 2.4). SCA mean squares was significant (P<0.05) for only ear height (Table 2.4).

Hybrid x environment (E) interaction was highly significant (P<0.001) for grain yield and not significant for other traits, suggesting that the hybrids performed differently across locations. There was significant (P<0.05) GCA x E interaction for all traits except ears per plant. SCA x environment interaction was significant (P<0.001) for only grain yield. Significant GCA x environment for traits other than ears per plant indicate that GCA effects associated with parents were not consistent over locations. The larger magnitude of GCA mean squares compared to GCA x E mean squares for plant and ear height, anthesis and silking date suggests that interaction effects may be of relatively minor importance for these traits.

Drought stress environments

Highly significant differences (P<0.01) were observed among the hybrids for all traits except ears per plant and grain yield across drought stress environments (Table 2.5). Mean days to anthesis was 104.68 d (range 98.46 to 112.84 d) while days to silking ranged from 98.46 to 112.84 d with a mean of 105.99. Mean anthesis silking interval was 1.32 d (range -1.84 to 5.71 d) while mean number of ears per plant was 0.98 (range 0.65 to 1.37). Mean grain yield ranged from 1.48 to 4.53 Mg ha^{-1}. The highest yielding hybrid across drought stress environments was CML258 x CML343 (4.53 Mg ha^{-1}). Combining ability analysis revealed highly significant (P<0.01) GCA mean squares for all traits except grain yield, plant height and ears per plant (Table 2.5). SCA mean squares were not significant for grain yield, ears per plant, and grain moisture (Table 2.5). Hybrid x environment interaction was significant (P<0.05) for all traits

Table 2.4. Combined analysis of variance and means for grain yield and agronomic traits across low N stress environments.

Source of variation	df	Mean squares						
		GY†	AD	SD	ASI	PH	EH	EPP
		Mg ha^{-1}	**d**			**cm**		**no.**
Environment (E)	1	238.26***	3570.58***	1974.70***	234.90***	54930.31***	18435.39***	1.03***
Reps(E)	2	5.61***	40.11***	29.15*	5.97	11543.53***	2735.61***	0.01
Hybrids	104	0.60	17.67***	16.84***	4.73	293.63**	156.75***	0.01
GCA	14	1.64	96.11***	86.97**	15.18	1055.14	491.59*	0.02**
SCA	90	0.43	5.46	5.93	3.11	175.17	104.67**	0.01
Hybrids x E	104	0.69***	5.11	6.92	4.23	173.40	74.97	0.01
GCA x E‡	14	0.78*	11.55**	18.16***	9.56**	489.07*	171.82**	0.00
SCA x E§	90	0.68***	4.11	5.17	3.40	124.29	59.91	0.01
Error	208	0.38	4.41	6.32	3.78	146.56	76.83	0.01
Mean		**1.66**	**87.08**	**90.34**	**3.26**	**149.71**	**63.61**	**0.90**
Min.		**0.91**	**81.31**	**85.94**	**0.61**	**127.45**	**49.23**	**0.61**
Max.		**3.85**	**91.63**	**94.72**	**6.71**	**168.68**	**79.50**	**1.10**
LSD (0.05)		**0.85**	**2.93**	**3.50**	**2.71**	**16.88**	**12.22**	**0.12**

*, **, *** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.

† AD, anthesis date; ASI, anthesis silking interval; EH, ear height; EPP, ears plant^{-1}; GCA, general combining ability; GY, grain yield; PH, plant height; SCA, specific combining ability; SD, silking date.

‡ GCA x E was used to test the significance of MS for GCA

§ SCA x E was used to test the significance of MS for SCA.

Table 2.5. Combined analysis of variance and means for grain yield and agronomic traits across drought stress environments.

Source of variation	df	Mean squares							
		GY†	AD	SD	ASI	PH	EH	EPP	GM
		Mg ha^{-1}	**d**			**cm**		**no.**	**g kg-1**
Environment (E)	1	996.03***	2499.05***	418.60***	883.72***	91391.00***	26.35	1.55***	472.12***
Reps(E)	2	13.72***	2.63	2.89	6.59	6855.53***	4717.68***	0.15*	7.31
Hybrids	104	2.43	24.66***	39.37***	9.60***	753.79**	421.08***	0.08	19.28***
GCA	14	7.14	153.47***	226.85***	39.18**	1754.23	1264.58**	0.28	106.04***
SCA	90	1.70	4.63*	10.11*	4.97*	598.16**	289.88*	0.04	5.79
Hybrids x E	104	1.81*	3.13**	6.94***	3.90**	423.12	215.75	0.06*	7.50**
GCA x E‡	14	4.21***	4.48*	11.15***	8.27***	918.16**	322.72	0.13***	14.86***
SCA x E§	90	1.44	2.92*	6.30**	3.19	346.11	199.12	0.05	6.35*
Error	207	1.35	2.07	4.02	2.51	380.92	185.99	0.04	4.52
Mean		**2.92**	**104.68**	**105.99**	**1.32**	**204.73**	**119.04**	**0.98**	**16.77**
Min.		**1.48**	**98.41**	**98.46**	**-1.84**	**169.63**	**89.34**	**0.65**	**12.30**
Max.		**4.53**	**110.13**	**112.84**	**5.71**	**239.69**	**147.47**	**1.37**	**21.78**
LSD (0.05)		**1.62**	**2.00**	**2.80**	**2.21**	**27.21**	**19.01**	**0.28**	**2.96**

*, **, *** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.

† AD, anthesis date; ASI, anthesis silking interval; EH, ear height; EPP, ears plant^{-1}; GCA, general combining ability; GM, grain moisture; GY, grain yield; PH, plant height; SCA, specific combining ability; SD, silking date; SEN, leaf senescence.

‡ GCA x E was used to test the significance of MS for GCA

§ SCA x E was used to test the significance of MS for SCA.

except plant and ear height. Significant GCA x environment (E) interaction ($P<0.05$) was observed for all traits except ear height. SCA x environment interaction was significant ($P<0.001$) for only anthesis and silking date and grain moisture.

Across environments

Highly significant differences ($P<0.01$) were observed among the hybrids for all traits across environments (Table 2.6). Mean days to silking was 93.39 d (range 87.90 to 97.87 d). Days to anthesis ranged from 87.19 to 97.18 d with a mean of 92.52. Mean anthesis silking interval was 1.62 d (range -0.14 to 4.29) while mean number of ears per plant was 1.00 (range 0.81 to 1.31). Leaf senescence ranged from 4.48 to 5.79 across environments. Mean grain yield ranged from 2.29 to 4.03 Mg ha^{-1}. The highest yielding hybrid across environments was CML258 x CML343 (4.03 Mg ha^{-1}). This cross was also the best hybrid under drought stress conditions. General combining ability (GCA) mean squares were significant ($P<0.05$) for all traits except leaf senescence (Table 2.6). Specific combining ability (SCA) mean squares were highly significant ($P<0.01$) for all traits except leaf senescence. Hybrid x environment interaction was highly significant for all traits ($P<0.001$). This suggested that the hybrids did not perform consistently across locations and stresses. There was highly significant ($P<0.001$) GCA x environment (E) interaction for all traits except yield ($P<0.05$). SCA x environment interaction was significant ($P<0.05$) for all traits except leaf senescence. The larger magnitude of GCA mean squares compared to GCA x E mean squares for plant and ear height, anthesis and silking date suggests that interaction effects may be of relatively minor importance for these traits.

Table 2.6. Combined analysis of variance and means for grain yield and agronomic traits across environments.

Source of variation	df	Mean squares GY†	SD	PH	EH	df	Mean squares AD	ASI	EPP	GM	df	Mean squares SEN
		Mg ha^{-1}	**d**	**cm**			**d**		**no.**	**g kg^{-1}**		**rating 1-10**
Environment (E)	7	875.95***	23611.68***	429301.56***	211424.92***	6	27459.27***	484.00***	2.62***	4039.91***	1	20.82***
Reps(E)	8	6.97***	9.49**	4764.04***	1941.17***	7	14.16***	4.19	0.05*	19.35***	2	1.88**
Hybrids	104	2.59***	11.44***	1139.04***	785.67***	104	53.27***	3.08***	0.11***	30.20***	104	0.46***
GCA	14	8.26*	487.70***	5157.06***	3919.04***	14	339.83***	48.07***	0.54***	171.19***	14	1.76
SCA	90	1.71**	12.76***	514.02***	298.26***	90	8.69***	4.17***	0.04**	8.27***	90	0.26
Hybrids x E	728	1.54***	6.71***	280.09***	171.81***	624	4.33***	3.28***	0.04***	7.57***	104	0.37*
GCA x E‡	98	4.55*	20.18***	717.35***	454.17***	84	12.89***	8.10***	0.11***	23.77***	14	1.30***
SCA x E§	630	1.08***	4.61***	212.08*	127.89***	540	2.99**	2.51*	0.03***	5.05*	90	0.23
Error	828	0.90	3.38	185.54	101.45	728	2.39	2.20	0.02	4.21	208	0.27
Mean		**3.26**	**93.39**	**212.12**	**106.34**		**92.52**	**1.62**	**1.00**	**15.43**		**5.13**
Min.		**2.29**	**87.90**	**192.25**	**91.15**		**87.19**	**-0.14**	**0.81**	**12.58**		**4.48**
Max.		**4.03**	**97.87**	**231.78**	**129.75**		**97.18**	**4.29**	**1.31**	**20.72**		**4.48**
LSD (0.05)		**0.66**	**1.28**	**9.45**	**6.99**		**1.15**	**1.10**	**0.11**	**1.50**		**0.72**

*, **, *** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.

† AD, anthesis date; ASI, anthesis silking interval; EH, ear height; EPP, ears plant^{-1}; GCA, general combining ability; GM, grain moisture; GY, grain yield; PH, plant height; SCA, specific combining ability; SD, silking date; SEN, leaf senescence.

‡ GCA x E was used to test the significance of MS for GCA.

§ SCA x E was used to test the significance of MS for SCA.

General and specific combining ability effects

The estimates of GCA effects for ASI varied significantly among the lines and between environments (Table 2.7). Lines CML339, CML341, and SPLC-F showed consistently negative GCA effects for ASI at all locations and across environments. The exception was at WEWW where CML339 and SPLC-F had positive but small GCA effects (0.06 and 0.03 d, respectively). SPLC-F had the highest negative and highly significant GCA effect for ASI at TLWW (-1.44 d), PRLN (-1.09 d), and across well-watered conditions (-0.63 d). Line CML341 had the highest negative and highly significant GCA effect at TLSS (-1.6 d) and across low N, drought, and environments (-0.73, -1.28, and -0.751 d, respectively). Across well-watered environments lines CML78, CML339, CML341, SPLC-F showed highly significant negative GCA effects. Across low N stress environments, CML339 and CML341 had highly significant negative GCA effects for ASI. Across drought stress environments lines CML339, CML341, SPLC-F, and CML343 had highly significant negative GCA effects for ASI (Table 2.7). Lines CML339, CML341, and CML343 were selected from the La Posta Sequía population that has been undergoing improvement for stress tolerance at CIMMYT (Bolaños and Edmeades, 1993a, b). Lines CML339 and CML343 were selected for drought tolerance while CML341 was selected for both drought and low N stress tolerance. Bolaños and Edmeades (1993b) reported that selection for drought tolerance in the Tuxpeño Sequía population improved yield by progressively reducing the ASI and indicated that reduction in ASI is associated with a higher proportion of fertile ears. A shorter ASI indicates increased partitioning of assimilates to the developing ear under stress (Dow et al., 1984; Edmeades et al., 1993).

Estimates of GCA effects for EPP are presented in Table 2.8. Lines CML254, CML339, and SPLC-F had significant positive GCA effect at TLWW and ZBWW. CML254 and CML343 had positive and significant GCA effects at ZBSS (Table 2.8). Line P502 had positive and significant GCA effects for EPP at PRLN (0.04 EPP), ZBSS (0.15 EPP), across well-watered (0.03 EPP), and drought stress environments (0.09 EPP). Lines CML343 and CML254 showed significant positive GCA for EPP across well-watered and drought stress conditions, indicating their ability to increase the number of ears under both optimal and stress conditions. Across environments, the highest GCA effect was observed for line CML339 (0.11 EPP). Lines selected for drought tolerance had mostly positive GCA for ears per plant. Bolaños and Edmeades (1993a) reported that selection for drought tolerance in a lowland tropical maize population resulted in a significant gain in the number of EPP.

Table 2.7. General combining ability effects (GCA) of fifteen maize inbred lines for anthesis silking interval per environment and across environments.

								Across			
	TLWW†	WEWW	ZBWW	PRLN	ZBLN	TLSS	ZBSS	WW	Low N	Drought	Env.
	d										
P502	0.28	-0.05	0.07	-0.36	-0.09	0.15	-0.83***	0.11	-0.27	-0.32	-0.13
P501	-0.06	-0.01	0.06	-0.43	-0.08	-0.47	-0.07	0.00	-0.28	-0.29	-0.16
CML 78	-1.02***	-0.05	-0.57**	0.84*	-0.15	-0.96**	-0.89***	-0.55***	0.31	-0.91***	-0.41***
CML 321	0.17	-0.01	-0.26	-0.74	0.31	0.59	-0.35	-0.03	-0.26	0.14	-0.06
CML 311	-0.24	-0.05	-0.21	-0.01	0.50	0.12	0.26	-0.18	0.30	0.18	0.07
CML 202	0.29	-0.05	-0.08	1.11**	1.04**	0.25	1.24***	0.05	1.10***	0.71***	0.54***
CML 206	1.26***	0.06	0.75***	1.57***	-0.14	0.66	2.09***	0.69***	0.68**	1.38***	0.88***
CML 216	0.42	-0.01	0.64***	1.34**	0.17	1.05**	1.68***	0.34***	0.79**	1.35***	0.75***
CML 247	1.59***	0.06	0.42*	-0.36	-0.02	2.03***	0.82***	0.69***	-0.13	1.41***	0.67***
CML 254	0.69**	0.03	-0.13	-0.55	-0.37	0.65	0.01	0.19	-0.45	0.33	0.05
CML 258	0.27	0.06	0.02	-0.13	-0.09	0.13	-0.21	0.12	-0.03	-0.03	0.03
CML 339	-1.00***	0.06	-0.01	-0.70	-0.73**	-1.05**	-0.99***	-0.32**	-0.70**	-1.03***	-0.63***
CML 341	-0.92***	-0.05	-0.30	-0.90*	-0.52	-1.60***	-0.98***	-0.43***	-0.73**	-1.28***	-0.75***
SPLC7-F	-1.44***	0.03	-0.47**	-1.09**	0.47	-1.27***	-0.76**	-0.63***	-0.32	-0.98***	-0.64***
CML 343	-0.27	-0.01	0.08	0.41	-0.39	-0.26	-1.00***	-0.07	-0.01	-0.66**	-0.22*
LSD (0.05) ‡	**0.50**	**0.11**	**0.34**	**0.83**	**0.62**	**0.65**	**0.45**	**0.47**	**0.86**	**0.80**	**0.39**

*, **, *** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.

† PRLN, Poza Rica low N; TLSS, Tlaltizapán, drought stress; TLWW, Tlaltizapán well-watered; WEWW, Weslaco well-watered; WW, Well-watered environments; ZBLN, Harare low N; ZBSS, Chiredzi drought stress; ZBWW, Harare well-watered.

‡ Least significant difference for the difference between two GCA effects.

Table 2.8. General combining ability effects (GCA) of fifteen maize inbred lines for ears per plant per environment and across environments.

								Across			
	TLWW†	WEWW	ZBWW	PRLN	ZBLN	TLSS	ZBSS	WW	Low N	Drought	Across
	no.										
P502	0.05	0.02	0.03	0.04**	0.01	0.05	0.15***	0.03*	0.02	0.09***	0.05***
P501	-0.12***	-0.09	-0.12***	0.01	0.01	0.04	-0.07	-0.08***	0.01	-0.02	-0.04***
CML 78	-0.12***	0.00	-0.11***	0.02	0.02	0.04	-0.06	-0.07***	0.02	-0.02	-0.03**
CML 321	-0.12***	-0.01	-0.03	-0.02	-0.02	-0.06*	-0.01	-0.05***	-0.02	-0.04	-0.04***
CML 311	-0.08*	-0.01	-0.10***	0.01	-0.03	-0.01	-0.00	-0.06***	-0.01	-0.00	-0.03**
CML 202	-0.04	-0.02	0.03	-0.01	0.03	-0.03	-0.04	-0.01	0.01	-0.03	-0.01
CML 206	-0.10**	-0.01	-0.05	-0.05***	-0.03	-0.04	-0.15***	-0.05**	-0.04**	-0.10***	-0.06***
CML 216	-0.07	-0.03	-0.12***	-0.02	-0.03	-0.06*	-0.19***	-0.07***	-0.03*	-0.13***	-0.07***
CML 247	-0.16***	0.02	-0.04	-0.01	-0.02	-0.08**	-0.15***	-0.06***	-0.02	-0.12***	-0.07***
CML 254	0.13***	0.02	0.11***	0.01	0.01	0.04	0.22***	0.09***	0.01	0.13***	0.08***
CML 258	-0.06	-0.00	0.04	-0.01	-0.01	0.00	0.06	-0.01	-0.01	0.03	0.00
CML 339	0.36***	0.02	0.27***	0.01	0.03	0.06*	0.02	0.21***	0.02	0.04	0.11***
CML 341	0.05	0.02	-0.04	-0.00	0.01	-0.03	0.03	0.01	0.00	0.00	0.00
SPLC7-F	0.15***	0.01	0.08**	0.04**	0.03	0.06*	0.09*	0.08***	0.03**	0.07**	0.06***
CML 343	0.11***	-0.02	0.04	-0.01	0.01	0.03	0.12**	0.04**	0.00	0.08***	0.04***
LSD (0.05) ‡	**0.06**	**0.03**	**0.06**	**0.03**	**0.04**	**0.05**	**0.07**	**0.07**	**0.02**	**0.10**	**0.05**

*, **, *** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.

† PRLN, Poza Rica low N; TLSS, Tlaltizapán, drought stress; TLWW, Tlaltizapán well-watered; WEWW, Weslaco well-watered; WW, Well-watered environment; ZBLN, Harare low N; ZBSS, Chiredzi drought stress; ZBWW, Harare well-watered.

‡ Least significant difference for the difference between two GCA effects.

Significant GCA effects were observed for grain yield among lines and between environments (Fig. 2.1, Table 2.9). Line P501 showed high positive GCA for grain yield at the two low N stress environments (0.34 and 0.35 Mg ha^{-1} for PRLN and ZBLN, respectively) as well as the highest GCA across the low N environments (0.35 Mg ha^{-1}), showing its ability to perform well under low N stress conditions. Line CML254 had the highest positive and significant GCA for grain yield at ZBLN (0.37 Mg ha^{-1}) and the second best GCA across low N stress environments. Line CML339 had consistently positive GCA at all environments and across environments. Line CML258 had the highest GCA at TLWW (1.24 Mg ha^{-1}), TLSS (0.29 Mg ha^{-1}), and ZBSS (1.11 Mg ha^{-1}) and across drought stress and environments (0.70 and 0.33 Mg ha^{-1} respectively). Betrán et al (2003b) also identified CML258 as having high GCA under well-watered conditions and the second best GCA under intermediate stress. Betrán et al (2003b) noted that CML254 had consistent positive GCA effects in most of the environments and this was the case in this study. Line CML339 which was developed from the La Posta Sequia population also showed positive GCA effects in the study by Betrán et al (2003b). Betrán et al. (2003b) reported that line CML247 to show mostly negative GCA for grain yield in most environments. This was also true in this trial where line CML247 had negative GCA for grain yield in all environments and across environments except at ZBWW.

Estimates of GCA effects for anthesis date were significantly different between lines (Table 2.10). Lines P501, CML78, CML311, CML321, and SPLC-F had significant negative GCA effects for anthesis date at most locations and across stresses, thus showing that they flower earlier. Line CML311 had the highest negative GCA at TLWW (-2.92 d) and TLSS (-3.06 d) revealing less days to anthesis under optimal and stress environments. Line CML78 had the highest negative GCA across well-watered, low N, and drought stress environments (-2.45, -3.30, -3.40 d, respectively) and across environments (-2.95 d). Lines P501, CML78, CML311, CML321, CML202, CML341, and SPLC-F had significant negative GCA effects for silking date at most locations and across stresses, showing their ability to silk earlier than the other inbred lines (Table 2.11). Line CML78 had the highest negative GCA across well-watered, low N, and drought stress environments (-3.07, -2.98, and -4.30 d, respectively) and across environments (-3.35). Line CML341 has a history of selection for drought tolerance and showed high and significant negative GCA effects for silking date at drought stress environments (-1.20 and -0.73 d at TLSS and ZBSS, respectively).

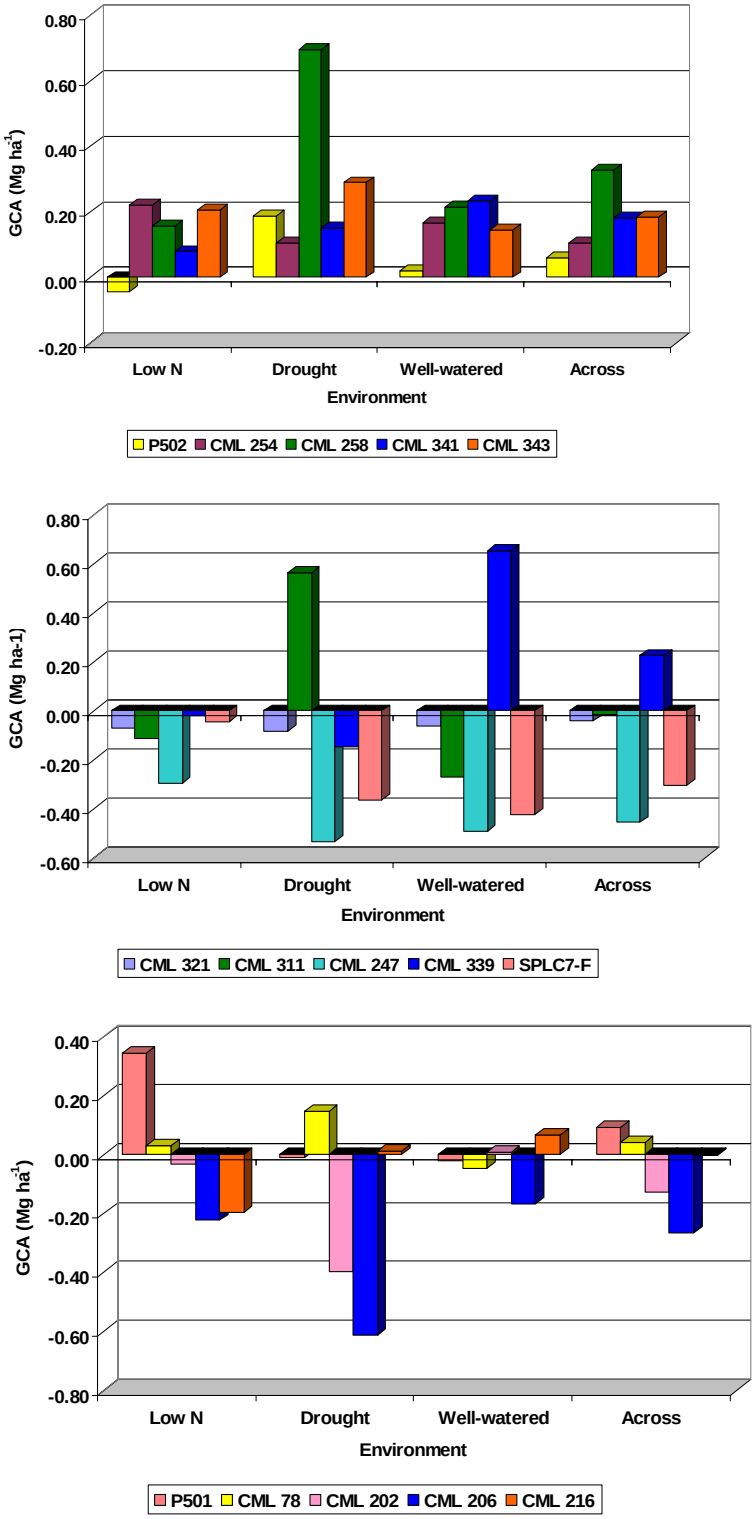


Fig. 2.1. General combining ability (GCA) effects for grain yield of 15 tropical maize inbred lines in a diallel study evaluated across stress and non-stress environments.

Table 2.9. General combining ability effects (GCA) of fifteen maize inbred lines for grain yield (Mg ha^{-1}) per environment and across environments.

									Across		
	TLWW†	CSWW	WEWW	ZBWW	PRLN	ZBLN	TLSS	ZBSS	WW	Low N	Drought	Env.
	Mg ha^{-1}											
P502	-0.07	0.35	0.60*	-0.74***	-0.010	-0.08	-0.10	0.48*	0.02	-0.04	0.19	0.06
P501	0.00	0.42*	0.16	-0.58***	0.34**	0.35**	0.18	-0.20	-0.02	0.35***	-0.01	0.09
CML 78	-0.13	0.94***	0.13	-1.04***	-0.03	0.09	-0.04	0.33	-0.05	0.03	0.15	0.04
CML 321	-0.14*	-0.68**	-0.24	0.94***	-0.03	-0.10	-0.23*	0.07	-0.06	-0.07	-0.08	-0.04
CML 311	0.11	-0.32	-0.24	-0.57***	-0.02	-0.21	0.16	0.97***	-0.27**	-0.11	0.56***	-0.02
CML 202	-0.03	-0.08	-0.24	0.39*	-0.13	0.07	-0.32***	-0.48*	0.01	-0.03	-0.40**	-0.13
CML 206	-0.23**	-0.42*	-0.20	0.28	-0.20	-0.25*	-0.18*	-1.05***	-0.17	-0.22**	-0.61***	-0.27***
CML 216	0.37***	-0.01	0.08	-0.13	-0.20	-0.19	-0.02	0.04	0.07	-0.20*	0.01	-0.00
CML 247	-0.566***	-0.67**	-1.11***	0.41**	-0.08	-0.52***	-0.11	-0.95***	-0.49***	-0.30***	-0.54***	-0.46***
CML 254	-0.08	-0.15	0.23	0.19	0.08	0.37**	0.05	0.16	0.17	0.22**	0.10	0.10
CML 258	0.27***	-0.27	-0.35	1.24***	0.27*	0.05	0.29**	1.12***	0.22*	0.16	0.70***	0.33***
CML 339	0.58***	0.35	0.42	0.76***	-0.01	-0.03	0.10	-0.40	0.65***	-0.02	-0.15	0.23***
CML 341	0.10	0.21	0.60*	0.15	0.04	0.12	0.13	0.17	0.23*	0.08	0.15	0.18**
SPLC7-F	-0.39***	0.09	0.27	-1.50***	0.06	-0.16	-0.17	-0.56*	-0.43***	-0.05	-0.37	-0.30***
CML 343	0.22**	0.25	-0.09	0.18	-0.08	0.50	0.27**	0.31	0.15	0.21*	0.29	0.18**
LSD (0.05) ‡	**0.13**	**0.41**	**0.47**	**0.30**	**0.22**	**0.24**	**0.17**	**0.44**	**0.52**	**0.24**	**0.57**	**0.30**

*, **, *** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.

† CSWW, College Station well-watered; PRLN, Poza Rica low N; TLSS, Tlaltizapán, drought stress; TLWW, Tlaltizapán well-watered; WEWW, Weslaco well-watered; WW, Well-watered environment; ZBLN, Harare low N; ZBSS, Chiredzi drought stress; ZBWW, Harare well-watered.

‡ Least significant difference for the difference between two GCA effects.

Table 2.10. General combining ability effects (GCA) of fifteen maize inbred lines for anthesis date per environment and across environments.

								Across			
	TLWW†	WEWW	ZBWW	PRLN	ZBLN	TLSS	ZBSS	WW	Low N	Drought	Env.
						d					
P502	0.90**	-0.09	0.33	-0.75*	0.53	0.26	-0.07	0.39**	-0.04	0.10	0.18
P501	-0.08	-0.11	-1.06***	0.06	-1.79***	-0.90***	-1.31***	-0.40**	-0.86**	-1.12***	-0.73***
CML 78	-2.55***	-1.40***	-3.41***	-3.33***	-3.22***	-2.99***	-3.79***	-2.45***	-3.30***	-3.40***	-2.95***
CML 321	-0.32	-1.57***	0.10	-1.14***	-0.37	-0.78**	-1.08***	-0.59***	-0.78**	-0.93***	-0.73***
CML 311	-2.92***	-0.98***	-1.75***	-1.17***	-1.12*	-3.06***	-2.92***	-1.87***	-1.17***	-2.98***	-1.97***
CML 202	-0.71*	0.02	-1.68***	-0.98**	-2.33***	-0.03	0.57	-0.79***	-1.70***	0.27	-0.74***
CML 206	1.72***	1.63***	0.86***	0.02	1.29**	2.28***	1.53***	1.39***	0.64*	1.91***	1.31***
CML 216	-0.82**	0.22	0.49*	0.44	1.23*	-0.07	-0.42	-0.04	0.89**	-0.23	0.16
CML 247	0.60*	0.60***	0.75***	0.98**	0.49	0.12	0.79**	0.63***	0.72*	0.46**	0.60***
CML 254	1.59***	0.73***	1.90***	1.29***	1.80***	2.12***	3.03***	1.40***	1.54***	2.57***	1.77***
CML 258	0.68*	-0.05	0.21	1.33***	0.87	0.70**	0.45	0.27*	1.09***	0.58***	0.59***
CML 339	0.77*	0.92***	0.90***	0.98**	0.89	1.22***	1.21***	0.87***	0.92**	1.21***	0.96***
CML 341	0.38	-1.11***	1.36***	0.60*	0.15	0.39	0.26	0.21	0.36	0.32	0.29**
SPLC7-F	-1.94***	-0.54***	-0.98***	-0.21	0.31	-1.65***	-1.11***	-1.16***	0.05	-1.37***	-0.87***
CML 343	2.70***	1.73***	1.98***	1.90***	1.27**	2.40***	2.86***	2.14***	1.62***	2.62***	2.12***
LSD‡	**0.55**	**0.22**	**0.34**	**0.60**	**0.92**	**0.43**	**0.51**	**0.74**	**0.94**	**0.59**	**0.50**

*, **, *** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.

† PRLN, Poza Rica low N; TLSS, Tlaltizapán, drought stress; TLWW, Tlaltizapán well-watered; WEWW, Weslaco well-watered; WW, Well watered environment; ZBLN, Harare low N; ZBSS, Chiredzi drought stress; ZBWW, Harare well-watered.

‡ Least significant difference for the difference between two GCA effects.

Table 2.11. General combining ability effects (GCA) of fifteen maize inbred lines for silking date per environment and across environments.

									Across			
	TLWW†	CSWW	WEWW	ZBWW	PRLN	ZBLN	TLSS	ZBSS	WW	Low N	Drought	Env.
	d											
P502	1.25***	0.67***	-0.15	0.44	-1.11	0.42	0.45	-0.85**	0.56***	-0.32	-0.20	0.13
P501	-0.13	-1.11***	-0.10	-0.96***	-0.38	-1.88***	-1.32***	-1.40***	-0.57***	-1.14***	-1.37***	-0.91***
CML 78	-3.50***	-3.35***	-1.45***	-3.97***	-2.50***	-3.37***	-3.95***	-4.65***	-3.07***	-2.98***	-4.30***	-3.35***
CML 321	-0.13	0.60*	-1.58***	-0.13	-1.90***	-0.05	-0.10	-1.37***	-0.29	-1.04**	-0.73**	-0.59***
CML 311	-3.11***	-1.34***	-1.05***	-1.92***	-1.17*	-0.62	-2.86***	-2.65***	-1.85***	-0.87**	-2.76***	-1.82***
CML 202	-0.42	-1.46***	-0.05	-1.77***	0.13	-1.26*	0.28	1.73***	-0.96***	-0.59	1.00***	-0.36**
CML 206	2.93***	1.44***	1.71***	1.58***	1.57***	1.14*	2.64***	3.63***	1.90***	1.32***	3.14***	2.06***
CML 216	-0.48	0.55*	0.20	1.12***	1.79***	1.40*	1.05**	1.25***	0.34*	1.69***	1.14***	0.86***
CML 247	2.17***	0.26	0.65***	1.10***	0.63	0.45	1.93***	1.62***	1.07***	0.58	1.78***	1.13***
CML 254	2.25***	2.37***	0.77***	1.75***	0.75	1.45**	2.82***	3.02***	1.79***	1.11**	2.92***	1.91***
CML 258	0.86	1.03***	0.01	0.20	1.20**	0.86	0.87*	0.29	0.53***	1.06**	0.58*	0.67***
CML 339	-0.18	1.43***	0.98***	0.91***	0.27	0.17	0.24	0.17	0.76***	0.22	0.21	0.48***
CML 341	-0.51	-0.13	-1.13***	1.07***	-0.30	-0.37	-1.20**	-0.73*	-0.18	-0.35	-0.96***	-0.40***
SPLC7-F	-3.44***	-2.07***	-0.51	-1.46***	-1.30**	0.76	-3.02***	-1.81***	-1.86***	-0.27	-2.41***	-1.60***
CML 343	2.43***	1.13***	1.69***	2.06***	2.32***	0.88	2.16***	1.75***	1.83***	1.61***	1.95***	1.81***
LSD‡	**0.53**	**0.48**	**0.23**	**0.48**	**0.92**	**0.92**	**0.71**	**0.59**	**0.85**	**1.18**	**0.93**	**0.62**

*, **, *** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.

† CSWW, College Station well-watered; PRLN, Poza Rica low N; TLSS, Tlaltizapán, drought stress; TLWW, Tlaltizapán well-watered; WEWW, Weslaco well-watered; WW, Well-watered environment; ZBLN, Harare low N; ZBSS, Chiredzi drought stress; ZBWW, Harare well-watered.

‡ Least significant difference for the difference between two GCA effects.

GCA effects for plant height were mostly negative for lines P502, CML78, CML311, CML206, CML247 and SPLC-F (Fig. 2.2, Table 2.12). Line CML247 had consistently negative GCA across locations and stresses and the highest negative GCA for plant height across well-watered (-10.12 cm), across low N stress (-7.23 cm), across drought stress (-14.65 cm), and across locations (-10.62 cm). GCA effects for ear height are presented in Table 2.13. GCA effects were mostly negative for inbred lines CML78, CML321, CML206, CML247 and SPLC-F (Table 2.13). Line CML78 had the highest negative GCA effect for ear height across well-watered and low N stress environments (-8.12 and -4.58 cm respectively). Line CML206 had the highest negative GCA effects across drought stress environments (-10.21 cm) while line CML247 had the highest negative GCA effect across environments (-6.47 cm). Thus, these two lines showed good general combining ability for reduced plant height and low ear placement across all locations and stresses. Inbred line CML247 line was also reported to have negative GCA for plant and ear height across 12 environments in a study by Betrán et al. (2003c).

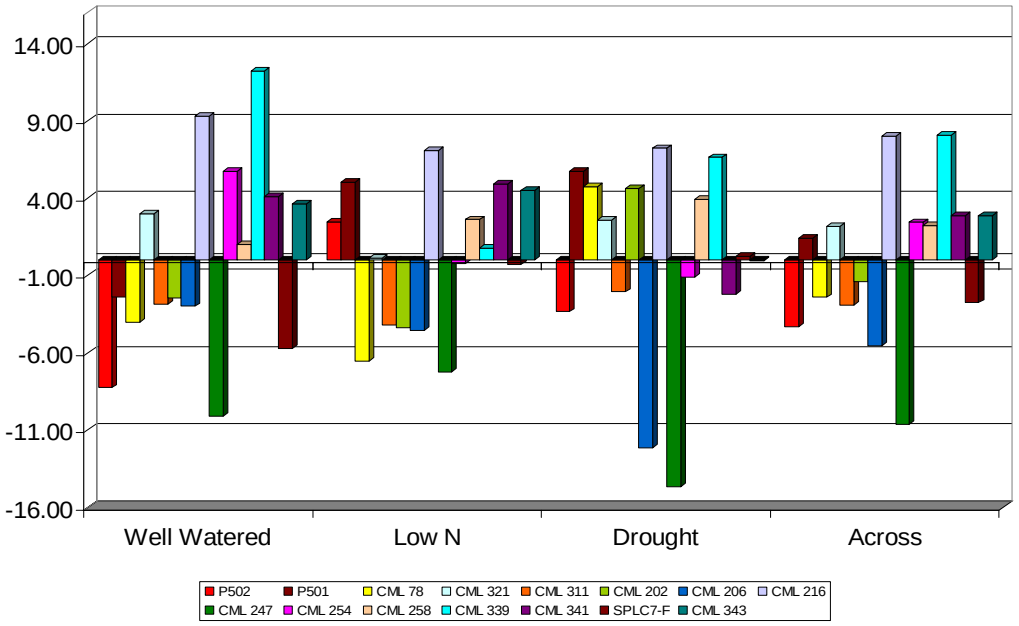


Fig. 2.2. General combining ability (GCA) effects for plant height across environments for 15 tropical and sub-tropical maize inbred lines.

Table 2.12. General combining ability effects (GCA) of fifteen maize inbred lines for plant height per environment and across environments.

									Across			
	TLWW†	CSWW	WEWW	ZBWW	PRLN	ZBLN	TLSS	ZBSS	WW	Low N	Drought	Env
	cm											
P502	-10.17***	-10.52***	-9.68***	-3.42*	-1.98	7.15*	-2.08	-4.63	-8.27***	2.47	-3.36	-4.34***
P501	-3.78*	-4.88	-0.33	-0.39	1.84	7.36*	10.64***	0.73	-2.42**	5.08**	5.74**	1.39
CML 78	-0.52	0.18	-7.06***	-7.40***	-5.07**	-7.96**	3.79	5.72*	-4.03***	-6.53**	4.71*	-2.42**
CML 321	-5.57**	4.40	7.82***	5.17***	0.32	0.04	-2.66	7.87**	2.99**	0.14	2.57	2.18**
CML 311	-4.87*	1.26	-3.73***	-4.11**	-0.99	-7.57**	-2.34	-1.95	-2.88**	-4.21*	-2.08	-2.90***
CML 202	9.07***	-4.61	-9.58***	-5.16***	-4.23**	-4.49	1.40	7.81**	-2.46**	-4.37**	4.64	-1.41
CML 206	-6.40**	-4.55	1.78**	-2.58	-0.79	-8.15**	-14.35***	-9.88**	-3.01**	-4.54**	-12.15***	-5.54***
CML 216	7.05***	8.14***	11.44***	10.48***	0.10	14.20***	5.40	8.95**	9.27***	7.07***	7.22***	8.01***
CML 247	-14.29***	-8.08***	-4.34***	-13.69***	-5.11***	-9.88***	-13.12***	-16.18***	-10.12***	-7.23***	-14.65***	-10.62***
CML 254	5.35**	5.75*	7.19***	4.36**	3.42*	-3.73	3.74	-6.00*	5.71***	-0.24	-1.09	2.43**
CML 258	3.50	-0.58	3.81***	-2.72	3.67*	1.47	9.00**	-1.13	0.99	2.60	3.90	2.22**
CML 339	16.28***	13.08***	5.92***	13.20***	0.35	0.70	7.95**	5.35	12.23***	0.74	6.64**	8.07***
CML 341	-0.34	1.77	1.71**	12.65***	4.23**	6.47	-4.33	-0.10	4.09***	4.89**	-2.24	2.85***
SPLC7-F	-4.49*	-5.43*	-2.87***	-9.89***	1.54	-1.80*	-2.90	3.39	-5.74***	-0.31	0.21	-2.78***
CML 343	9.18***	4.07	-2.06***	3.51*	2.69	6.20*	-0.13	0.06	3.64***	4.51**	-0.06	2.87***
LSD‡	**3.57**	**5.24**	**1.06**	**2.88**	**2.67**	**5.91**	**5.24**	**5.62**	**4.54**	**6.12**	**8.39**	**3.71**

*, **, *** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.

† CSWW, College Station well-watered; PRLN, Poza Rica low N; TLSS, Tlaltizapán, drought stress; TLWW, Tlaltizapán well-watered; WEWW, Weslaco well-watered; WW, Well-watered environment; ZBLN, Harare low N; ZBSS, Chiredzi drought stress; ZBWW, Harare well-watered.

‡ Least significant difference for the difference between two GCA effects.

Table 2.13. General combining ability effects (GCA) of fifteen maize inbred lines for ear height per environment and across environments.

									Across		
	TLWW†	CSWW	WEWW	ZBWW	PRLN	ZBLN	TLSS	ZBSS	WW	Low N	Drought	Env
	cm											
P502	-6.17***	-2.08	-3.68***	0.47	1.25	5.88**	-2.38	-4.22	-2.75***	3.59**	-3.20	-1.25
P501	-9.09***	-7.64***	-0.13	-7.23***	-2.55	2.02	-0.96	0.98	-5.96***	-0.21	0.16	-3.00***
CML 78	-6.38***	-6.64***	-9.57***	-9.62***	-5.22***	-3.80**	-1.23	-0.27	-8.12***	-4.58***	-0.81	-5.32***
CML 321	-9.07***	-6.18**	1.40*	-2.02	-0.48	-0.58	-5.93***	2.99	-3.93***	-0.57	-1.55	-2.46***
CML 311	-1.69	1.48	-0.38	0.85	4.06**	0.88	1.74	-4.85	0.11	2.57*	-1.38	0.34
CML 202	11.46***	6.15**	-4.23***	-1.62	-3.44*	-1.10	9.57***	5.11	2.65	-2.36*	7.36***	2.54***
CML 206	-6.29***	-3.98*	-4.88***	-2.42	0.36	-3.45	-11.58***	-8.70***	-4.31***	-1.58	-10.21***	-5.07***
CML 216	9.89***	7.91***	11.54***	6.93***	4.11**	9.76***	6.70***	6.21*	9.03***	6.96***	6.47***	7.76***
CML 247	-14.40***	-0.66	-0.57	-7.64***	-1.42	-6.57***	-12.79***	-7.56*	-5.92***	-4.05***	-10.11***	-6.47***
CML 254	6.29***	9.70***	9.33***	10.08***	3.57*	-2.32	4.92**	3.23	8.86***	0.65	4.09*	5.56***
CML 258	8.73***	3.82*	5.71***	0.97	1.96	0.20	8.62***	2.07	4.83***	1.04	5.33*	4.06***
CML 339	11.80***	6.66***	3.33***	5.96**	-1.59	-2.88	4.05*	4.13	7.20***	-2.19	4.11*	4.03***
CML 341	4.89**	0.31	-0.28	10.76***	2.34	1.76	-0.32	-1.65	3.94***	2.04	-1.07	2.24***
SPLC7-F	-3.88*	-5.84**	-3.27***	-6.54***	0.37	-0.87	1.01	1.81	-4.99***	-0.24	1.38	-2.21***
CML 343	3.90*	-3.01	-4.33***	1.07	-3.31*	1.07	-1.42	0.73	-0.63	-1.08	-0.57	-0.74
LSD‡	**2.95**	**3.92**	**1.40**	**3.33**	**2.67**	**3.71**	**3.28**	**5.52**	**4.05**	**3.63**	**4.97**	**2.95**

*, **, *** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.

† CSWW, College Station well-watered; PRLN, Poza Rica low N; TLSS, Tlaltizapán, drought stress; TLWW, Tlaltizapán well-watered; WEWW, Weslaco well-watered; WW, Well-watered environment; ZBLN, Harare low N; ZBSS, Chiredzi drought stress; ZBWW, Harare well-watered.

‡ Least significant difference for the difference between two GCA effects.

Table 2.14. General combining ability effects (GCA) of fifteen maize inbred lines for grain moisture per environment and across environments.

								Across		
	TLWW†	CSWW	WEWW	ZBWW	ZBLN	TLSS	ZBSS	Well-watered	Drought	Across
					g kg^{-1}					
P502	-1.42***	0.42	1.14*	0.140	0.06	-1.03**	-0.89*	0.06	-0.96***	-0.25
P501	2.37***	1.36**	2.47***	-0.36	-0.16	2.16***	1.80***	1.45***	1.96***	1.37***
CML 78	-3.69***	-0.83	-1.91***	-1.06***	-0.07	-4.06***	-2.31***	-1.86***	-3.17***	-1.98***
CML 321	0.08	-2.85***	-0.87	0.62**	0.30	-0.37	-0.29	-0.63**	0.04	-0.30*
CML 311	-0.73	-0.27	-0.78	-1.35***	-0.37	0.37	0.62	-0.78***	0.10	-0.45**
CML 202	-1.08**	-1.12*	-1.11*	0.65**	0.05	-1.23***	0.24	-0.67**	-0.51*	-0.55***
CML 206	1.22***	0.60	1.31*	0.48*	0.16	0.53	0.33	0.86***	0.50	0.66***
CML 216	0.20	0.64	-1.27*	-0.51**	-0.15	0.02	-0.25	-0.25	-0.13	-0.20
CML 247	0.40	-1.30**	0.54	0.33	0.13	0.88**	0.60	0.01	0.73**	0.24
CML 254	2.38***	3.06***	2.77***	0.60**	0.28	2.29***	1.43***	2.32***	1.91***	1.92***
CML 258	1.20***	0.92*	1.26*	0.25	-0.32	1.88***	2.53***	0.89***	2.22***	1.09***
CML 339	0.40	0.51	-0.73	0.61**	0.14	-0.56	-1.45***	0.14	-1.01***	-0.19
CML 341	-1.23***	0.43	0.23	-0.33	-0.26	0.11	-0.86	-0.27	-0.40	-0.30*
SPLC7-F	-1.62***	-0.77	-2.09***	-0.30	0.06	-2.15***	-1.57***	-1.25***	-1.86***	-1.23***
CML 343	1.54***	-0.83	-0.97	0.22	0.15	1.18***	0.07	-0.03	0.60	0.16
LSD‡	**0.63**	**0.92**	**1.06**	**0.39**	**0.38**	**0.61**	**0.80**	**0.99**	**1.07**	**0.68**

*, **, *** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.

† CSWW, College Station well-watered; TLSS, Tlaltizapán, drought stress; TLWW, Tlaltizapán well-watered; WEWW, Weslaco well-watered; ZBLN, Harare low N; ZBSS, Chiredzi drought stress; ZBWW, Harare well-watered.

‡ Least significant difference for the difference between two GCA effects.

Table 2.15. General combining ability effects (GCA) of fifteen maize inbred lines for leaf senescence at two environments and across environments.

	ZBLN†	ZBSS	Across
	rating 1-10		
P502	0.41***	0.17	0.29***
P501	-0.25***	-0.04	-0.14*
CML 78	0.38***	-0.03	0.17**
CML 321	-0.17*	0.11	-0.03
CML 311	0.42***	-0.24**	0.09
CML 202	-0.03	0.09	0.03
CML 206	-0.22***	-0.07	-0.15**
CML 216	0.31***	0.01	0.16**
CML 247	-0.25***	-0.19*	-0.22***
CML 254	-0.34***	-0.15	-0.24***
CML 258	0.02	-0.05	-0.02
CML 339	0.08	0.31**	0.20***
CML 341	0.04	0.09	0.06
SPLC7-F	-0.00	0.15	0.08
CML 343	-0.40***	-0.18	-0.29***
LSD‡	**0.12**	**0.17**	**0.16**

*, **, *** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.
† ZBLN, Harare low N; ZBSS, Chiredzi drought stress.
‡ Least significant difference for the difference between two GCA effects.

Estimates for GCA effects for grain moisture differed significantly among lines (Table 2.14). Lines CML78, CML311, CML202, and SPLC-F showed mostly good GCA effects for grain moisture at most locations and across environments. CML78 had the highest negative GCA for grain moisture across well-watered (-1.86 g kg^{-1}), drought (-3.17 g kg^{-1}), and across environments (-1.98 g kg^{-1}). Line CML247 had good general combining ability for reduced leaf senescence at ZBLN (-0.34) and across locations (-0.22) (Table 2.15). Line CML343 had the highest highly significant negative GCA for leaf senescence at ZBLN (-0.40) and across locations (-0.29). Lines CML247, CML254, CML258, and CML339 had negative GCA effects for leaf senescence in a diallel study by Betrán et al. (2003c).

Specific combining ability for grain yield was highest and significant for the cross CML78 x SPLC-F (1.513***, 5.34 Mg ha^{-1}) followed by CML202 x CML343 (0.893**, 5.24 Mg ha^{-1}) across well-watered conditions. Across low N stress environments, the highest SCA was for the cross P501 x CML258 (1.019***, 1.26 Mg ha^{-1}) followed by CML311 x CML202 (0.623*, 2.17 Mg ha^{-1}). Across drought stress environments the highest SCA was for the cross CML216 x SPLC-F (1.015*, 3.55 Mg ha^{-1}). The cross CML78 x SPLC-F had the highest SCA for grain yield across environments (0.891***, 3.91 Mg ha^{-1}) followed by CML321 x CML311 (0.658**, 3.92 Mg ha^{-1}).

GCA and SCA variance components

The relative importance of GCA and SCA was expressed as the ratio between additive to total genetic variance. This ratio varied with trait but was generally higher under optimal conditions compared to stress environments (Table 2.16, Fig. 2.3). Additive genetic variance accounted for 79% of the genetic variance for grain yield under well-watered conditions (TLWW). In drought stress environments, additive genetic variance accounted for 40% and 64% of the total genetic variance for grain yield at TLSS and ZBSS, respectively. Under low N stress environments, additive variance accounted for 53% and 40% of the total genetic variance for grain yield at PRLN and ZBLN, respectively. Additive variance accounted for 42%, 67%, and 71% of total genetic variance for grain yield across low N, drought and well-watered environments, respectively. Additive genetic effects appear to be more important under drought and well-watered conditions, but nonadditive genetic effects seem to be more important under low N stress conditions in this set of maize inbred lines and environments. With predominance

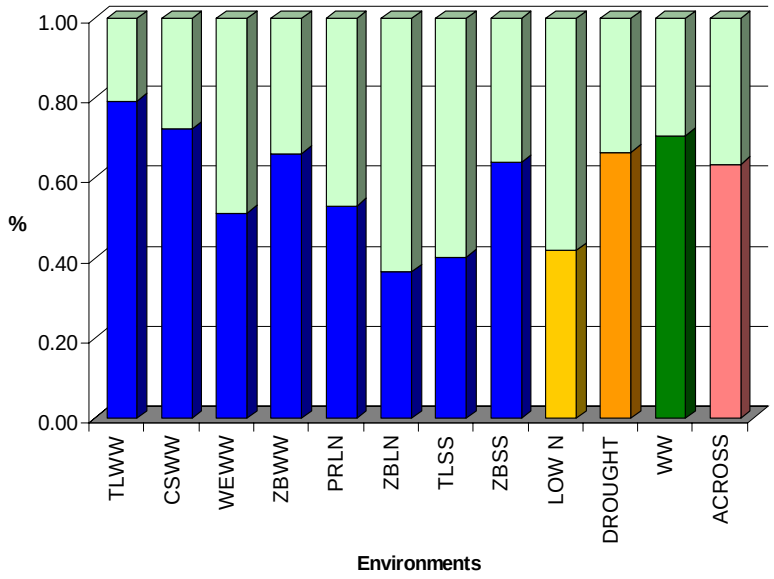


Fig. 2.3. Proportion of additive (lower bar) and nonadditive (upper bar) genetic variance for grain yield at 8 environments in a diallel among 15 tropical and subtropical maize inbreds.

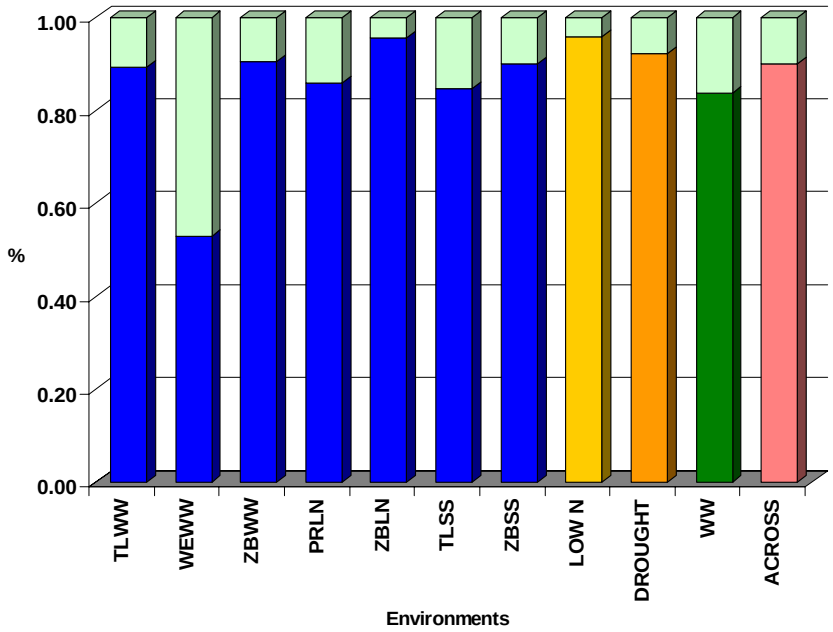


Fig. 2.4. Proportion of additive (lower bar) and nonadditive (upper bar) genetic variance for anthesis date at 7 environments in a diallel among 15 tropical and subtropical maize inbreds.

of GCA over SCA variance, early testing may be more effective and promising hybrids can be identified and selected mainly based on the prediction from GCA effects. Betrán et al. (2003b) reported additive genetic variance for grain yield to be of more importance under drought stress conditions. Beck et al. (1990) and Vasal et al. (1992) also reported additive effects to be more important for grain yield in maize populations. Betrán et al. (2003b) also found lower contribution of additive variance under low N stress environments.

Additive genetic variance accounted for 53 to 91% of the total genetic variation for anthesis date under well-watered conditions and 86 to 96% of the total genetic variation under low N stress conditions (Table 2.16, Fig. 2.4). Across environments, additive genetic variance appears to be more important that nonadditive genetic variance for anthesis date in this set of materials (Fig. 2.4). A similar trend was observed for silking date, plant and ear height, and grain moisture (Table 2.16). Beck et al. (1990) and Vasal et al. (1992) reported similar results with additive effects being more important than nonadditive effects for silking date, plant height, and ear height. The large proportion of additive genetic variance in these traits suggests that selection which takes advantage of additive variation can be effective. Additive genetic variance accounted for 78% and 71% of total genetic variance for ears per plant at two well-watered environments (TLWW and ZBWW), respectively (Table 2.16). Across low N stress environments, additive genetic variance accounted for 17% of the total genetic variance for ear per plant. Under low N stress, nonadditive genetic variation, which accounted for 83% of total genetic variance, seems to be more important than additive genetic effects for ears per plant (Fig. 2.5). Wang et al. (1999) indicated nonadditive gene effects to be more important than additive effects for ear-filling rate in maize.

Table 2.16. Ratio of additive genetic variance to total genetic variance for grain yield and agronomic traits at each environment and across environments.

								Across			
Trait	TLWW†	CSWW	WEWW	ZBWW	PRLN	ZBLN	TLSS	ZBSS	Low N	Drought	WW	Across
Grain yield	0.79	0.72	0.51	0.66	0.53	0.37	0.40	0.64	0.42	0.67	0.71	0.64
Anthesis date	0.89	-	0.53	0.91	0.86	0.96	0.85	0.90	0.96	0.92	0.84	0.90
Silking date	0.74	0.92	0.53	0.92	-	0.88	0.70	0.87	-	0.86	0.88	0.89
Plant height	0.63	0.81	0.56	0.88	0.38	-	0.71	0.53	0.96	0.62	0.78	0.78
Ear height	0.80	0.60	0.57	0.88	0.54	-	0.75	0.33	0.72	0.81	0.85	0.77
ASI	0.57	-	-	0.71	-	0.37	0.52	0.80	-	0.71	0.69	0.79
Ears per plant	0.78	-	-	0.71	-	-	0.28	0.80	0.17	0.71	0.84	0.81
Grain moisture	0.79	0.54	0.79	0.89	-	-	-	0.85	-	0.95	0.84	0.88

†ASI, Anthesis silking interval; CSWW, College Station well-watered; PRLN, Poza Rica low N; TLSS, Tlaltizapán, drought stress; TLWW, Tlaltizapán well-watered; WEWW, Weslaco well-watered; WW, Well-watered environments; ZBLN, Harare low N; ZBSS, Chiredzi drought stress; ZBWW, Harare well-watered.

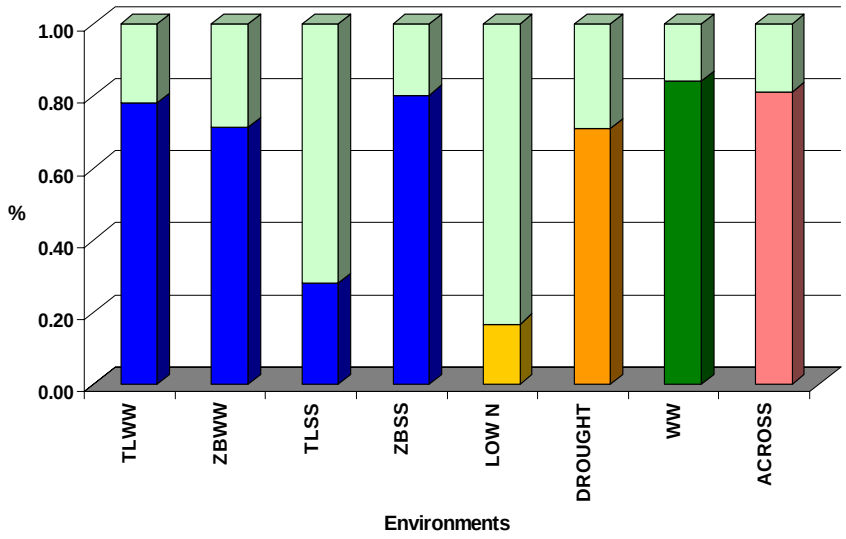


Fig. 2.5. Proportion of additive (lower bar) and nonadditive (upper bar) genetic variance for ears per plant at 4 environments in a diallel among 15 tropical and subtropical maize inbreds.

Correlation between grain yield, specific combining ability, and agronomic traits

Genotypic correlation between grain yield and anthesis and silking dates were positive across well-watered environments (Table 2.17). Genetic correlation between grain yield and anthesis silking interval was significant and negative (-0.76; Fig. 2.6) while the genetic correlation between grain yield and ears per plant was significant and positive (0.48). Anthesis silking interval was negatively correlated with ears per plant (-0.30). Phenotypic correlation between grain yield and anthesis date was positive, but the correlation with silking date and anthesis silking interval was negative (Table 2.17). Ears per plant and anthesis silking interval had a negative and significant genetic and phenotypic correlation (-0.29 and -0.22), respectively.

Across drought stress environments, the genetic correlation between grain yield, anthesis and silking dates, and anthesis silking interval (ASI) was negative (Table 2.18). Fischer et al. (1989) and Bolaños and Edmeades (1996) also reported negative phenotypic correlation between grain yield and ASI in tropical maize under moisture stress. Anthesis silking interval and ears per plant were negatively correlated. This indicates that increases in ASI will result in a reduced number of ears per plant. Edmeades et al. (1993) reported that delayed silking under

drought or high density was related to less assimilate being partitioned to growing ears around anthesis, which resulted in lower ear growth rates, increased ear abortion and more barren plants. The phenotypic correlation between grain yield and anthesis and silking dates was negative. Grain yield was positively correlated with ears per plant (0.58*). Bolaños and Edmeades (1996) reported a strong positive genetic correlation (0.90) between grain yield and ears per plant across 50 trials grown under well-watered, intermediate stress, and severe stress conditions. Bolaños and Edmeades (1996) noted that the ability of a genotype to produce an ear under stress is the most important characteristic associated with drought tolerance. Anthesis silking interval and anthesis date were negatively correlated with grain yield across all environments used by Bolaños and Edmeades (1996).

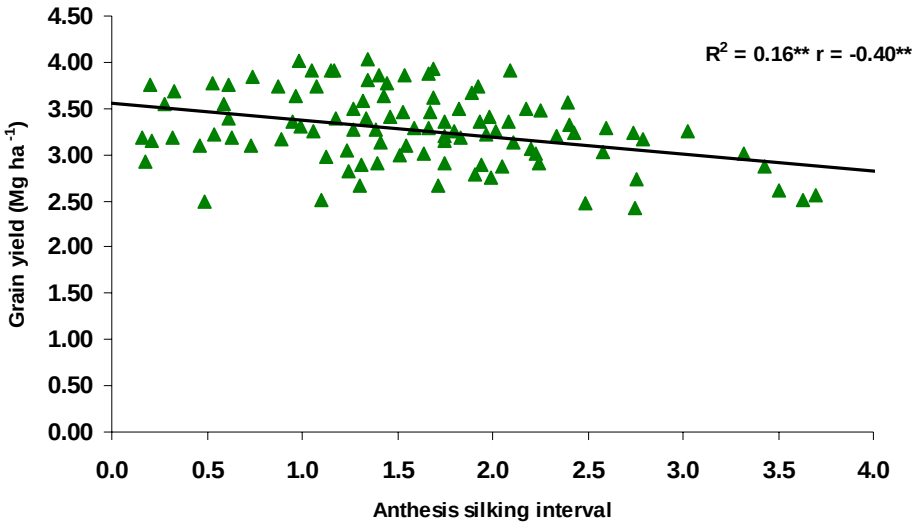


Fig. 2.6. Relationship between anthesis silking interval and grain yield across environments for 15 tropical maize inbred lines.

Table 2.17. Genetic correlations (upper diagonal) and phenotypic correlations (below diagonal) between grain yield and agronomic traits across well-watered environments.

	GY†	AD	SD	ASI	PH	EPP	EH	GM
GY		0.30*	0.27	-0.76*	-	0.48*	-	0.29
AD	0.06		0.98**	0.56**	0.26*	0.43**	0.33**	0.75**
SD	-0.02	0.89**		0.70**	0.31**	0.36**	0.42**	0.78**
ASI	-0.07	0.14*	0.56**		0.06	-0.30*	0.31*	0.56**
PH	0.20**	0.14*	0.05	-0.18*		0.56**	0.76**	0.18*
EPP	0.26**	0.11	0.01	-0.22**	0.23**		0.54**	0.04
EH	0.18**	0.15*	0.10	-0.16*	0.66**	0.24**		0.35**
GM	0.20**	0.29**	0.29**	0.14**	0.06	0.04	0.10*	

† AD, anthesis date; ASI, anthesis silking interval; EH, ear height; EPP, ears plant^{-1}; GM, grain moisture; GY, grain yield; PH, plant height; SD, silking date.

Table 2.18. Genetic correlations (upper diagonal) and phenotypic correlations (below diagonal) between grain yield and agronomic traits across drought stress environments.

	GY†	AD	SD	ASI	PH	EPP	EH	GM
GY		-0.26*	-0.41**	-0.54*	0.74**	0.54*	0.83**	0.15
AD	-0.21*		0.92**	0.27*	-0.28*	0.21*	0.02	0.54**
SD	-0.35**	0.81**		0.63**	-0.49**	-0.10	-0.16*	0.62**
ASI	-0.33**	0.09	0.65**		-0.66**	-0.64**	-0.44**	0.43**
PH	0.38**	-0.24*	-0.34**	-0.30**		0.24	-	-0.16
EPP	0.63**	-0.04	-0.32**	-0.50**	0.29		0.60*	-0.15
EH	0.20**	-0.12*	-0.21*	-0.23**	0.72	0.14*		0.20
GM	0.39**	0.33*	0.31*	0.11*	0.09	0.21*	0.02	

† AD, anthesis date; ASI, anthesis silking interval; EH, ear height; EPP, ears per plant; GM, grain moisture; GY, grain yield; PH, plant height; SD, silking date.

Table 2.19. Genetic correlations (upper diagonal) and phenotypic correlations (below diagonal) between grain yield and agronomic traits across environments.

	GY†	AD	SD	ASI	PH	EPP	EH	GM	SEN
GY		0.11	-0.03	-0.52**	0.95*	0.39*	0.85**	0.22*	0.72**
AD	-0.07		0.95**	0.20*	0.19*	0.32**	0.29**	0.68**	-0.73**
SD	-0.17**	0.82**		0.48**	0.10	0.10	0.27**	0.71**	-0.88*
ASI	-0.21**	-0.02	0.54**		-0.33**	-0.68**	-0.04	0.29*	-0.70*
PH	0.29**	-0.03	-0.12**	-0.21**		0.39	0.79**	0.14*	0.32
EPP	0.43**	0.01	-0.15**	-0.31**	0.24		0.40**	-0.08	0.71*
EH	0.19**	0.03	-0.04	-0.15**	0.68**	0.19**		0.30**	0.42*
GM	0.26**	0.27**	0.27**	0.09	0.07	0.11*	0.06		-
SEN	-0.40**	-0.10*	-0.08	0.03	0.01	-0.23**	0.12*	-0.48**	

† AD, anthesis date; ASI, anthesis silking interval; EH, ear height; EPP, ears per plant; GM, grain moisture; GY, grain yield; PH, plant height; SD, silking date; SEN, leaf senescence.

Correlations across environments are presented in Table 2.19. Grain yield had a low genetic correlation with anthesis date (0.11) and silking date (-0.03). Genetic correlation between grain yield and anthesis silking interval was negative and high (-0.52) while that between grain yield and ears per plant was positive. Genetic correlation between ASI and SD was positive. Genetic correlation between anthesis silking interval and ears per plant was high and negative (-0.68). The phenotypic correlations between grain yield and AD, SD, and ASI were all negative. Several studies have reported negative correlation between grain yield and ASI under stress conditions (Bolaños and Edmeades, 1993b; Lafitte and Edmeades, 1995; Bolaños and Edmeades, 1996; Chapman and Edmeades, 1999). Several studies have shown also the importance of the relationship between ASI and EPP (Bolaños and Edmeades, 1996; Bänziger and Lafitte, 1997; Betrán et al., 2003c). Grain yield was strongly correlated with specific combining ability across environments (Fig. 2.7), with a high predictive value at all environments.

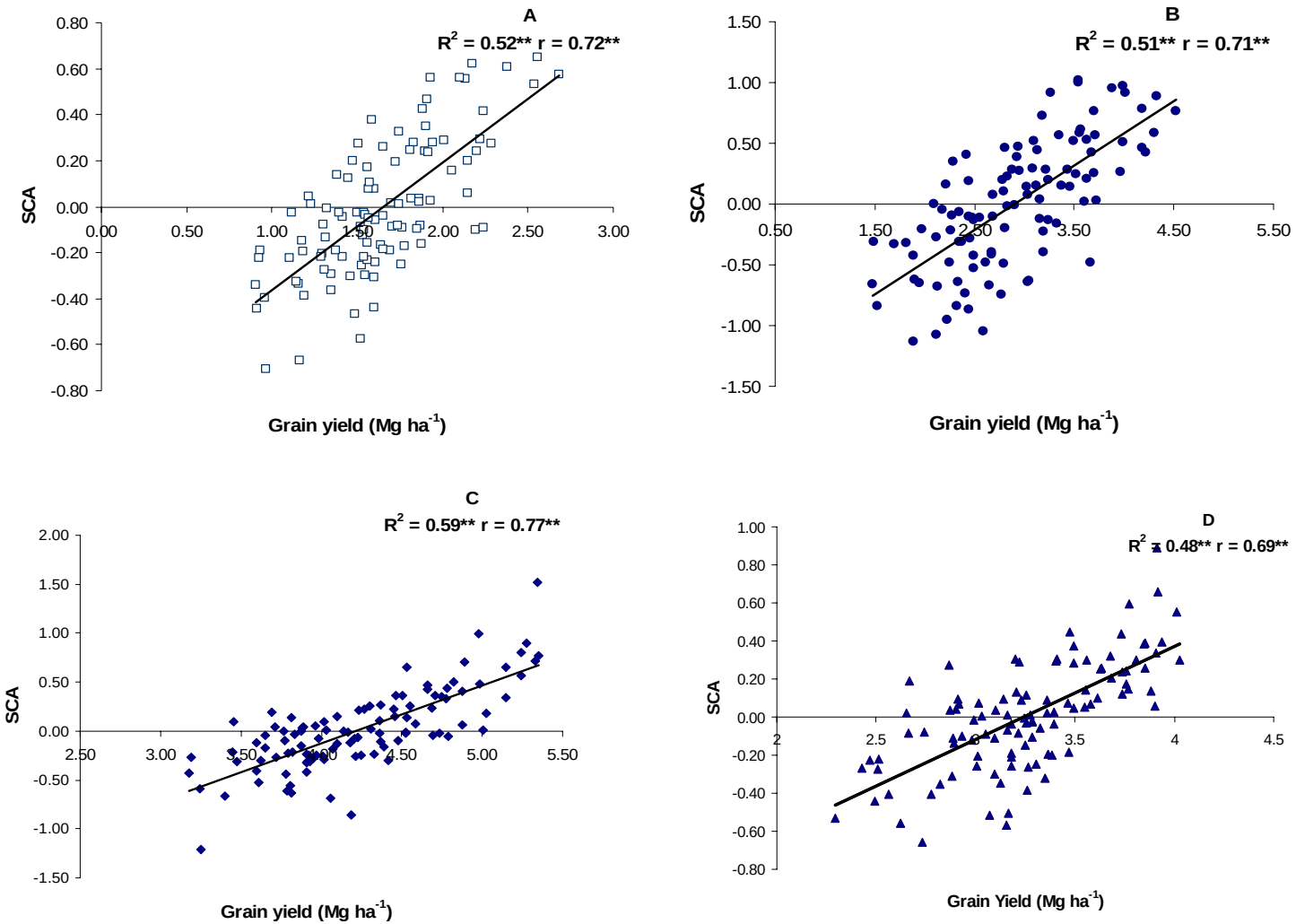


Fig. 2.7. Relationship between grain yield and specific combining ability across (A) low N, (B) drought stress, (C) well-watered and (D) environments.

Repeatability of grain yield and agronomic traits

Repeatability sets an upper limit to broad sense and narrow sense heritability and can thus provide information on heritability (Falconer and Mackay, 1996). Repeatability varied among environments and traits. Repeatability for grain yield was high for two of the well-watered environments (0.74 ± 0.06 at TLWW and 0.82 ± 0.04 at ZBWW) and low for CSWW and WEWW (Table 2.20). Repeatability for grain yield was low at PRLN (0.11 ± 0.18) but relatively high at ZBLN (0.56 ± 0.11). Anthesis and silking dates showed high repeatability at all environments except PRLN. Anthesis silking interval had a high repeatability at TLWW, TLSS, and ZBSS and low repeatability at other environments. Bolaños and Edmeades (1996) reported a broad-sense heritability of 0.60 and 0.69 for ASI measured in S_1 and S_2 progeny of tropical maize under well-watered conditions, while under severe stress broad-sense heritability was 0.51 and 0.71 for ASI of the same S_1 and S_2 progeny. Leaf senescence had a high repeatability at ZBLN and a very low repeatability at ZBSS. The low repeatability for grain yield and other traits suggests that actual heritability estimates for these traits might be low and progress to be made might be slow. The low repeatability for grain yield at PRLN was due to low genotypic variance (5.7%) and high error variance (89.6%) (Table 2.21). Bänziger et al. (1997) in a study on maize reported that under low N stress, broad-sense heritabilities decreased compared to that under high N. At other stress environments (TLSS and ZBSS), genotypic variance again explained a small proportion of the total variance for grain yield (Table 2.21). The genotypic variance for grain at TLWW was 2.4 times that at TLSS while genotypic variance at ZBWW was 3.1 times that at ZBSS and twice that at ZBLN (Table 2.21).

There was variation in repeatability across environments (Table 2.22). Grain yield had low repeatability across well-watered environments (0.16 ± 0.14) and moderate repeatability across all environments (0.47 ± 0.08). Anthesis and silking dates, ear height, and grain moisture showed high repeatability across all environments. Anthesis silking interval had low repeatability across low N stress and well-watered environments but high repeatability across drought stress environments. Bolaños and Edmeades (1996) reported grain yield to have a broad sense heritability of 0.43 under severe stress and 0.59 across environments. Low broad sense heritability was reported for anthesis silking interval across environments in a study involving 250 progenies (Bolaños and Edmeades, 1996). The lower heritability at stressed environments is a result of reduced genotypic variance (Bänziger et al., 1997). This was observed across

Table 2.20. Repeatability on mean basis (± standard error) for grain yield and agronomic traits at each environment.

	TLWW†	ZBWW	CSWW	WEWW	PRLN	ZBLN	TLSS	ZBSS
Grain yield	0.74 ± 0.06	0.82 ± 0.04	0.33 ± 0.14	0.26 ± 0.15	0.11 ± 0.18	0.56 ± 0.09	0.51 ± 0.11	0.51 ± 0.11
Anthesis date	0.83 ± 0.04	0.87 ± 0.03	-	0.95 ± 0.01	0.75 ± 0.05	0.56 ± 0.89	0.90 ± 0.02	0.88 ± 0.03
Silking date	0.92 ± 0.02	0.88 ± 0.02	0.85 ± 0.03	0.95 ± 0.01	0.48 ± 0.10	0.51 ± 0.10	0.86 ± 0.03	0.89 ± 0.02
ASI	0.71 ± 0.06	0.40 ± 0.13	-	-	0.21 ± 0.16	0.09 ± 0.19	0.62 ± 0.09	0.77 ± 0.05
Plant height	0.81 ± 0.04	0.82 ± 0.04	0.44 ± 0.11	0.97 ± 0.01	0.53 ± 0.11	0.32 ± 0.14	0.49 ± 0.12	0.51 ± 0.11
Ears per plant	0.76 ± 0.05	0.71 ± 0.06		0.05 ± 0.19	-	-	0.51 ± 0.11	0.61 ± 0.08
Ear height	0.85 ± 0.03	0.67 ± 0.07	0.63 ± 0.07	0.94 ± 0.01	0.44 ± 0.12	0.30 ± 0.14	0.71 ± 0.06	0.26 ± 0.16
Grain moisture	0.82 ± 0.04	0.59 ± 0.08	0.60 ± 0.09	0.54 ± 0.09		-	0.84 ± 0.03	0.56 ± 0.06
Leaf senescence	-	-	-	-	-	0.77 ± 0.05	-	0.03 ± 0.21

† ASI, Anthesis silking interval; CSWW, College Station well-watered; PRLN, Poza Rica low N; TLSS, Tlaltizapán, drought stress; TLWW, Tlaltizapán well-watered; WEWW, Weslaco well-watered; ZBLN, Harare low N; ZBSS, Chiredzi drought stress; ZBWW, Harare well-watered.

Table 2.21. Variance component estimates for grain yield of 15 maize inbred lines at 8 environments.

	Component					
	Rep	Block(Rep)	Genotype	Residual	% genetic variance	% error variance
TLWW†	0.02	0.04	0.17	0.12	48.8	34.6
ZBWW	0.05	0.05	1.40	0.62	66.1	29.0
CSWW	0.02	0.12	0.28	1.16	17.8	73.4
WEWW	0.03	0.07	0.22	1.30	13.7	80.3
PRLN	0.00	0.02	0.02	0.33	5.7	89.6
ZBLN	0.10	0.00	0.25	0.40	33.4	52.9
TLSS	0.00	0.19	0.10	0.19	20.2	39.3
ZBSS	0.17	1.08	0.69	1.32	21.1	40.6

†CSWW, College Station well-watered; PRLN, Poza Rica low N; TLSS, Tlaltizapán, drought stress; TLWW, Tlaltizapán well-watered; WEWW, Weslaco well-watered; ZBLN, Harare low N; ZBSS, Chiredzi drought stress; ZBWW, Harare well-watered.

Table 2.22. Repeatability on mean basis for grain yield and agronomic traits across environments.

	Low N	Drought	Well-watered	Across
Grain yield	-	0.35 ± 0.14	0.16 ± 0.14	0.47 ± 0.08
Anthesis date	0.72 ± 0.06	0.91 ± 0.02	0.83 ± 0.03	0.93 ± 0.01
Silking date	0.58 ± 0.09	0.87 ± 0.03	0.85 ± 0.02	0.92 ± 0.01
Anthesis silking interval	0.11 ± 0.18	0.62 ± 0.08	0.38 ± 0.11	0.69 ± 0.05
Plant height	0.49 ± 0.11	0.60 ± 0.08	0.78 ± 0.04	0.80 ± 0.03
Ear height	0.52 ± 0.10	0.58 ± 0.09	0.75 ± 0.04	0.80 ± 0.03
Ears per plant	0.15 ± 0.14	0.47 ± 0.11	0.57 ± 0.07	0.70 ± 0.05
Grain moisture	-	0.70 ± 0.06	0.64 ± 0.06	0.77 ± 0.04
Leaf senescence	-	-	-	0.24 ± 0.16

stress environments (Table 2.23). Reduction in genetic variance under stress conditions has been reported in other crops. In wheat, Ud-Din et al. (1992) reported that genetic variance was 3.5 times greater in irrigated environments than in the stress environments. In a study on oats, Atlin and Frey (1990) reported that low productivity environments had lower genetic variance and heritability compared to high productivity environments. In alfalfa and wheatgrass, heritability and genetic variances declined as amount of irrigation water was reduced (Rumbaugh et al., 1984). Allen et al. (1978) analyzed data from five different crops and found lower genotypic variance for the unfavorable environments. However, lower error variance for stressed environments has also been reported by Atlin and Frey (1990).

Inbred line *per se* performance and correlation with hybrid performance.

The analyses of variance combined over environments for inbred lines showed significant differences among inbreds for anthesis date, anthesis silking interval, and plant and ear height (Table 2.24). Significant inbred x environment interaction was observed for all traits. Mean grain yield was 1.01 Mg ha^{-1} (range 0.59 to 1.43 Mg ha^{-1}) across environments. Mean anthesis date was 96 d while mean anthesis silking interval was 1.07 d (range -1.75 to 4.72 d). The genetic correlations between grain yield and anthesis date was high and positive (0.69) while that between grain yield and anthesis silking interval was negative but low (-0.002) across environments (Table 2.25). Betrán et al. (2003c) reported highly significant and negative correlation between grain yield, anthesis date and anthesis silking interval among inbred lines evaluated in stress and nonstress environments. Grain yield showed a negative correlation with leaf senescence and this in agreement with results obtained by Betrán et al. (2003c). Reduced senescence should allow for better grain filling in the genotypes that maintain more green leaves. The correlation between grain yield and plant and ear height was positive indicating that among this set of inbred lines, the taller inbreds gave higher yield. Anthesis silking interval was negatively correlated with ears per plant, showing that reduced anthesis silking interval results in fewer barren ears.

Table 2.23. Variance component estimates for agronomic traits of 15 maize inbred lines across low N stress, drought stress, and well-watered environments.

Trait	Component					
	Environment (E)	Reps(E)	Blocks(Rep*E)	Genotype	Genotype*E	Residual
Across Low N						
Grain yield	1.11	0.05	0.00	0.00	0.13	0.38
Anthesis date	16.85	0.31	0.49	3.04	0.40	3.92
Silking date	9.30	0.18	0.55	2.33	0.47	5.72
Anthesis silking interval	1.07	0.02	0.04	0.13	0.23	3.74
Plant height	206.80	105.98	19.11	34.17	3.56	133.90
Ears per plant	0.01	0	0	0	0	0.01
Ear height	74.82	24.57	9.54	18.32	0.47	67.88
Across Drought						
Grain yield	4.64	0.08	0.64	0.16	0.22	0.76
Anthesis date	11.81	0	0.65	5.76	0.41	1.47
Silking date	1.86	0	1.22	8.74	1.29	2.79
Anthesis silking interval	4.26	0.01	0.34	1.52	0.80	2.12
Plant height	396.32	47.22	210.42	83.53	13.82	195.61
Ears per plant	0.01	0	0.01	0.01	0.01	0.03
Ear height	0	23.95	55.20	54.36	8.57	138.63
Grain moisture	2.27	0	1.42	3.28	1.27	3.22
Across Well-watered						
Grain yield	4.64	0.03	0.06	0.04	0.48	0.80
Anthesis date	170.13	0.02	0.17	2.84	1.23	1.15
Silking date	117.08	0	0.40	3.82	1.96	1.28
Anthesis silking interval	0.26	0	0.16	0.20	0.55	0.79
Plant height	277.69	0	32.94	77.47	45.44	81.01
Ears per plant	0.01	0	0	0.01	0.01	0.02
Ear height	670.09	0	16.41	55.83	42.83	60.04
Grain moisture	23.60	0.18	0.56	1.80	1.94	4.19

Table 2.24. Combined analysis of variance and means for grain yield and agronomic traits across environments for inbred lines.

Source of variation	df	Mean squares								
		GY†	AD	ASI	PH	EH	df	EPP	df	SEN
		Mg ha^{-1}	**d**		**cm**			**no.**		**rating 1-10**
Environment (E)	3	19.95**	3055.75***	180.42*	67463.07***	28595.69***	2	0.36	1	0.55***
Reps (E)	8	2.61	20.01***	23.93**	680.78***	220.43***	6	0.46***	4	11.93***
Inbreds	14	0.81	111.12***	40.46*	1134.27**	495.16***	14	0.22	14	1.03
Inbreds x E‡	42	0.65*	22.19**	16.33**	364.43***	155.80***	28	0.11***	14	0.73*
Error	112	0.10	11.09	8.74	95.10	38.47	84	0.03	56	0.31
Mean		**1.01**	**96.08**	**1.07**	**133.72**	**38.47**		**1.00**		**5.18**
Min		**0.59**	**90.63**	**-1.75**	**117.32**	**50.75**		**0.69**		**4.58**
Max		**1.43**	**100.25**	**4.72**	**150.71**	**74.17**		**1.19**		**6.10**
LSD (0.05)		**0.26**	**2.69**	**2.39**	**7.89**	**5.02**		**0.17**		**0.64**

*,**,*** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.
† AD, anthesis date; ASI, anthesis silking interval; EH, ear height; EPP, ears per plant; GY, grain yield; PH, plant height; SEN, leaf senescence.
‡ Hybrid x E was used to test the significance of MS for inbreds

Table 2.25. Genetic correlations (upper diagonal) and phenotypic correlations (below diagonal) between grain yield and agronomic traits across environments for inbred lines.

	GY†	AD	ASI	PH	EH	EPP	SEN
GY		0.69*	0.00	0.54	0.71*	-0.33	-0.15
AD	0.08		0.17	-0.12	0.03	0.37	-
ASI	-0.21*	-0.49**		0.05	0.43	-	0.12
PH	0.18	0.03	-0.16*		0.86**	0.25	-0.17
EH	0.23*	0.10	-0.07	0.75**		-0.26	-0.23
EPP	0.32*	0.26*	-0.44**	0.03	-0.06		-0.51
SEN	-0.37*	-0.42*	0.12*	-0.10	-0.14	-0.08	

† AD, anthesis date; ASI, anthesis silking interval; EH, ear height; EPP, ears per plant; GY, grain yield; SEN, leaf senescence.

Repeatability varied among environments for inbred line traits (Table 2.26). Repeatability was high for grain yield at ZBWW (0.95) and low at ZBDR (0.56). Anthesis silking interval had varying repeatability at the low N stress environments, 0.40 at ZBLN and 0.89 at PRLN. Plant and ear height showed consistently high repeatability at all environments. Repeatability for ears per plant was high at PRLN and ZBDR but low at ZBWW. Across environments, grain yield showed a low repeatability (0.20). This suggests that estimates for heritability for grain yield are expected to be relatively low. Anthesis date, plant height, ear height, and leaf senescence maintained high repeatability across environments. It is possible that the environment had a big effect on the yield and its components thus, the lower repeatability due to reduced genetic variance.

Table 2.26. Repeatability on mean basis (± standard error) for 15 maize inbred lines at four environments and across environments.

	PRLN†	ZBLN	ZBDR	ZBWW	ACROSS
Grain yield	0.72 ± 0.13	0.77 ± 0.11	0.56 ± 0.23	0.95 ± 0.02	0.20 ± 0.35
Anthesis date	0.96 ± 0.02	0.58 ± 0.19	0.75 ± 0.13	0.84 ± 0.08	0.79 ± 0.09
ASI	0.89 ± 0.05	0.40 ± 0.31	0.60 ± 0.21	0.77 ± 0.11	0.58 ± 0.19
Plant height	0.77 ± 0.12	0.73 ± 0.14	0.89 ± 0.05	0.88 ± 0.06	0.68 ± 0.14
Ear height	0.82 ± 0.09	0.82 ± 0.09	0.83 ± 0.08	0.87 ± 0.06	0.69 ± 0.14
Ears per plant	0.73 ± 0.13	-	0.83 ± 0.08	0.52 ± 0.23	0.51 ± 0.23
Leaf senescence	-	0.81 ± 0.09	0.73 ± 0.14	-	0.56 ± 0.36

† ASI, Anthesis silking interval; PRLN, Poza Rica low N; ZBLN, Harare low N; ZBSS, Chiredzi drought stress; ZBWW, Harare well-watered.

The relationship between inbred line and hybrid performance was investigated by correlation between inbred lines and hybrid traits under the same environment. Grain yield for inbred lines was correlated with hybrid grain yield at PRLN (0.57) and ZBLN (0.54) (Fig. 2.8). Anthesis silking interval for inbred lines was correlated with ASI for hybrids at PRLN, ZBDR, and across locations. Plant and ear height of inbred lines was significantly correlated with that of hybrids at all locations.

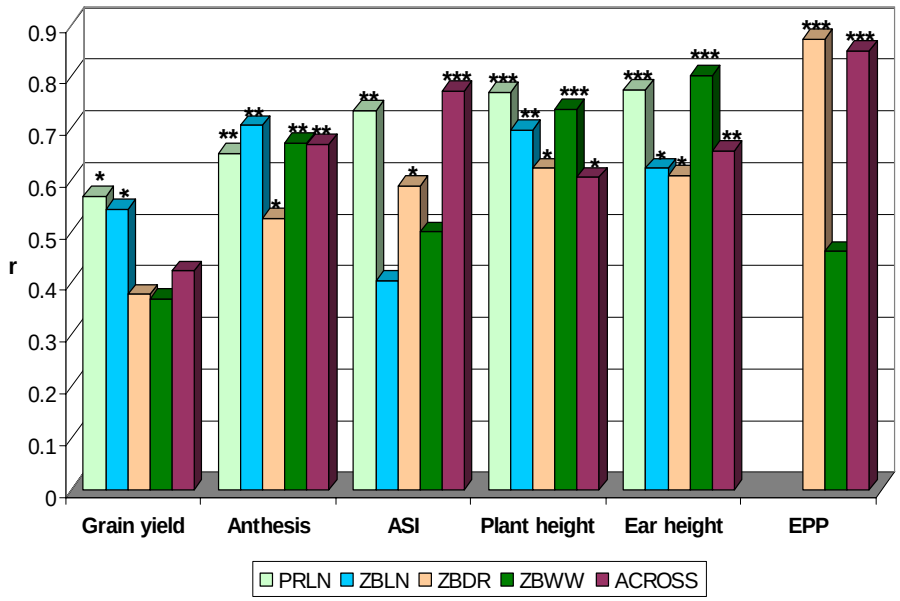


Fig. 2.8. Correlation between inbred and hybrid performance at 4 environments and across environments.

The correlation between hybrid and inbred ears per plant was highly significant at ZBDR and across locations (0.87 and 0.85), respectively. Gama and Hallauer (1977) reported significant correlation between inbred and hybrid plant height (r = 0.98), ear height (r = 0.94), and days to silking (r = 0.92) for temperate maize grown in 8 environments. Lafitte and Edmeades (1995) reported significant correlations between line and hybrid performance for anthesis date, plant and ear height in three eight parent diallel studies conducted under low N and high N conditions. Betrán et al. (2003b) in a study with tropical maize inbred lines reported that correlation between line and hybrid performance for grain yield was low but significant under severe stress but noted greater correlation under low N stress than under high N. In this study, the correlation between inbred and hybrid performance for grain yield was not significant under drought stress and well-watered conditions and the results of correlation under low N stress agree with those by Betrán et al. (2003b). The degree of inbreeding could cause the low correlation between inbred and hybrid performance under stress as early generation lines can tolerate drought intensity (Betrán et al., 2003b).

Heterosis for grain yield and agronomic traits

Heterosis was estimated both as mid-parent and high-parent heterosis in four environments where the hybrids and inbreds were evaluated in adjacent experiments. Mid-parent heterosis (MPH) and high-parent heterosis (HPH) for grain yield were highest in the drought stressed environment (ZBSS) with a mean of 367% for MPH (Fig. 2.9) and 289% for HPH (Fig.10). MPH ranged from 74% to 1119% in the drought stress environments. MPH for grain yield was low for PRLN compared to ZBLN. Mid-parent heterosis and HPH were low for plant and ear height and similar in magnitude across environments (Fig. 2.9 and Fig. 2.10). Mid-parent heterosis and HPH for anthesis silking interval were negative, showing that the hybrids had shorter anthesis silking interval compared to their parental inbreds. Betrán et al. (2003a) in

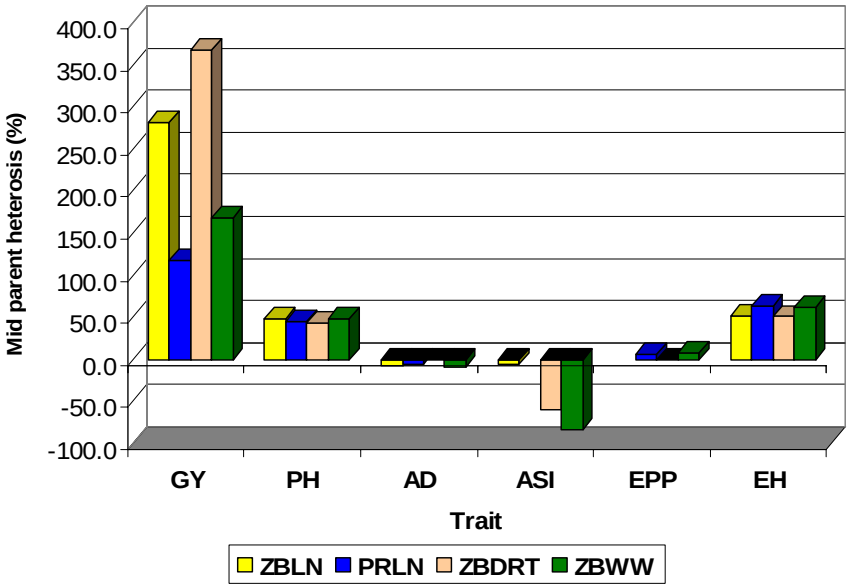


Fig. 2.9. Mid-parent heterosis for 6 traits at 4 environments (PRLN, Poza Rica low N; ZBLN, Harare low N; ZBSS, Chiredzi drought stress; ZBWW, Harare well-watered; GY, grain yield; PH, plant height; AD, anthesis date; ASI, anthesis silking interval; EPP, ears per plant; EH, ear height).

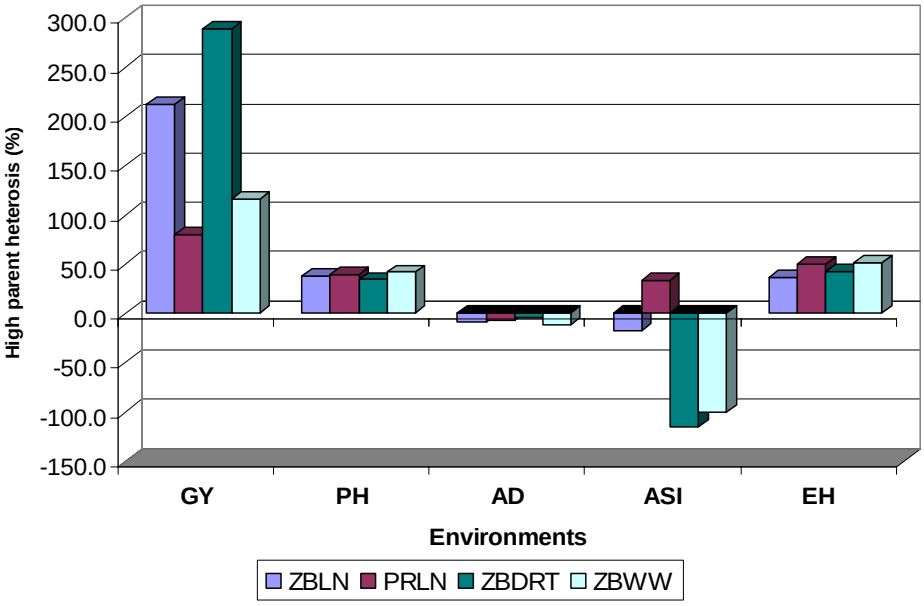
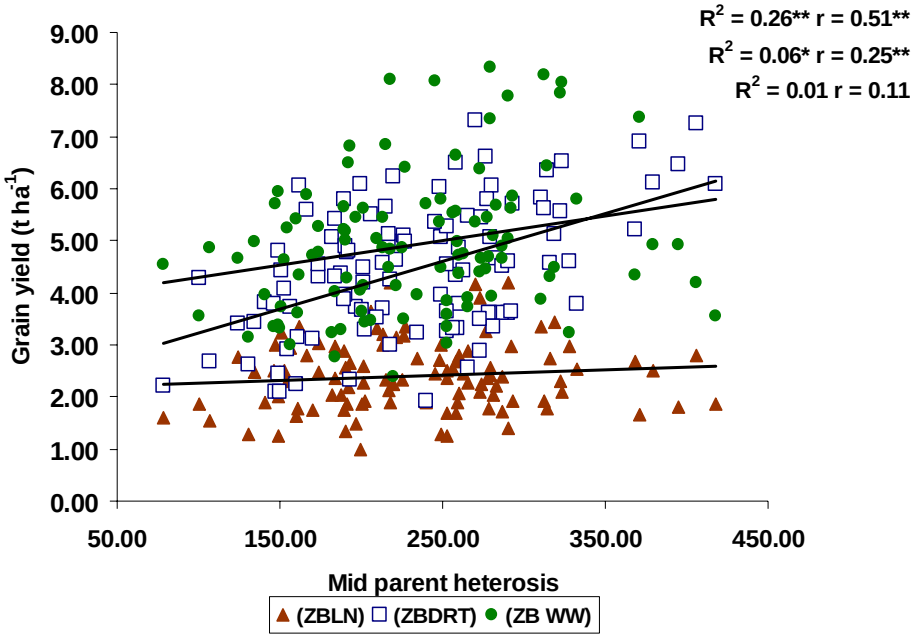


Fig. 2.10. High-parent heterosis for 5 traits at 4 environments (PRLN, Poza Rica low N; ZBLN, Harare low N; ZBSS, Chiredzi drought stress; ZBWW, Harare well-watered; GY, grain yield; PH, plant height; AD, anthesis date; ASI, anthesis silking interval; EH, ear height).

a 17 parent diallel reported average MPH for grain yield that was 2225% under severe stress conditions and 34% under low N stress conditions. A similar trend was observed in this study in which low N stress showed lower MPH and HPH for grain yield compared to drought stress environments. In the study by Betrán et al. (2003a), average HPH for grain yield was 1225% under severe stress. Saleh et al. (2002) in a study with tropical maize single cross, double cross, and three-way cross hybrids reported MPH ranging from 306 to 478% and HPH ranging from 281 to 398% for grain yield. Xu et al (2004) in a study using SSR markers to predict hybrid grain yield and yield heterosis in maize, reported low heterosis values that ranged from -38.6 to 17.2%. Shieh and Thseng (2002) analyzed diversity of RAPD markers in 13 white-grained maize inbred lines and reported MPH values in the range -21.2 to 151% for grain yield.

Simple linear correlations were used to investigate the relationship between heterosis and F_1 hybrid performance under different stresses. Mid-parent heterosis (MPH) was significantly correlated with grain yield under drought stress ($R^2 = 0.26$, $r = 0.51$; Fig. 2.11). MPH was significantly correlated with grain yield under well-watered conditions ($R^2 = 0.06$, $r = 0.25$). The correlation between MPH and grain yield under low N was weak ($R^2 = 0.01$, $r = 0.11$). The relatively strong correlation between MPH and grain yield under drought conditions might suggest that MPH could be used to predict performance of F_1 hybrids under drought stress better than under well-watered conditions. Under low N stress conditions, MPH would not be a good predictor of F_1 hybrid performance. Across environments, Betrán et al. (2003a) reported a low correlation ($r = 0.34$) between MPH and F_1 hybrid performance. The correlation between MPH and SCA was positive and significant ($R^2 = 0.28$, $r = 0.53$), indicating some value of MPH in predicting SCA across stress conditions. Betrán et al. (2003a) also reported a positive correlation between mid-parent heterosis and SCA ($r = 0.47$) in diallel study across 12 environments.

1



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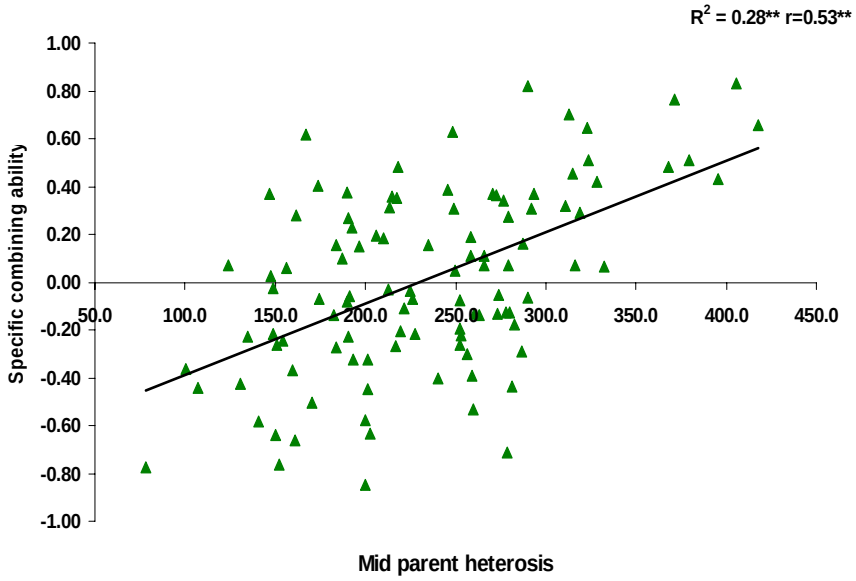

Fig. 2.11. Relationship between mid parent heterosis and (1) grain yield (2) specific combining ability for 15 maize inbred lines.

Relationships among environments

Pattern analysis was used to investigate genotype x environment interaction in this study. The lattice adjusted mean grain yield (GY) and the GCA effect for grain yield for each line were added to create a new variable (GY + GCA) that was used in this analysis. A dendrogram was constructed to examine similarities among environments. The clustering based on grain yield revealed three groups of environments (Fig. 2.12). The first group of environments was well-watered environments (WEWW and CSWW) followed by the drought stress environments (TLSS and ZBSS). This analysis clearly showed that grouping was based on growing conditions prevailing at the eight different environments (Fig. 2.12). Similar stress environments were grouped together. For example, the low N stress environments (PRLN and ZBLN), which are distant geographical locations, were grouped together (Fig. 2.12). This analysis showed marked differences between the different stress levels in this study. Chapman et al. (1997) reported similar results in a study involving topical maize populations grown under drought and well-watered environments. They reported that the high yielding environments clustered differently from the severe stress environments. Alagarswamy and Chandra (1998) reported clustering of environments that was largely geographical for sorghum grain yield across countries in Africa, Asia and Central America.

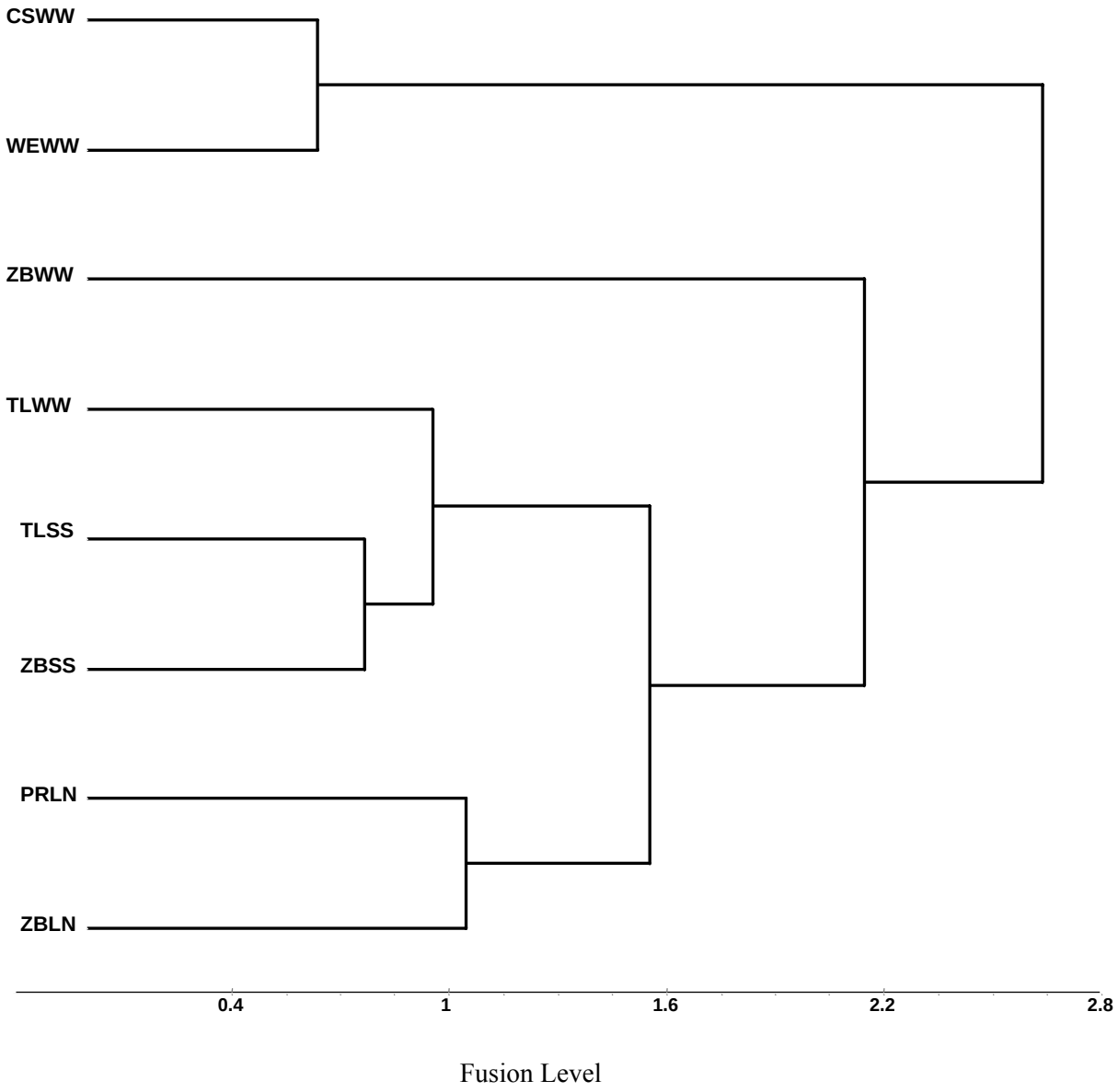

Fig. 2.12. Cluster analysis based on grain yield in hybrids of 15 maize inbred lines grown at 8 environments (PRLN, Poza Rica low N; ZBLN, Harare low N; ZBSS, Chiredzi drought stress; ZBWW, Harare well-watered).

Stability and AMMI analysis

Stability analysis was conducted to assess the performance of the inbred lines in hybrid combination and inbred lines *per se* in different environments. A stable variety is defined as one with b = 1.0 and $\sigma^2_{di} = 0$, where b for a genotype is the slope of a linear regression of the yield of that genotype at a given location against the mean yield of all hybrids grown at that location, and σ^2_{di} is the mean squared deviation from regression (Eberhart and Russell, 1966). Results showed that there is variation in stability of the inbred lines used in this study when considered in hybrid combination and as inbred lines *per se* as measured by the b value and mean squared deviation (Table 2.27). For grain yield, stability as measured by the slope b, ranged from 0.82 to 1.14 for inbred lines in hybrid combination. Inbred line CML341 was the most stable with b = 1.14 and $\sigma^2_{di} = 0.04$. CML254 (b=1.07, $\sigma^2_{di} = 0.10$) and CML216 (b = 1.04, $\sigma^2_{di} = 0.14$) were also stable. The least stable lines were CML247 and CML311 for grain yield. Stability values for anthesis silking interval ranged from 0.88 to 1.25. The most stable line for anthesis silking interval was CML258 (b = 1.01, $\sigma^2_{di} = 0.03$) followed by CML311 (b = 1.04, $\sigma^2_{di} = 0.07$). As lines *per se*, the most stable line for grain yield was CML341 (b = 1.14, $\sigma^2_{di} = 0.04$). Average grain yield was positively correlated with the slope of regression b, for both inbreds in hybrid combination (r = 0.53*) and as lines *per se* (r = 0.61*), suggesting that lines that performed well were more stable.

Table 2.27. Mean grain yield and anthesis silking interval of inbred lines in hybrid combination and grain yield of inbred lines *per se* and their phenotypic stability (b).

Line	Hybrid combination						Per se		
	Grain yield	b†	σ^2_{di}	ASI	b	σ^2_{di}	Grain yield	b	σ^2_{di}
	Mg ha^{-1}			**d**			**Mg ha^{-1}**		
P502	3.36	1.12	0.72	1.39	1.04	0.14	1.27	1.31	0.01
P501	3.42	0.85	0.38	1.34	0.89	0.02	1.43	0.66	0.22
CML78	3.33	0.92	1.28	0.85	1.25	0.30	0.71	0.46	0.03
CML321	3.16	1.13	0.83	1.54	1.02	0.21	0.79	0.60	0.09
CML311	3.23	0.96	0.93	1.75	1.04	0.07	0.82	0.94	0.00
CML202	3.06	1.01	0.30	2.67	1.12	0.30	1.17	1.60	0.00
CML206	2.72	1.00	0.59	3.34	0.93	0.64	1.16	1.43	0.12
CML216	3.25	1.04	0.14	3.08	1.04	0.39	1.14	2.20	0.19
CML247	2.39	0.82	0.90	2.90	0.91	0.77	0.72	0.81	0.01
CML254	3.46	1.07	0.10	1.72	0.93	0.21	0.90	0.04	0.11
CML258	3.89	1.06	1.43	1.68	1.01	0.03	1.37	1.84	0.04
CML339	3.69	1.10	0.56	0.41	0.92	0.21	0.81	0.95	0.08
CML341	3.63	1.14	0.04	0.18	0.88	0.24	1.07	1.14	0.04
SPLC-F	2.69	0.90	1.28	0.39	0.95	0.51	0.59	0.08	0.03
CML343	3.42	0.89	0.16	1.18	1.07	0.12	1.20	0.94	0.05

†ASI, anthesis silking interval; b, slope of regression; σ^2_{di}, mean squared deviation.

An AMMI biplot (Gabriel, 1971) was used to show both genotypes and environments simultaneously. In a biplot, genotypes are represented as points and environments are represented by vectors. An acute angle between any two vectors indicates a strong positive correlation among the environments. Such environments would then discriminate genotypes in a similar way. Environment vectors at 90^{o} or greater indicate that discrimination among genotypes in these environments is different. The biplot was generated using the principal component scores to visualize the relationship between environments and hybrids. The first two principal components explained 82.6% of the total variation in genotype x environment (G x E) sums of squares (Table 2.28, Fig. 2.13). The biplot showed that environments ZBSS and ZBWW were the most discriminating for the genotypes. The angle between the vectors for these two environments was large indicating they were very different in discriminating genotypes. Similarly, environment ZBWW and CSWW, ZBSS and CSWW had large angles between them suggesting they were different in discriminating genotypes. Well-watered environments CSWW and WEWW, both in Texas, had a very small angle between them showing how closely associated they are. These two environments are expected to have a strong positive correlation of genotype yield between them and discriminate genotypes similarly. The two low N stress environments (PRLN and ZBLN) although different geographically, were close suggesting that these two environments are similar in genotype discrimination. Inbred line P501 had a small projection on the vector for environment WEWW indicating it performed well in that environment. Line SPLC-F had a small projection on CSWW and thus performed well in that environment. Line CML311 performed well at ZBSS. Lines CML258 and CML321 had positive projections on ZBWW and ZBSS showing that they performed well on average in both environments.

Table 2.28. Analysis of variance for the Additive Main Effect and Multiplicative Interaction (AMMI) model.

Source of variation	df	Sum of squares	Mean square	% SS explained
Genotypes	14	17.83	1.27	
Environments (E)	7	437.07	62.44	
Genotype x E	98	62.44	0.64	
AMMI 1	20	36.86	1.84**	59.04
AMMI 2	18	14.71	0.82**	23.55
AMMI 3	16	4.81	0.30*	6.55
AMMI 4	14	2.78	0.19	4.46
G x E Residual	30	3.28		

*, ** Indicates significance at 0.05, and 0.01 probability levels, respectively.

Analysis of data for inbred lines revealed that the first two principal components accounted for 92.3% of the total variation in G x E sums of squares (Fig. 2.14). Environments ZBWW and ZBWW were the most discriminating among the inbred lines as these had the largest angle between them. The stressed environments ZBSS and PRLN had a small angle between them, suggesting that they discriminated the inbred lines similarly. Inbred line P501 had a small projection on environment ZBLN suggesting it performed well at that location. Indeed P501 had the highest yield at ZBLN (1.62 Mg ha^{-1}). CML254 performed well at PRLN where it had the highest yield (0.70 Mg ha^{-1}). CML216 had a small projection on environment vector for ZBWW suggesting good performance at that environment. Line CML258 had positive projection on both ZBSS and ZBWW where it was among the best performers at those environments.

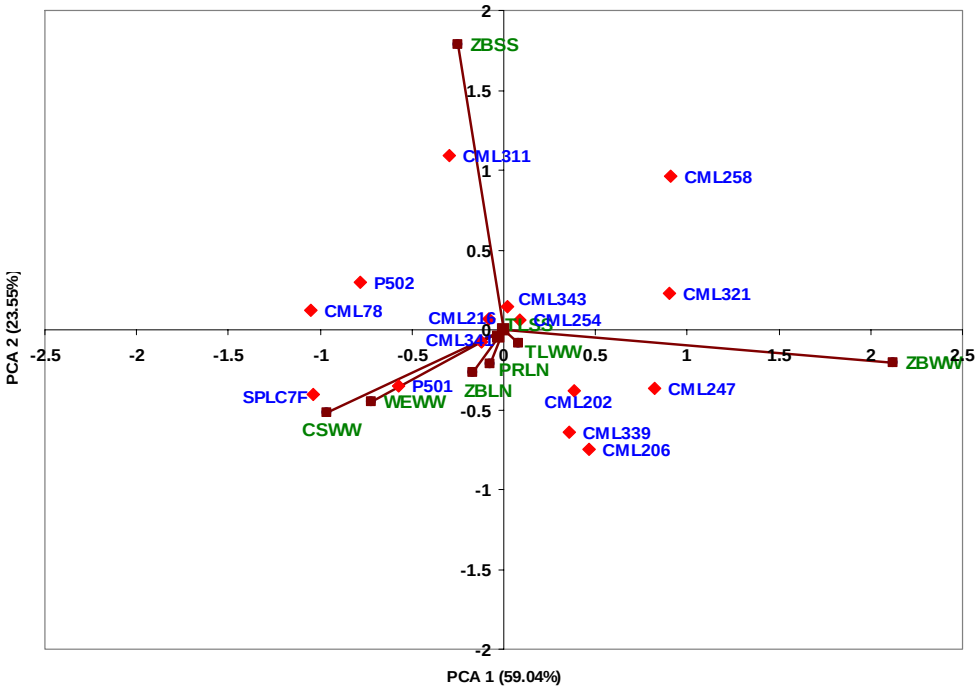

Fig. 2.13. Biplot of first two principal components for grain yield of 15 maize inbred lines in hybrid combination at 8 environments.

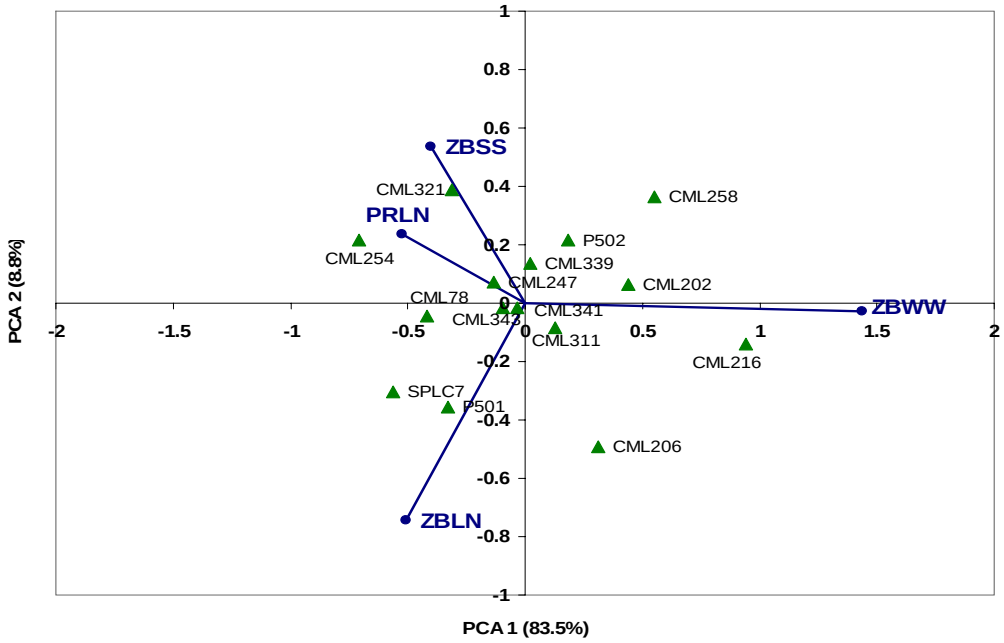

Fig. 2.14. Biplot of first two principal components for grain yield of 15 maize inbred lines *per se* at 4 environments.

Genetic diversity

Three types of markers were used to investigate diversity among this set of 15 maize inbred lines. The 32 SSR primers produced 114 alleles. The average number of alleles was 3.6, and this was relatively smaller than the number found in other studies on maize. Senior et al. (1998), reported an average of 5 alleles for 70 SSR markers in 94 U.S. maize inbred lines, Pejic et al. (1998) 6.8 alleles for 27 SSR markers in 33 U.S. maize inbred lines, Warburton et al. (2002) 4.9 alleles for 85 SSR markers in 57 inbred lines and 7 populations, Reif et al. (2003) 7.7 alleles for 83 SSR markers in 20 subtropical maize populations, and Xia et al. (2004) 7.4 alleles for 79 SSR markers in 155 tropical maize lines. Garcia et al. (2004), however, reported a lower number of alleles (2.9) when using 68 SSR markers on 18 maize inbred lines. The total number of alleles in diversity studies is usually proportional to sample size and that could explain the differences (Xia et al., 2004). The PIC, which is a measure of allele diversity at a locus, ranged from 0.38 to 0.78 with an average of 0.59 for SSR markers (Fig. 2.15). The average value obtained in this study is similar to that reported by Senior et al. (1998) that reported 0.59 for 70 SSR and Reif et al. (2003) that reported an average of 0.60 for 83 SSR markers. Smith et al. (1997) reported an average PIC value of 0.62 with 131 SSR markers.

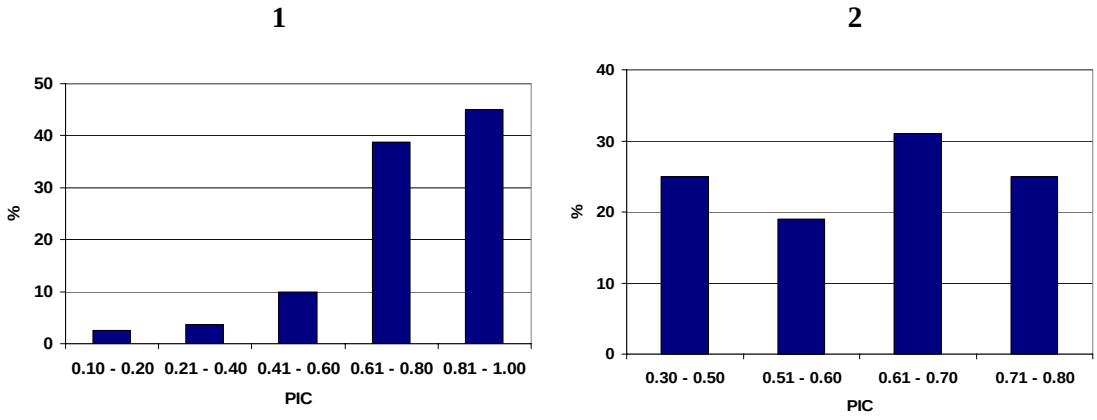

Fig. 2.15. Distribution of polymorphism information content (PIC) for (1) RFLP and (2) SSR markers.

The number of alleles for RFLP markers ranged of 2 to 28. Other studies have reported average number of alleles as 5.3 (Garcia et al., 2004), 4.0 for the BSSS population (Hagdorn et al., 2003), and 4.65 (Betrán et al., 2003a). The average PIC value for RFLP markers was 0.73 with a range of 0.12 to 0.94 (Fig 2.15). Betrán et al. (2003a) reported a range of 0.11 to 0.82 and Garcia et al. (2004) reported an average PIC value of 0.96 for RFLP markers.

Genetic distance among inbred lines

Genetic distance between pairs of inbred lines was computed for each of the marker data sets and a combination of markers. Estimates of genetic distance using the methods of Nei and Li (1979) and Modified Roger's distance are presented in Table 2.29. Mean genetic distance estimated with AFLP markers was the lowest (0.48). Genetic distance ranged from 0.36 to 0.64 for AFLP markers with Nei and Li's method (Table 2.28). The mean genetic distance estimated with RFLP and SSR data using the Nei and Li method was the same (0.60). The mean genetic distance estimated using Modified Roger's distance was higher than that estimated using Nei and Li for all markers. The situation was the same when RFLP and SSR data were combined and this was true also for pooled data. The mean genetic distance for the 15 inbred lines using pooled marker data was 0.57 with a range 0.45 to 0.63. Ajmone Marsan et al. (1998) reported that genetic distance estimated with AFLP and RFLP marker data following the method of Nei and Li agreed very closely.

Table 2.29. Mean and range of genetic distance for 15 maize inbred lines estimated from AFLP, RFLP and SSR data using two methods (Nei & Li, Modified Roger's Distance).

	Nei & Li		Modified Roger's Distance	
	Mean	Range	Mean	Range
AFLP	0.48	0.36 - 0.64	0.73	0.65 - 0.81
RFLP	0.60	0.46 - 0.66	0.61	0.54 - 0.64
SSR	0.60	0.35 - 0.81	0.72	0.59 - 0.80
RFLP + SSR	0.60	0.46 - 0.66	0.63	0.56 - 0.66
All Markers	0.57	0.45 - 0.63	0.65	0.59 - 0.68

Pearson correlation coefficients were computed among genetic distance estimates obtained with the different markers. Genetic distance estimated with AFLP had a small correlation with that based on SSR (0.03) and RFLP (0.04). The correlation coefficient between genetic distance based on SSR and that based on RFLP was low as well (0.06). This is in contrast with results obtained in other studies in maize. Pejic et al. (1998) reported high correlation between AFLP and RFLP (0.70), AFLP and SSR (0.67), RFLP and SSR (0.59) based genetic similarities among temperate maize inbred lines. Lübberstedt et al. (2000) reported a highly significant correlation (0.87) among genetic similarity estimates based on AFLP and RFLP markers in European maize inbreds. Barbosa et al. (2003) reported a strong correlation (0.78) between AFLP and SSR based genetic distance in tropical maize. Ajmone Marsan (1998) reported a high correlation (r = 0.65) between RFLP and AFLP based genetic distance. SSR and RFLP based genetic distances were highly correlated in a study on maize by Smith et al. (1998). Garcia et al. (2004) reported high correlation between genetic distance based on AFLP and RFLP (0.87), RFLP and SSR (0.71), SSR and AFLP (0.78). Powell et al. (1996) reported that in soybean, genetic similarities based on SSR marker data were in agreement with those from RFLP, AFLP, and RAPD markers. In a study on wheat, Bohn et al. (1999) found low correlation between genetic similarity based on AFLP and RFLP (0.13), AFLP and SSR (0.00), and RFLP and SSR (0.05) among 55 wheat lines. Powell et al. (1996) suggested that the number of markers affects the variance of the similarity estimates.

Cluster analysis

Similarity values were used to construct a dendrogram using the UPGMA method to assess genetic diversity among this set of inbred lines for each of the marker system and pooled marker data. Clustering based on AFLP marker data revealed 4 clusters (Fig. 2.16). Some lines clustered together but pedigree information does not show them to be related. For example line CML254 and CML341 have different origins, but they clustered together. Lines that are closely related like CML339, CML341 and CML343 were grouped in different clusters. Lines CML254 and CML258, originating from the same population, clustered together. The dendrogram produced from SSR marker data is shown in Fig. 2.17. This dendrogram also had four clusters that differed from that obtained with AFLP data, but many of the lines known to be related based on pedigree ended up in separate clusters. Some lines related by pedigree were classified in the same cluster (CML339 and CML343) although not very close.

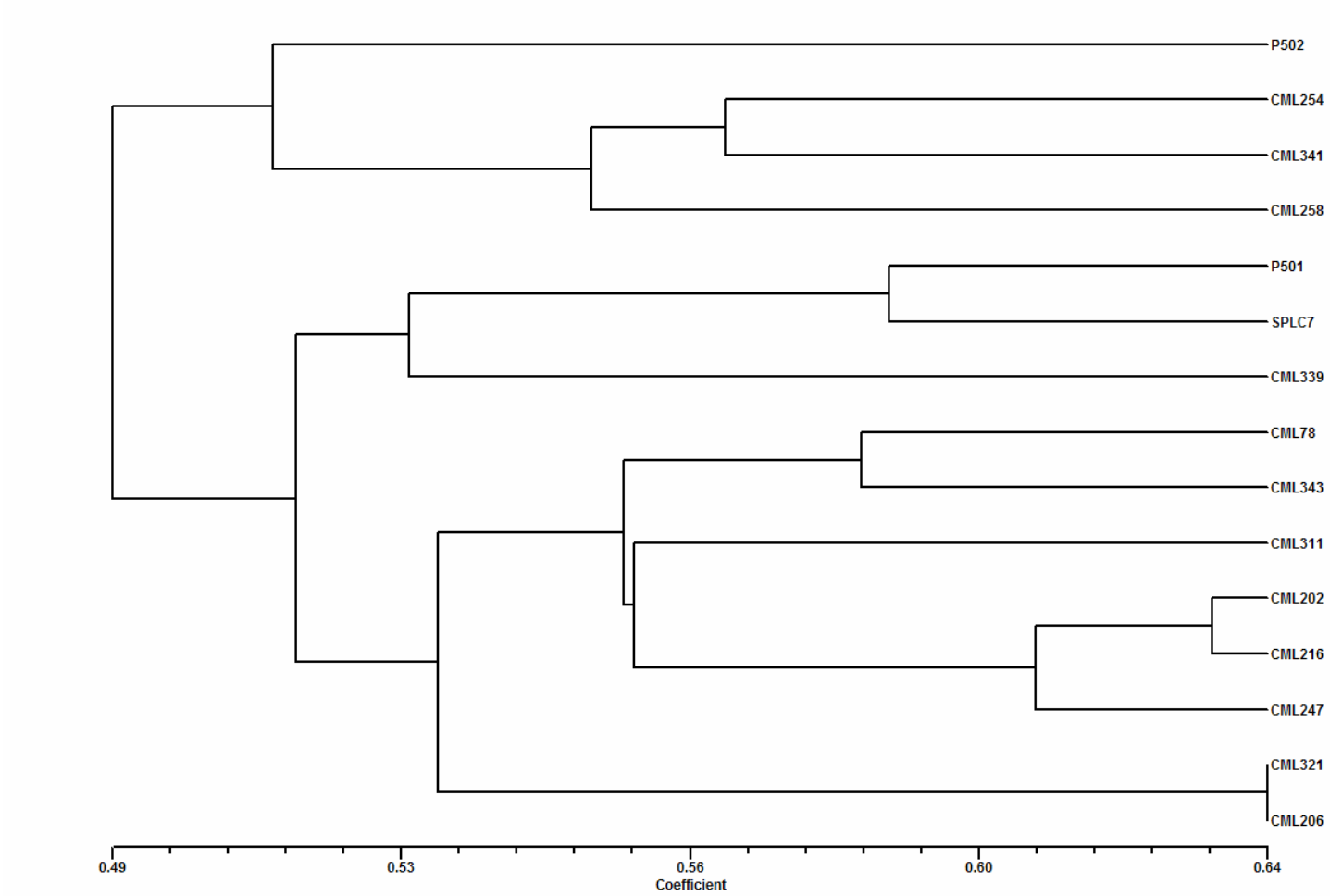

Fig. 2.16. Dendrogram of 15 maize inbred lines revealed by UPGMA cluster analysis of genetic similarity based on AFLP marker data.

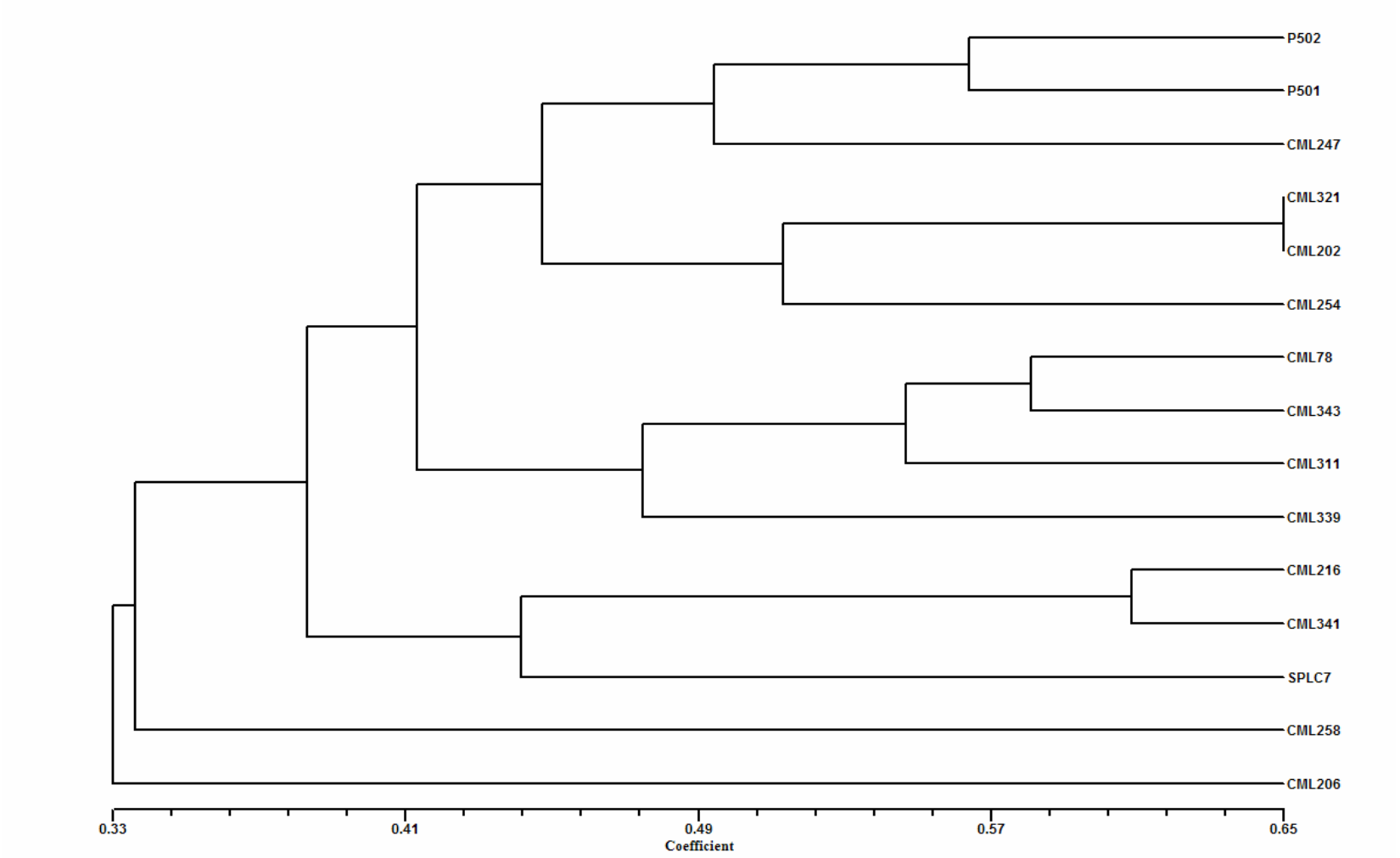

Fig. 2.17. Dendrogram of 15 maize inbred lines revealed by UPGMA cluster analysis of genetic similarity based on SSR marker data.

Clustering based on RFLP data revealed four clusters (Fig. 2.18) with many of the related lines falling in the same clusters. Lines CML399, CML341, and CML343, originating from Population 43, clustered together. Lines CML254 and CML258, both from Population 21, clustered together as would be expected.

Data from the three marker systems was then pooled and cluster analysis conducted. The dendrogram showed 4 clusters that had most lines grouped together in accordance with known pedigree and origin (Fig. 2.19). Drought tolerant lines CML339, CML341, and CML343 that were developed from the same population clustered together. Lines CML202, CML206 and CML216 from the mid-altitude maize breeding program in Zimbabwe clustered together. CML254 and CML258 clustered together. Analysis based on AFLP, RFLP, and pooled data consistently classified lines CML254 and CML258 in the same cluster. Classification based on SSR, RFLP, and pooled data produced the same result as regards grouping of lines CML339 and CML341 in the same cluster. The dendrogram produced from RFLP data and that from the pooled data classified the lines almost in identical patterns with three clusters agreeing closely. Similarity in clustering has been reported with different marker systems. Pejic et al, (1998) reported AFLP, SSR and RFLP to group material mostly according to pedigree data with AFLP showing the highest correlation with pedigree data. Ajmone Marsan (1998) reported similar clustering of temperate maize using AFLP and RFLP markers. Barbosa et al. (2003) also reported close agreement between clustering based on AFLP and SSR markers for tropical maize single crosses. Powell et al. (1996) reported that RFLP, SSR, AFLP and RAPD markers discriminated two subspecies of soybean clearly.

Relationship between genetic distance, F_1 hybrid performance, specific combining ability, and heterosis

Linear correlation coefficients were computed between genetic distance (GD), F_1 performance, specific combining ability, and heterosis. Correlation between genetic distance and F_1 grain yield was positive and significant (r = 0.24*) (Fig. 2.20). This low correlation between genetic distance and F_1 grain yield suggests that genetic distance in this set of maize inbred lines is of limited value in predicting F_1 hybrid grain yield. Significant correlations between genetic distance and grain yield of varying magnitude have been reported in tropical maize (Benchimol et al., 2000; Betrán et al., 2003; Barbosa et al., 2003) and temperate maize

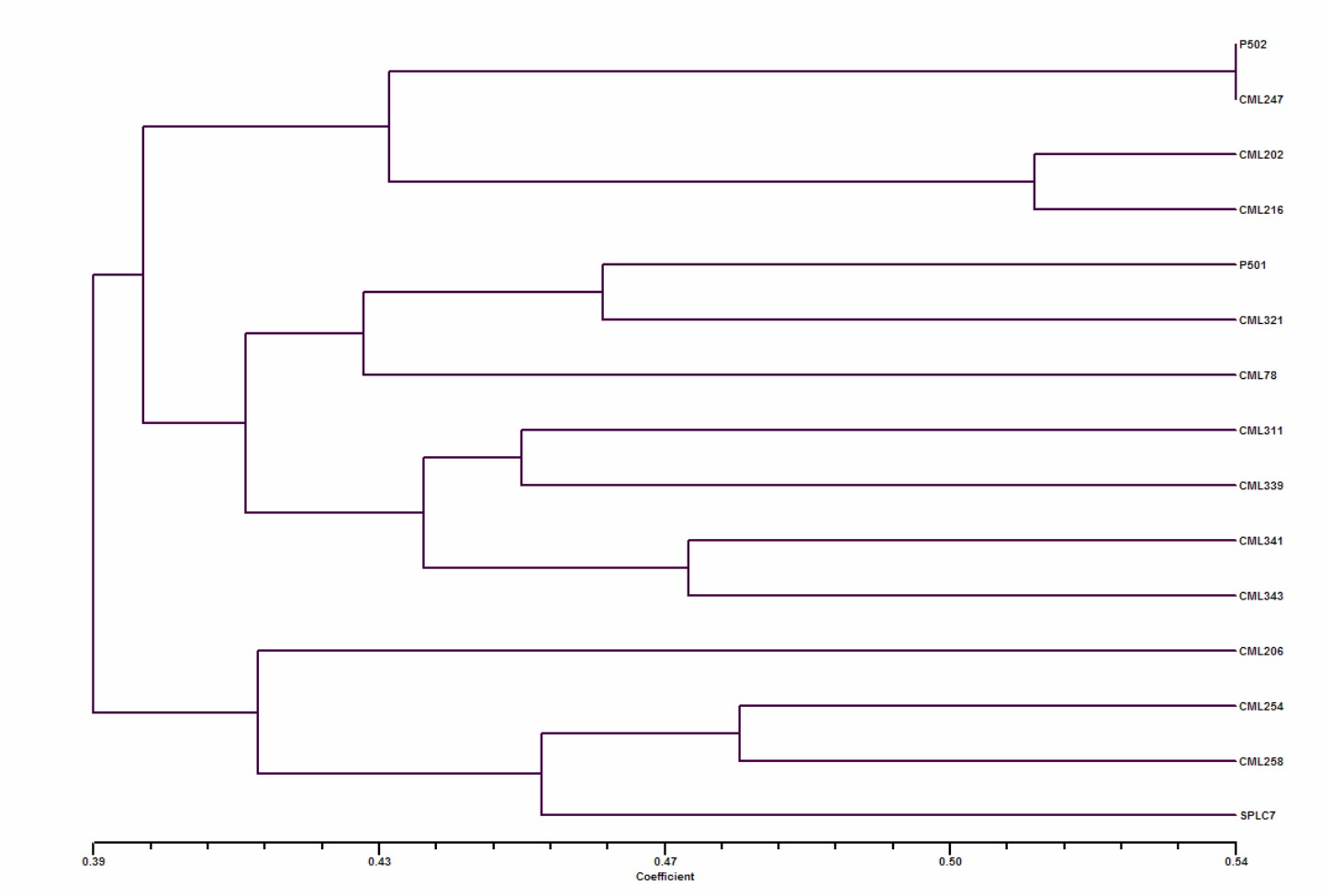

Fig. 2.18. Dendrogram of 15 maize inbred lines revealed by UPGMA cluster analysis of genetic similarity based on RFLP marker data.

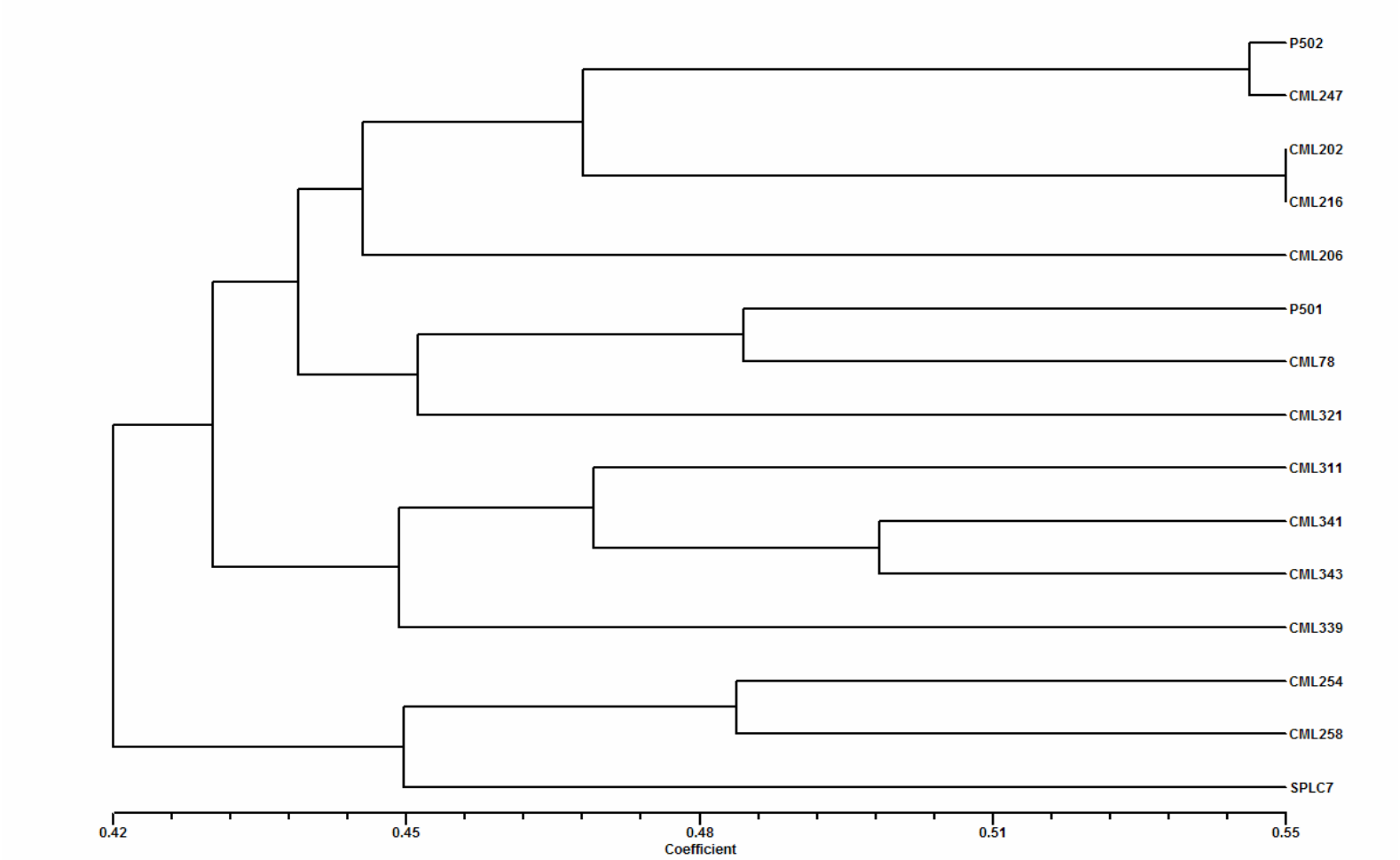

Fig. 2.19. Dendrogram of 15 maize inbred lines revealed by UPGMA cluster analysis of genetic similarity based on combined marker data.

(Lee et al., 1989; Melchinger et al., 1990a; Ajmone Marsan, 1998). No significant correlation was found between genetic distance and grain yield in studies by Melchinger et al. (1990b) and Shieh and Thseng (2002) in temperate maize.

Genetic distance and average mid-parent heterosis showed a positive and significant correlation (Fig. 2.20). Positive correlation between genetic distance and heterosis has been reported in studies by Melchinger et al. (1990a, b), Benchimol et al. (2000), Shieh and Thseng (2002), and Reif et al (2003b). The correlation between genetic distance and mid-parent heterosis in this study was quite low with a very low predictive value ($R^2 = 0.06$). The low predictive value implies that GD may not be suitable as a predictor of F_1 hybrid performance and heterosis in this set of materials. Melchinger (1999) indicated that high estimates of *r*(GD, MPH) can be expected if correlations are calculated across different types of crosses because GD and MPH are expected to increase from crosses among related lines to intra-group crosses and further into inter-group crosses. The range of genetic distances obtained in this study (0.45-0.63) is within the range of genetic distances for crosses among unrelated lines in which the correlation between marker-estimated GD and MPH is expected to be weak (Melchinger, 1999).

Specific combining ability had a positive but low correlation with genetic distance (Fig. 2.20) suggesting that genetic distance may not be a good indicator of high specific combining ability in this set of materials. Melchinger et al. (1990a, b) reported slightly higher correlation ($r = 0.26$ and $r = 0.39$ respectively) while Lee et al. (1990) reported a much higher correlation ($r = 0.74$) between SCA and genetic distance among temperate germplasm. Parentoni et al. (2001) reported a low and positive correlation ($r = 0.16$) between genetic distance based on RAPD markers and specific combining ability. Genetic distance based on SSR was significantly correlated with hybrid yield in maize in a study by Xu et al. (2004). Betrán et al. (2003a) reported a highly significant correlation ($r = 0.80$) between GD and specific combining ability in tropical maize inbreds grown under stress and non-stress environments. Melchinger et al. (1990a) noted that differences in correlations could be a result of evaluating different types of materials. Melchinger et al. (1990a) suggested that marker based genetic distance is not sufficiently associated with grain yield, heterosis, and SCA to identify superior single crosses.

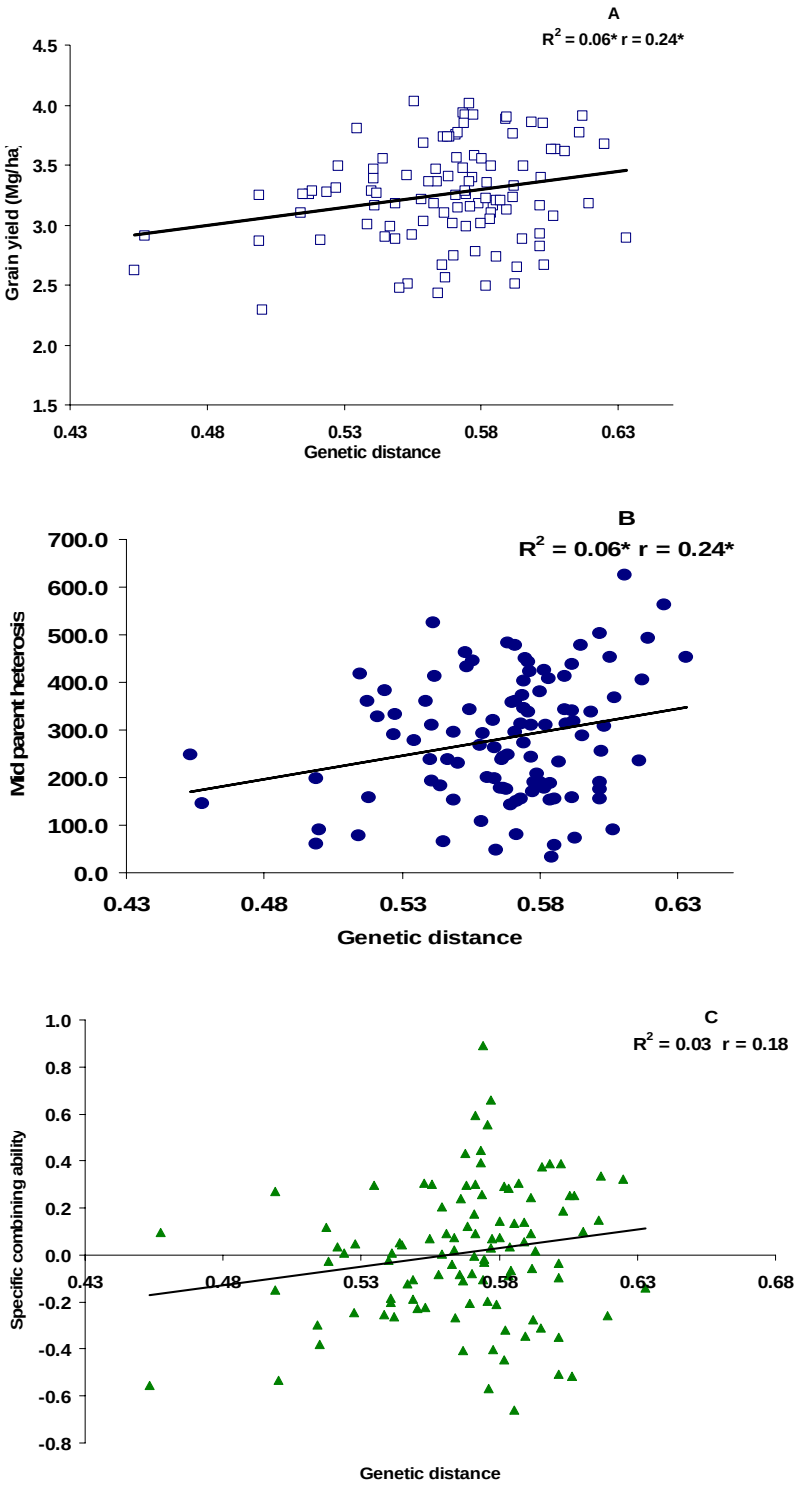

Fig. 2.20. Relationship between genetic distance and (A) grain yield, (B) average mid-parent heterosis, and (C) specific combining ability.

CONCLUSIONS

Significant GCA was observed for most traits except grain yield and ears per plant across low N stress, drought stress, and well-watered conditions. Significant GCA x environment interaction was observed across low N, drought, and well-watered conditions for all traits except ear height. Inbred lines CML254, CML258, CML341, and CML343 had consistently positive GCA effects for grain yield across low N, drought stress, well-watered, and across locations. Inbred lines CML339, CML341, and SPLC7-F had good GCA effects for anthesis silking interval across stresses. The best hybrids were from crosses between testers from different programs. Additive genetic effects appear to be more important for grain yield under drought and well-watered conditions, but non-additive genetic effects seem to be more important under low N stress conditions for ears per plant in this set of inbred lines. Repeatability was low for grain yield under stress conditions. AMMI analysis showed that some environments explained more of the genotype x environment variation than others. Mid-parent and high-parent heterosis were highest in drought stress followed by low N stress conditions. Molecular marker genetic distance was positively correlated with specific combining ability and grain yield, but the predictive value was not strong.

CHAPTER III

PERFORMANCE OF SYNTHETIC MAIZE HYBRIDS UNDER LOW NITROGEN STRESS AND OPTIMAL CONDITIONS

INTRODUCTION

Maize (*Zea mays* L.) in many tropical regions is produced by small scale farmers who face a number of constraints that include both abiotic and biotic stresses, and a general lack of inputs. The major abiotic stresses are drought and low soil fertility. Low soil fertility is mainly due to low soil nitrogen. Nitrogen deficiency is common where nitrogen (N) is applied at below-optimal levels because of high cost relative to economic returns, or where there are significant risks of drought (Lafitte and Edmeades, 1994a). In the case of eastern and southern Africa, a combination of climatic risk, declining soil fertility, the need to increase food production into marginal areas as population pressure increases, high input costs, lack of credit schemes, and poverty result in smallholder farmers producing maize and other crops in extremely low-input/low risk systems (Bänziger and Diallo, 2004). Maize yield averages 1.3 Mg ha^{-1}. Most of the maize varieties grown in the eastern and southern Africa regions were developed for good performance under optimal conditions rather than those faced by the smallholder farmers (Bänziger and Diallo, 2004). Stress tolerant germplasm can be very helpful in alleviating the effects of drought and low N stress. Low N stress tolerant germplasm would be particularly of interest in those tropical areas where fertilizer application is limited and not readily affordable. CIMMYT-Zimbabwe in collaboration with the National Agricultural Research Systems (NARS) of the different countries in eastern and southern Africa, has developed stress tolerant germplasm adapted to the region and a number of open-pollinated varieties (OPVs) have been released (Bänziger and Diallo, 2004).

Open-pollinated varieties are important in this region because farmers do not readily buy hybrid seed every year, and they commonly replant harvested seed the following season. It is estimated that less than 30% of the maize area in sub-Saharan Africa is planted with hybrid seed (Hassan et al., 2001) with the remainder planted to OPVs and recycled hybrid grain (Pixley and Bänziger, 2004). Pixley and Bänziger (2004) noted that in some farming systems in Africa where yield levels are inherently low (below 1.5 Mg ha^{-1}), recycling improved OPVs may be more profitable and sustainable than purchasing annually fresh hybrid seed. Growing OPVs can

become more profitable if farmers use monetary savings that could have been used to buy seed to purchase additional inputs such as fertilizer (Pixley and Bänziger, 2004). Other than OPVs, farmers can also use synthetic maize seed without buying seed every season. Seed production of OPVs and synthetics is easier and cheaper than that of hybrids. Synthetic varieties developed from stress tolerant lines would be particularly very useful. Improved synthetic varieties of maize are important as germplasm sources for inbred line development and for alleviating the problems of genetic vulnerability (Hallauer and Malithano, 1976). Synthetic varieties are developed usually to increase the frequency of alleles for specific traits and to incorporate exotic germplasm into adapted varieties. A well known example of a synthetic is the Iowa Stiff Stalk Synthetic that is a source of many valuable inbred lines used in temperate maize breeding in the United States (Hallauer and Miranda, 1988). Synthetic varieties have been improved for grain yield (Hallauer and Malithano, 1976; Vales et al., 2001), drought tolerance (Gama et al., 2004), and weevil resistance (Dhliwayo and Pixley, 2003). CIMMYT in Zimbabwe has developed synthetic varieties to combine different sources of stress tolerances and agronomic traits. Obtaining information on the performance of these synthetics and their hybrids under stress and non-stress conditions will be helpful in understanding their value for breeding and potential use by farmers. Therefore, the objectives of this study were to: (i) estimate the general and specific combining abilities among synthetics for grain yield and other agronomic traits, (ii) investigate genotype x environment interaction across stress conditions and testing locations for synthetics and their hybrids, and (iii) evaluate the performance of synthetic hybrids.

REVIEW OF LITERATURE

Synthetic varieties

Synthetic varieties were first suggested by Hayes and Garber (1919). Lonnquist (1961) defined synthetic varieties as "open-pollinated populations derived from the intercrossing of selfed plants or lines and subsequently maintained by routine mass selection procedures from isolated plantings". Kinman and Sprague (1945) and Lonnquist (1949) observed that relatively little attention was given to the development of synthetic varieties yet their value as reservoirs of desirable germplasm was pointed out by Sprague and Jenkins (1943). The greater genetic variability of a synthetic variety (i.e., mixture of different hybrids) should permit finer adjustment to the more variable growing conditions (Lonnquist, 1949). An advantage of a synthetic variety is that farmers can use harvested grain as source seed to plant the next crop. If care can be taken to avoid contamination by foreign pollen, and to select a sufficiently large number of plants to avoid inbreeding, the synthetics can be maintained for several years from open-pollinated seed. Unlike hybrid varieties, the farmer does not have to purchase new seed every year (Mochizuki, 1970; Singh, 1993). In variable environments, synthetics are likely to do better than hybrid varieties. This expectation is based on the wider genetic base of synthetic varieties in comparison to that of hybrids. The cost of seed in the case of synthetic varieties is relatively lower than that of hybrids. Where farmers have limited financial resources, such as is the case of sub-Saharan Africa, synthetic varieties are more attractive than hybrids. There is evidence that the performance of synthetic varieties can be considerably improved through population improvement without appreciably reducing variability. Lonnquist (1949) indicated that inbreeding in a synthetic variety would permit the extraction of inbred lines with far greater numbers of favorable yield genes and consequently of higher combining ability. Therefore synthetic varieties would have value for commercial purpose and also as a germplasm reservoir highly suitable for the extraction of superior inbred lines. Hallauer and Eberhart (1966) indicated that the main objective in the development of synthetic varieties was to increase the gene frequency for specific attributes. A higher frequency of either better or more desirable genotypes would be expected in these synthetic varieties. Lonnquist (1949) observed that synthetics would be of considerable value where the cost of hybrid seed was high relative to the value of the expected crop if the synthetic would yield satisfactorily.

A synthetic variety is produced by crossing in all combinations a number of lines that combine well with each other. Once synthesized, a synthetic is maintained by open-pollination in isolation. The lines that make up a synthetic variety may be inbred lines, clones, open-pollinated varieties, or other populations tested for general combining ability. The general combining ability of the lines is evaluated because synthetic varieties exploit the portion of heterosis produced by general combining ability. General combining ability is highly important in developing high yielding synthetics (Lonnquist, 1949). The lines that have high general combining ability are selected as parents of synthetic varieties. It is necessary that in the development of high yielding synthetics, some selection on the basis of other agronomic characteristics be done before testing for combining ability (Lonnquist, 1949). Allard (1960) pointed out that three factors theoretically affect the yield of a Syn-2 generation of a synthetic variety. These are (i) the sum of the yields of parent varieties or inbred lines (ii) the sum yields of variety crosses or single crosses, and (iii) the number of parent varieties or inbred lines. From prediction equations for the yield of synthetics, Mochizuki (1970) indicated that the number of parents might have an optimum value corresponding to the yield and combining ability of the parents. Kinman and Sprague (1945), using yield data from single crosses between maize inbred lines, indicated that four to six lines is the optimum number for highest yield in a synthetic variety. The performance of synthetic varieties is usually lower than that of single-cross hybrids because synthetics exploit mainly general combining ability and to a less extent specific combining ability while hybrid varieties exploit both general combining ability and specific combining ability. The performance of synthetics is adversely affected by lines with poorer general combining ability. Such lines often have to be included to increase the number of parental lines making up the synthetic as lines with outstanding general combining ability are limited in number (Singh, 1993).

Lonnquist (1949) developed two synthetic varieties (High Syn-2 and Low Syn-2) of corn from an open-pollinated variety Krug yellow dent and also developed the Syn-3 generation of these two. The Syn-2 and Syn-3 were compared to unselected parental open-pollinated variety and a commercial check and the relative yield of the High Syn-2 and Low Syn-2 synthetics was 142% and 85% respectively, compared to that of the Krug open-pollinated variety. Lonnquist (1949) also reported lower root lodging among the synthetics compared to the open-pollinated variety. For the Syn-3, the High and Low Syn-3 yields were 127% and 101% of the open-pollinated variety. Kinman and Sprague (1945) advocated for the use of S_1 lines in the

development of synthetic varieties as a means of increasing yields of synthetic varieties since S_1 yield considerably higher than long-time inbred (homozygous) lines and this was also noted by Lonnquist (1949).

Hallauer and Eberhart (1966) used nine maize synthetic varieties in a diallel mating design and evaluated them for yield performance *per se* and in crosses, and estimated heterosis, average heterosis, and specific heterosis. Hallauer and Eberhart (1966) indicated that higher yielding synthetic crosses were obtained by crossing high yielding synthetic varieties and noted that high yielding crosses were due to a greater accumulation of favorable yield factors. They detected highly significant differences for entries, among synthetic varieties, heterosis and average heterosis at all locations except for one year at one location. Hallauer and Eberhart (1966) also detected significant specific heterosis in two experiments. When data were combined over the six experiments, significant differences among varieties, heterosis, and variety heterosis were revealed while specific heterosis was not significant (Hallauer and Eberhart, 1966). The total sum of squares due to heterosis, average heterosis accounted for 73% while variety heterosis accounted for only 11%. Hallauer and Eberhart (1966) reported average heterosis on the basis of mid-parent, high-parent and constant parent to be 11, 6, and 12%, respectively, while the average estimated heterosis was 11%. Hallauer and Eberhart (1966) indicated that genetic dissimilarity among the synthetic varieties, as measured by the synthetic variety heterosis included in their study, appeared to be less than among the open-pollinated North Carolina varieties studied.

Hallauer and Sears (1968) evaluated nine maize synthetic varieties that were crossed in a diallel mating design for yield performance for two years at three locations. From the analysis of variance for yield, significant differences were noted for heterosis and variety heterosis in all experiments except one. In one experiment, they did not find significant variation among synthetic varieties. Specific heterosis appeared to be of minor importance in individual experiment analyses while in the combined analysis of the six experiments, specific heterosis was significant. Hallauer and Sears (1968) calculated average heterosis relative to the mid-parent and high-parent to be 9.8 and 4.2% respectively and observed that this was lower than that reported by Hallauer and Eberhart (1966) in a related experiment conducted earlier.

Hallauer (1972) evaluated thirty six variety crosses obtained from diallel mating of nine synthetic maize varieties at six locations. Significant differences among entries for grain moisture and yield as well as significant entry by location interaction for grain yield were

observed. Average constant parent heterosis was calculated to be 14% and the lowest-yielding varieties *per se* had the largest variety heterosis. Stability analysis showed that the variety crosses had similar regression coefficients to those of the checks and had lower deviation mean squares. Hallauer (1972) noted that on the average, the variety crosses responded more to improved environments than the varieties *per se*. Hallauer and Malithano (1976) evaluated seven maize synthetic varieties that included 'Iowa Stiff Stalk Synthetic' (BSSS C0) in a diallel mating design. Constant parent heterosis for 'BSSS C0' was 15.5% and mid-parent heterosis ranged from 5.1% for 'BSSS C0' x 'BSTE C0' to 24.1% for 'BSSS C0' x 'Teoza'. Average heterosis for the diallel was 950 kg ha^{-1}. Stability analysis showed that the 7 varieties showed a slightly higher response to favorable environments than their variety crosses (Hallauer and Malithano, 1976). Hallauer and Malithano (1976) also evaluated ten synthetic populations that had undergone recurrent selection for population improvement in a diallel. Average heterosis for the 10-variety diallel was 1120 kg ha^{-1} (19.6%) and ranged from 800 kg ha^{-1} (13.7%) to 1770 kg ha^{-1} (39.4%).

Population improvement in synthetics and populations

Hallauer et al. (2004) noted that the main goal of selection is to increase the frequency of favorable alleles for the target trait(s). For germplasm enhancement, selection emphasizes the improvement of a limited number of traits of broad-based populations and the maintenance of genetic variation for continued selection (Hallauer et al., 2004). Vales et al. (2001) evaluated two synthetic populations that had been subjected to recurrent selection and reported that the recurrent selection program was effective of improving grain yield in the two populations. The synthetic populations obtained after the first, second, and third cycles of selection had significantly better grain yields than the original populations. Days to silking and grain moisture increased in the third cycle of selection, a trend that was undesirable. Vales et al. (2001) also reported that mid-parent heterosis of grain yield did not change significantly from the cross of original populations to the cross of the populations of the third cycle of selection. Dhliwayo and Pixley (2003) evaluated divergently selected maize synthetic population for weevil resistance and noted significant differences in synthetics developed by different selection methods for resistance parameters. High and low rind penetrometer resistance populations selected for stalk strength from Missouri second cycle Stiff Stalk Synthetic were evaluated by Martin et al. (2004). Martin et al. (2004) showed that rind penetrometer resistance selection was effective at

separating the original population into two significantly different populations. They reported a decrease in grain yield at an average of 2.5% per cycle in both directions of selection and a greater response to selection for the high direction of selection for stalk lodging resistance.

Lopez-Reynoso and Hallauer (1998) evaluated twenty seven cycles of divergent mass selection in Iowa Long Ear Synthetic (BSLE). Divergent mass selection reduced ear length by 1.9% cycle^{-1} and increased ear length by 1.4% cycle^{-1} of selection. Lopez-Reynoso and Hallauer (1998) reported that selection for shorter ears was accompanied by a significant decrease of grain yield of 44% or 1.7% cycle^{-1} and selection for longer ears reduced grain yield by 5.6%. Genetic variation for ear length was not reduced after 24 cycles of selection for shorter and longer ears. Smith (1983) estimated response to selection in diallel crosses from C0, C4, and C7 cycles of selection in BS13, BSSS, and BSCB1 synthetic populations and reported that reciprocal recurrent selection was effective in improving grain yield of the cross between populations BSSS(R) and BSCB1(R). The response of the population cross to reciprocal recurrent selection was estimated to be 4.3% per cycle when averaged over all cycles. Martin and Hallauer (1980) evaluated seven cycles of recurrent selection in BSSS and BSCB1 synthetic populations. They reported that mid-parent heterosis for grain yield for the population crosses increased from 14.9% for C0 x C0 cross to 41.7% for the C7 x C7 cross. Average gain per cycle for the population crosses was 2.97% per cycle based on C0 x C0 yield. Keeratinijakal and Lamkey (1993a) evaluated response to selection in a population diallel among cycles of BSSS(R) and BSCB1(R). Response to grain yield of the BSSS(R) x BSCB1(R) cross was 0.28 Mg ha^{-1} per cycle. Correlated response for BSSS(R) was 0.06% Mg ha^{-1} per cycle. Mid-parent heterosis for grain yield increased from 25 to 76% from C0 to C11. They reported that selection was effective in reducing stalk lodging in BSCB1(R) (40% in C0 to 9.7% in C11) and that this response was greater than that observed in BSSS(R). Keeratinijakal and Lamkey (1993b) reported that the observed response of 0.28 Mg ha^{-1} per cycle was primarily due to dominance effects.

Dudley and Lambert (2004) summarized results of selection for oil and protein in maize. They reported that in the Illinois High Oil (IHO), change per generation decreased slightly in generation 0-58 but was relatively constant at about 0.15% per generation from generation 58 onwards. In the Illinois Low Oil (ILO) corn, they reported that change per generation was -0.21% for generation 0-9 and decreased to -0.01% for generation 58 onwards. Selection in the Illinois High Protein (IHP) resulted in 0.30% change per generation for generation 0-9 but dropped in generations 10-58. Rosulj et al. (2002) evaluated nine cycles of mass selection in two

populations of maize synthetics for oil content and reported an increase of 16.1% per cycle in DS7u population and 12.8% per cycle in YuSSSu population. They reported a decrease of 1.41% and 1.24% per cycle in grain yield for DS7u and YuSSSu populations, respectively. Johnson et al. (1986) reported a change of -2.39% per cycle in total plant height after 15 cycles of selection for reduced total plant height in tropical maize population Tuxpeño, with plant height in the final selection cycle being 63% of the height in the original cycle. They also reported a 3% change per cycle in grain yield after the 15 cycles of selection.

Mikkilineni and Rocheford (2004) used RFLPs to study frequency changes in two cycles of selection in Illinois High Protein (IHP), Illinois Low Protein (ILP), Reverse High Protein (RHP), and Reverse Low Protein (RLP) strains. They reported a higher percentage of RFLP loci fixed in IHP generation 91. The IHP strain at generation 91 showed the highest level of inbreeding at 36%. Reverse strain showed lower levels of inbreeding. They noted that inbreeding values calculated from RFLP data were lower than those calculated without molecular marker data. Natural selection could have played part in selection for more vigorous strains and more heterozygous plants (Mikkilineni and Rocheford, 2004). The effective population size due to bulked pollen used to pollinate many ears may be larger than previously calculated, contributing to less inbreeding depression than estimated earlier (Walsh, 2004). Goodnight (2004) conducted simulation studies and indicated that large amounts of epistasis lead to significantly greater response to selection. Larger population sizes achieve a slightly greater overall response to selection, probably because there are more alleles in larger populations, and thus a greater probability that highly advantageous alleles or combinations of alleles are present.

MATERIALS AND METHODS

Germplasm

Nineteen synthetics used in this study were derived from different source germplasm. Some of the lines used to form the synthetics are adapted to the region and some had temperate germplasm previously introgressed into available germplasm in the region by CIMMYT-Zimbabwe (Table 3.1). These synthetics have been improved for both biotic and abiotic stress that affect maize in the region and have been classified into two heterotic type groups, A and B (Table 3.1). Ten of the synthetics used in this study were from heterotic type A and nine from heterotic type B. The nineteen synthetics were crossed in a North Carolina (NC) II mating design at CIMMYT-Zimbabwe between 1999 and 2000 (Table 3.2). A total of 69 synthetics hybrids were generated from crossing the synthetics. The synthetic hybrids were grown together with the parental synthetics and two checks in the trials.

Environments and stress management

The synthetic hybrids were evaluated at six locations in three countries (Table 3.3). These locations represented the following growing conditions:

(i) low nitrogen stress conditions
(ii) optimal fertilization.

Low nitrogen stress conditions were achieved at the sites by continuous cropping of maize without N fertilizer application. In the optimal growing conditions, fertilizer was applied at the recommended rates for the different locations. Two low N stress experiments were grown at Harare and Namulonge, and one at Alupe, making a total of five low N stress environments. Two experiments under optimal environments were grown at ART Farm, Rattray Arnold, Namulonge and one each at Kadoma, Matopos, and Alupe, making a total of nine optimal environments. Standard cultural and agronomic practices were followed during trial management.

Table 3.1. Synthetics used to form synthetic hybrids, checks, their origin and description.

Synthetic	Source and description
P501	Sub-tropical A Population from Mexico, Streak resistant-converted (SR)
P502	Sub-tropical B Population from Mexico, SR-converted
SYNN3-SR-F2	SR-converted N3, an important non-CIMMYT synthetic in southern Africa, A
SYNK64R-SR-F2	SR-converted K64R, an important non-CIMMYT synthetic in southern Africa, B
SYNSC-SR-F2	SR-converted SC, an important non-CIMMYT synthetic in southern Africa, B
SYNI137TN-SRF1	SR-converted I137TN, an important non-CIMMYT synthetic in southern Africa
SYNTemperateA-SR-F2	Temperate, based on public lines from Iowa Stiff Stalk Synthetic (B73) background, SR-converted
SYNTemperateB-SR-F2	Temperate based on public lines from Lancaster (Mo17) background, SR-converted
99SADVIA-#	Intermediate A synthetic among stress tolerant CIMMYT synthetic, SR, adapted
99SADVIB-#	Intermediate B synthetic among stress tolerant CIMMYT synthetic, SR, adapted
99SADVLA-#	Late A synthetic among stress tolerant CIMMYT synthetic, SR, adapted
99SADVLB-#	Late B synthetic among stress tolerant CIMMYT synthetic, SR, adapted
SYNA00-F2	Intermediate/late maturing synthetic formed by recombining best lines from heterotic type A
SYNB00-F2	Intermediate/late maturing synthetic formed by recombining best lines from heterotic type B
SZSYNKITII-F2	SR and weevil resistant synthetic among Kitale lines, important in eastern Africa, A
SZSYNUCA-F2	SR and weevil resistant synthetic among UCA lines, important in eastern Africa, A
SZSYNECU573-F2	SR and weevil resistant synthetic among ECU573 lines, important in eastern Africa, B
Z97SYNGLS(A)-F3	SR and GLS resistant A synthetic from CIMMYT-Zimbabwe, adapted
Z97SYNGLS(B)-F5	SR and GLS resistant B synthetic from CIMMYT-Zimbabwe, adapted
SC627	Check – Commercial hybrid
ZM621-FLINT F2	Check - Open pollinated variety

Table 3.2. Crossing plan used to develop synthetic hybrids with A and B parental synthetics.

			A Synthetics									
			1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
			99SADVIA-#	99SADVLA-#	SZSYNKITII-F2	SZSYNUCA-F2	Z97SYNGLS(A)-F3	SYNA00F2	P501-SRc0-F2	SYNN3-SR-F2	SYNTemperateA-SR-F2	SYNI137TN-SRF1
B Synthetics	1	P502-SRc0-F3	x	x	x	x	x	x	x	x	x	x
	2	SYNK64R-SR-F2	x	x	x	x	x	x	x	x	x	x
	3	SYNSC-SR-F2	x	x	x	x	x	x	x	x	x	x
	4	SYNTemperateB-SR-F2	x	x	x	x	x	x	x	x	x	x
	5	SYNI137TN-SRF1	x	x	x	x	x	x	x	x	x	
	6	99SADVIB-#							x	x	x	x
	7	99SADVLB-#							x	x	x	x
	8	SYNB00-F2							x	x	x	x
	9	SZSYNECU573-F2							x	x	x	x
	10	Z97SYNGLS(B)-F5							x	x	x	x

Table 3.3. Locations, type of environment and plot size used in the evaluations of synthetics and their hybrids.

Location, Country	Latitude	Longitude	Altitude	Type of environment	Plot size
			masl†		**m**
Alupe, Kenya	00°30' N	34°07' E	1189	Low N stress	3.50 x 0.75
Harare, Zimbabwe	17°48' N	31°02' E	1506	Low N stress	4.25 x 0.75
Namulonge, Uganda	00°32' N	34°07' E	1150	Low N stress	5.00 x 0.75
Alupe, Kenya	00°30' N	34°07' E	1189	Optimal	4.00 x 0.75
ART Farm, Harare, Zimbabwe	17°80' S	31°05' E	1468	Optimal	4.25 x 0.75
Harare, Zimbabwe	17°48' S	31°02' E	1506	Optimal	4.25 x 0.75
Kadoma, Zimbabwe	18°32' S	30°90' E	1155	Optimal	4.50 x 0.75
Matopos, Zimbabwe	20°23' S	28°31' E	1370	Optimal	4.25 x 0.75
Namulonge, Uganda	00°32' N	34°07' E	1150	Optimal	5.00 x 0.75
Rattray Arnold, Zimbabwe	17°67' S	31°17' E	1308	Optimal	4.00 x 0.75

†masl, meters above sea level.

Field measurements

The experimental field design used was an alpha lattice (Paterson and Williams, 1976) with 2 replications at all locations. Plot sizes varied at each location (Table 3.3). Measurements on plot basis were recorded on the following agronomic traits: anthesis date (days from planting to 50% pollen shed), silking date (days from planting to 50% silking), plant height (distance in cm from the ground to the top of tassel), and ears per plant (ratio of number of ears to number of plants harvested). An ear was counted if it had at least one fully developed grain. Anthesis silking interval was calculated as the difference between silking and anthesis dates (ASI = SD – AD). Leaf senescence was scored on a scale from 0 to 10 by dividing the percentage of estimated total leaf area that is dead by 10. A score of 1 = 10%; 2 = 20%; 3 = 30%, 4 = 40%; 5 = 50%; 6 = 60%; 7 = 70%; 8 = 80%; 9 = 90%, and 10 = 100% dead leaf area (Bänziger et al, 2000). Grain weight was adjusted to 12.5% grain moisture content and expressed in Mg ha^{-1}. Grain moisture (g kg^{-1} moisture) of grain at harvest was measured using a moisture meter, and 100-kernel weight (the weight of a sample of 100 kernels in g) was measured using an electronic scale.

Statistical analyses

Analysis of variance for each environment and adjusted means were computed with the PROC MIXED procedure (SAS, 1997) considering genotypes as fixed effects and reps and blocks within reps as random effects. Combined analyses of variance across locations were computed using PROC GLM in SAS (SAS, 1997). Analysis was done following the line x tester (L x T) analysis (Kempthorne, 1957), considering synthetics from heterotic type A as lines and synthetics from heterotic type B as testers for each environment and across environments. Tests of significance for line, tester, and line x tester mean squares were conducted using their respective interaction with the environment as the error term in the analysis across environments. The genotypes sums of squares were partitioned into sources due to hybrids, parents, a contrast between synthetic hybrids and parental synthetics, checks, and a contrast between synthetic hybrids and checks. The hybrids source was partitioned into variation due to A synthetics, B synthetics, and the A x B interaction. In L x T analysis, variance due to lines and testers is equivalent to variation due to general combining ability (GCA) effects while variance due to L x T interaction is equivalent to variation due to specific combining ability (SCA) effects.

For all traits across environments, GCA (g_i or g_j) and SCA (s_{ij}) effects were estimated as follows:

$$g_i = (y_{i\cdot} - y_{\cdot\cdot})$$

$$g_j = (y_{\cdot j} - y_{\cdot\cdot})$$

$$s_{ij} = (y_{ij} - y_{\cdot\cdot} - g_i - g_j)$$

where y_{ij} is the mean of the hybrid of crossing the i^{th} A synthetic with the j^{th} B synthetic, $y_{i\cdot}$ is the mean of all hybrids involving the i^{th} A synthetic, $y_{\cdot j}$ is the mean of all hybrids involving the j^{th} B synthetic, and $y_{\cdot\cdot}$ is the mean of all hybrids (Sharma, 1998). Standard errors for GCA and SCA effects were calculated following Cox and Frey (1984) and Sharma (1998). Standard error of GCA, $SE_{GCA} = \{MS_{fl}(f\text{-}1)/mflr\}^{0.5}$ or $\{MS_{ml}(m\text{-}1)/mflr\}^{0.5}$ for A or B synthetics, respectively. MS_{fl} and MS_{ml} are the respective A synthetic x location and B synthetic x location mean squares, and f, m, l, r, are the number of A synthetics, B synthetics, locations, and replications, respectively. Standard error of SCA, $SE_{SCA} = \{(MS_{fml})(f\text{-}1)(m\text{-}1)/mflr\}^{0.5}$. Two tailed *t*-tests were used to test the significance of the GCA and SCA effects where $t = GCA/SE_{GCA}$ or SCA/SE_{SCA}, respectively (Singh and Chaudhary, 1977; Sharma, 1998).

Genotypic and phenotypic correlations were calculated between traits for each environment and across environments by considering genotypes as random effects for synthetics and their hybrids. Repeatability was estimated for each trait per environment and across environments assuming genotypes random. Repeatability was calculated as $R = \dfrac{\sigma^2_g}{\sigma^2_g + \dfrac{\sigma^2_e}{r}}$

where σ^2_g is the genotypic variance, σ^2_e is the error variance and r is the number of replications for a single environment.

Across environments, repeatability was calculated as $R = \frac{\sigma^2_g}{\sigma^2_g + \frac{\sigma^2_{ge}}{e} + \frac{\sigma^2_e}{re}}$ where σ^2_g is the genotypic variance, σ^2_{ge} is the genotype x environment variance, σ^2_e is the error variance, e is the number of environments, and r is the number of replications for a single environment. Genotypic and phenotypic correlations and repeatability were calculated using SAS (Holland, 2003).

Additive Main Effects and Multiplicative Interaction (AMMI) analysis of grain yield for hybrids was carried out to assess the relationship among synthetics, synthetic hybrids and environments. AMMI analysis was also used to visualize the phenotypic correlations among traits (Yan and Tinker, 2005). This analysis was carried out using IRRISTAT (IRRI, 1998) and Biplot v1.1 (Dr. E.P. Smith, Virginia Tech; http://www.stat.vt.edu/facstaff/epsmith.html). Stability analysis of hybrids across locations was conducted with joint linear regression method (Eberhart and Russell, 1966) using IRRISTAT (IRRI, 1998) and SAS. Mid-parent and high-parent heterosis were calculated using the adjusted means of synthetics and their hybrids. Mid-parent heterosis was calculated as $\text{MPH} = \frac{(\text{F}_1 - \text{MP})}{\text{MP}} \text{x}100$ where, F_1 is the mean of the F_1 synthetic hybrid performance and $\text{MP} = (\text{P}_1 + \text{P}_2)/2$ in which P_1 and P_2 are the means of the two parental synthetics. High-parent heterosis was calculated as $\text{HPH} = \frac{(\text{F}_1 - \text{HP})}{\text{HP}} \text{x}100$, where HP is the mean of the best parental synthetic.

RESULTS AND DISCUSSION

Low N stress environments

There were highly significant differences (P<0.001) among environments and genotypes for all traits across low N stress environments (Table 3.4). Significant differences among genotypes indicated that there was variation between synthetic hybrids, the parental synthetics, and checks for the traits studied. Highly significant differences (P<0.001) were observed between synthetic hybrids for all traits. Partition of variation among hybrids into sources due to A, B, and A x B interaction revealed significant differences between A synthetics and B synthetics for all traits except leaf senescence (Table 3.4). The A synthetics contributed 38% and B synthetics contributed 30% of the variation among synthetics hybrids for grain yield. Significant A and B synthetic source of variation indicates presence of significant general combining ability (GCA) for both the A and B synthetics. The A x B interaction variance was significant for only plant height and ears per plant (EPP). Non-significant A x B interaction for grain yield may indicate lack of significant specific combining ability (SCA). This implies that there were few crosses which were superior to others in grain yield among the synthetic hybrids. Significant differences (P<0.05) were observed among parental synthetics for all traits except anthesis silking interval. The single degree of freedom contrast (hybrids vs. parents) was significant for all traits except grain moisture and leaf senescence. This contrast indicates average heterosis and implies that some amount of heterosis was expressed in the hybrids for grain yield, anthesis date, anthesis silking interval (ASI), plant height, ears per plant, and kernel weight. No significant difference was detected for the contrast hybrids vs. checks for all traits except anthesis date, suggesting the hybrids and checks were equal in performance for most of the traits studied.

Genotype x environment effect was significant only for anthesis silking interval and 100-kernel weight (Table 3.4). This indicated that the synthetic hybrids, parents, and checks responded similarly at the different locations for grain yield, anthesis date, plant height, ears per plant, grain moisture, and leaf senescence. Significant hybrid x environment interaction was observed for only ASI, suggesting that the hybrids performed similarly at all locations for the other traits. Within the synthetic hybrids, variation due to A synthetic x environment was significant for ASI and grain moisture. Variation due to B synthetic x environment was significant for grain yield, anthesis date, ASI, ears per plant, and leaf senescence. There was no

Table 3.4. Combined analysis of variance and means for grain yield and agronomic traits across low N stress environments.

Source of variation	df†	Mean squares						df	Mean square	
		GY	AD	ASI	PH	EPP	GM		KWT	SEN
		Mg ha^{-1}	**d**		**cm**	**no.**	**g kg^{-1}**		**g**	**rating 1-10**
Environments (E)	4	20.92***	4211.72***	416.27***	107046.07***	0.48***	2573.16***	3	1462.80***	112.20***
Reps(Env)	5	2.34***	19.65***	28.78***	1103.93***	0.02	14.72***	4	40.82***	6.03***
Genotypes	89	0.63***	30.65***	19.59***	636.08***	0.06***	8.69***	89	31.34***	0.71***
Hybrids (H)	68	0.51***	26.22***	18.37***	491.31***	0.05***	7.22***	68	28.83***	0.61***
A Syn (A)	9	1.46***	87.82***	52.16***	640.04*	0.13***	18.83**	9	59.44***	2.02
B Syn (B)	9	1.13*	95.11***	46.05***	1414.16***	0.10**	20.76***	9	117.46***	1.21
A x B	50	0.22	4.33	7.37	305.74*	0.03*	2.88	50	7.69	0.23
Parents (P)	18	0.68*	41.23***	23.23	788.91***	0.06*	15.36***	18	44.13***	1.20**
H vs. P	1	5.91***	164.59***	51.59**	7204.46***	0.58***	0.08	1	28.51*	0.23
Checks (C)	1	3.62*	11.25	24.20	1296.05*	0.15	1.40	1	2.67	0.05
H vs. C	1	0.27	37.58**	0.04	837.20	0.00	0.35	1	3.55	0.13
Genotypes x E	356	0.31	4.62	9.79***	254.95	0.02	3.24	267	8.79*	0.29
H x E	272	0.29	4.59	8.11**	226.13	0.02	3.28	204	8.25	0.26
A x E	36	0.28	3.91	12.49***	252.94	0.02	6.14***	27	6.67	0.32
B x E	36	0.50**	6.03*	12.50***	318.66	0.03**	3.62	27	9.40	0.69***
A x B x E	200	0.25	4.43	6.45	204.17	0.02	2.68	150	8.32	0.17
P x E	72	0.37	4.88	15.98*	275.13	0.03	3.06	54	9.65	0.46***
H vs. P x E	4	0.60	1.70	4.71	421.96	0.02	1.87	3	6.48	0.05
C x E	4	0.29	3.63	19.58	72.80	0.03	6.50	3	32.07	0.07
H vs. C x E	4	0.86*	6.56	9.00	1737.29***	0.04	1.89	3	8.91	0.29
Error	441	0.26	4.35	7.12	235.55	0.02	3.02	354	7.08	0.25
Mean (overall)		**1.54**	**68.61**	**5.98**	**169.40**	**0.79**	**12.84**		**23.47**	**4.99**
Mean for Hybrids		**1.58**	**68.36**	**5.85**	**171.01**	**0.80**	**12.87**		**23.51**	**4.98**
Mean for Parents		**1.39**	**69.41**	**6.44**	**164.06**	**0.74**	**12.77**		**23.05**	**5.03**
Mean for Checks		**1.69**	**69.75**	**5.90**	**164.45**	**0.79**	**12.75**		**23.99**	**5.07**
LSD (0.05)		**0.45**	**1.83**	**2.35**	**13.49**	**0.12**	**1.53**		**2.62**	**0.50**

*,**,*** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.

† AD, anthesis date; ASI, anthesis silking interval; df, degrees of freedom; EPP, ears plant^{-1}; GM, grain moisture; GY, grain yield; KWT, 100-kernel weight; PH, plant height; SD, silking date; SEN, leaf senescence.

significant A x B x environment interaction for all traits. Parent x environment interaction was significant for ASI and leaf senescence, suggesting different responses among parents at the different locations for these traits. Mean grain yield was 1.58, 1.39, and 1.69 M ha^{-1}, for synthetic hybrids, parental synthetics, and checks respectively (Table 3.4). Mean days to anthesis for synthetic hybrids, parental synthetics, and checks were quite similar, with the synthetic hybrids flowering slightly earlier (68.4 d) than the parental synthetics (69.4 d) and checks (69.8 d). Anthesis silking interval was slightly shorter for the hybrids and checks compared to the parental synthetics (5.9 d against 6.4 d).

Optimal environments

There were highly significant differences ($P<0.001$) among environments for all traits across optimal environments (Table 3.5). Genotype source of variation was highly significant ($P<0.001$) for all traits except ears per plant which was significant at $P<0.05$. Highly significant differences ($P<0.001$) were observed among synthetic hybrids for grain yield, grain moisture, anthesis date, ASI, plant height, 100-kernel weight, and leaf senescence and significant differences ($P<0.05$) for ears per plant. Variation among hybrids due to A synthetics was significant ($P<0.05$) for grain yield, ASI, and leaf senescence, and highly significant ($P<0.01$) for grain moisture, anthesis date, plant height, ears per plant, and kernel weight (Table 3.5). Variation among B synthetics was significant ($P<0.05$) for grain yield, ASI, and leaf senescence, and highly significant for grain moisture, anthesis date, plant height, and kernel weight (Table 3.5). Significant A and B synthetics source of variation indicates presence of significant variation among general combining ability (GCA) effects among the A and B synthetics, respectively. The A x B interaction variance was significant for only grain yield indicating significant variation among specific combining ability (SCA) effects among A x B synthetic crosses. The A x B source of variation accounted for 60% of the variation among synthetic hybrids for grain yield, with A synthetics contributing 17% and B synthetics contributing 23% of the variation. Parents differed significantly ($P<0.05$) for all traits. The hybrids vs. parents contrast was significant for all traits except grain moisture, ASI, 100-kernel weight, and leaf senescence (Table 3.5).

Table 3.5. Combined analysis of variance and means for grain yield and agronomic traits across optimal environments.

Source of variation	df†	Mean squares GY	GM	df	Mean squares AD	ASI	df	PH	df	Mean squares EPP	df	Mean squares KWT	SEN
		Mg ha^{-1}	**g kg^{-1}**		**d**			**cm**		**no.**		**g**	**rating 1-10**
Environment (E)	8	1221.89***	2954.37***	5	73904.28***	491.62***	7	210765.05***	6	5.46***	2	7997.00***	140.81***
Reps(E)	9	5.49***	14.00***	6	10.68***	4.32	8	1226.55***	7	0.24***	3	12.20	0.07
Genotypes	89	4.96***	13.32***	89	29.37***	6.51***	89	1514.67***	89	0.04*	89	28.97***	0.60***
Hybrids (H)	68	2.09***	11.80***	68	22.79***	4.64*	68	1126.07***	68	0.03	68	22.41***	0.47***
A Syn (A)	9	2.73*	39.63***	9	77.68***	10.20*	9	4405.19***	9	0.05**	9	59.56***	1.64*
B Syn (B)	9	3.52*	33.87***	9	84.30***	11.35*	9	3312.62***	9	0.04	9	59.99**	1.06*
A x B	50	1.71*	3.40	50	3.92	2.37	50	222.68	50	0.02	50	8.46	0.18
Parents (P)	18	7.44***	20.72***	18	47.48***	13.93***	18	2459.37***	18	0.06*	18	53.30***	1.14***
H vs. P	1	119.52***	4.54	1	132.84***	0.02	1	6013.88***	1	0.14*	1	0.88	0.04
Checks (C)	1	43.49***	2.89	1	7.04	10.67*	1	7906.53**	1	0.00	1	46.73	0.46
H vs. C	1	0.03	3.94	1	85.31***	1.82	1	0.33	1	0.12*	1	47.70*	0.05
Genotypes x E	712	1.31***	4.35***	445	3.06	3.34**	623	285.01	534	0.03	178	10.08	0.24**
H x E	544	1.24**	4.39***	340	2.94	3.15**	476	275.17	408	0.03	136	9.25	0.23**
A x E	72	1.16	3.43***	45	2.86	4.51***	63	302.46	54	0.02	18	6.27	0.48***
B x E	72	1.43*	7.51***	45	2.57	4.33**	63	386.71**	54	0.04*	18	11.32	0.38**
A x B x E	400	1.20*	3.52	250	3.01	2.65	63	250.45	300	0.02	18	9.19	0.18
P x E	144	1.22***	4.37*	90	2.84	4.35	126	323.69	108	0.03	36	12.70	0.30
H vs. P x E	8	7.79***	0.97	5	3.11	0.13	7	436.70***	6	0.06*	2	2.45	1.23
C x E	8	1.46	2.60	5	12.14	1.27	7	287.03	6	0.02	2	18.46	0.29
H vs. C x E	8	1.67	0.21	5	6.22*	0.60	7	115.80*	6	0.07*	2	19.37	9.69
Error	793	0.92	3.19	534	2.66	2.68	712	252.51	622	0.03	267	9.11	0.17
Mean (overall)		**5.33**	**14.35**		**73.44**	**2.23**		**229.93**		**1.01**		**26.05**	**4.74**
Mean for Hybrids		**5.47**	**14.37**		**73.21**	**2.22**		**230.99**		**1.01**		**25.99**	**4.74**
Mean for Parents		**4.80**	**14.24**		**74.07**	**2.23**		**225.97**		**0.99**		**26.09**	**4.76**
Mean for Checks		**5.45**	**14.71**		**75.13**	**2.50**		**231.09**		**0.95**		**28.01**	**4.81**

*,**,*** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.
†AD, anthesis date; ASI, anthesis silking interval; df, degrees of freedom; EPP, ears plant^{-1}; GM, grain moisture; GY, grain yield; KWT, 100-kernel weight; PH, plant height; SD, silking date; SEN, leaf senescence.

The hybrids vs. parents contrast indicates average heterosis and implies that there was heterosis expressed in the hybrids for grain yield, anthesis date, plant height, and ears per plant. No significant difference was detected for the contrast hybrids vs. checks for all traits except anthesis date, ears per plant, and 100-kernel weight, suggesting that hybrids and checks were equal in performance for grain yield, grain moisture, ASI, plant height, and leaf senescence.

Significant genotype x environment variance was detected for only grain yield, grain moisture, ASI, and leaf senescence (Table 3.5), indicating that the synthetic hybrids, parents, and checks responded differently to environments for those traits. Hybrid x environment was significant ($P<0.05$) for only grain yield, grain moisture, ASI, and leaf senescence, suggesting that the hybrids performed similarly at all locations for the other traits. Within the synthetic hybrids, variation due to A synthetic x environment was significant for grain moisture, ASI and leaf senescence. Variation due to B synthetics x environment was significant for grain yield, grain moisture, ASI, plant height, ears per plant, and leaf senescence. Significant A x B x environment interaction was indicated for grain yield suggesting variation in A x B interaction depending on environment. Parent x environment interaction and hybrids vs. parents x environment sources of variation was significant for grain yield. Mean grain yield ranged from 4.80 Mg ha^{-1} for parental synthetics to 5.47 Mg ha^{-1} for synthetic hybrids (Table 3.5). Parental synthetics had the same mean ASI as the synthetic hybrids (2.2 d).

Table 3.6. Combined analysis of variance and means for grain yield and agronomic traits across environments.

Source of variation	df†	Mean squares GY	GM	df	Mean squares AD	ASI	df	Mean squares PH	df	Mean squares EPP	df	Mean squares KWT	SEN
		Mg ha^{-1}	**g kg^{-1}**		**d**			**cm**		**no.**		**g**	**rating 1-10**
Environments (E)	13	1390.37***	2972.37***	10	51563.02***	1252.88***	12	375143.74***	11	6.37***	6	3947.74***	139.78***
Reps(E)	14	4.42***	15.11***	11	18.36***	20.80***	13	1443.19***	12	0.19***	7	30.40***	4.00***
Genotypes	89	4.22***	18.86***	89	55.19***	19.76***	89	1808.79***	89	0.07***	89	51.60***	1.07***
Hybrids (H)	68	1.79***	15.77***	68	44.01***	16.38***	68	1251.18***	68	0.05	68	43.20***	0.82***
A Syn (A)	9	3.26***	54.18***	9	158.32***	47.05***	9	4118.67***	9	0.14***	9	110.46***	3.27***
B Syn (B)	9	3.40**	48.42***	9	171.40***	46.89***	9	4216.31***	9	0.08*	9	166.39***	1.80**
A x B	50	1.22*	3.70	50	4.18	5.30	50	277.65	50	0.03	50	9.02	0.21
Parents (P)	18	6.02***	33.07***	18	84.11***	32.62***	18	3026.19***	18	0.10***	18	88.51***	2.12***
H vs. P	1	103.94***	3.50	1	294.52***	24.56*	1	12876.43***	1	0.61***	1	11.80	0.25
Checks (C)	1	41.28***	4.29	1	17.82	32.82**	1	8478.77***	1	0.04	1	10.49	0.36
H vs. C	1	0.03	1.54	1	120.00***	1.28	1	305.92	1	0.11	1	35.36*	0.18
Genotypes x E	1157	1.01***	3.91***	890	3.86*	6.22***	1068	279.73*	979	0.03	534	9.19*	0.27**
H x E	884	0.91***	3.96***	680	3.81	5.48***	816	266.41	748	0.05	408	8.55	0.25*
A x E	117	0.87	6.18***	90	3.17	8.78***	108	337.96*	99	0.04***	54	7.85	0.38***
B x E	117	1.12***	6.21***	90	4.50*	8.22***	108	374.74**	99	0.04	54	6.35	0.38***
A x B x E	650	0.87**	3.19	500	3.68	4.35	600	235.05	550	0.05	300	8.41	0.17
P x E	234	1.02***	3.87*	180	3.84	9.02*	216	299.04	216	16.04***	108	10.45*	0.37**
H vs. P x Env	13	6.63***	27.94***	10	2.53	5.61	12	423.89	11	0.05	6	6.98	0.05
C x E	13	1.44	3.60	10	7.57	8.67*	12	252.02	11	0.03	6	28.67	0.15
H v C x E	13	1.31*	29.63***	10	6.02	4.44	12	690.95***	11	0.05	6	13.56	0.24
Error	1234	0.69	3.13	979	3.43	4.70	1157	245.99	1068	0.05	621	7.95	0.22
Mean (overall)		**3.98**	**13.82**		**71.24**	**3.93**		**206.65**		**0.92**		**25.31**	**4.89**
Mean for Hybrids		**4.08**	**13.84**		**71.00**	**3.87**		**207.92**		**0.93**		**25.34**	**4.88**
Mean for Parents		**3.59**	**13.72**		**71.95**	**4.15**		**202.16**		**0.89**		**25.10**	**4.91**
Mean for Checks		**4.11**	**14.01**		**72.68**	**4.05**		**205.46**		**0.88**		**26.32**	**4.96**
LSD (0.05)		**0.43**	**0.93**		**1.10**	**1.28**		**8.53**		**0.09**		**1.95**	**0.34**

*,**,*** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.

† AD, anthesis date; ASI, anthesis silking interval; df, degrees of freedom; EPP, ears plant^{-1}; GM, grain moisture; GY, grain yield; KWT, 100-kernel weight; PH, plant height; SD, silking date; SEN, leaf senescence.

Combined analysis across environments

Variance due to environments and genotypes was highly significant (P<0.001) for all traits (Table 3.6). Significant differences among genotypes indicated that there was variation in performance between synthetic hybrids, the parental synthetics, and checks for all traits. Highly significant differences (P<0.001) were observed between synthetic hybrids for all traits except ears per plant, implying differences in performance of the synthetic hybrids. Variation among synthetic hybrids was partitioned into sources due to A, B, and A x B interaction. The A and B synthetics showed highly significant differences (P<0.001) for all traits (Table 3.6). This indicated that both A and B synthetics performed differently. Significant A and B synthetics source of variation indicates presence of significant variation among GCA effects within both A and B synthetics. The A x B interaction variance was significant for only grain yield, indicating significant variation among SCA effects (Table 3.6). This implies that there were some crosses which were superior to others in grain yield among the hybrids. The A synthetics contributed 24%, B synthetics contributed 25%, and A x B interaction contributed 50% of the variation among hybrids for grain yield. Significant differences (P<0.05) were observed among parental synthetics for all traits, indicating varying performance. The single degree of freedom hybrids vs. parents contrast was significant for grain yield, anthesis date, ASI, plant height, and ears per plant. This implied presence of heterosis in the hybrids for these traits. Significant differences were detected for the contrast hybrids vs. checks for anthesis date and 100-kernel weight, suggesting that there were differences in performance between hybrids and checks for these traits.

Genotype x environment variance was highly significant (P<0.01) for grain yield, grain moisture, anthesis silking interval and leaf senescence, and significant (P<0.05) for anthesis date, plant height, and 100-kernel weight (Table 3.6). This indicated that the synthetic hybrids, parents, and checks responded differently across environments. Synthetic hybrid x environment interaction was highly significant (P<0.01) for grain yield, grain moisture, ASI, and significant (P<0.05) for leaf senescence suggesting that synthetic hybrids performed differently across environments. Significant G x E is probably due to the variable growing environments to which the genotypes were subjected. The environment effect accounted for 92% of the total sums of squares in this analysis. Within the synthetic hybrids, variation due to A synthetics x environment was highly significant (P<0.001) for grain moisture, ASI, and ears per plant. Variation due to B synthetics x environment was significant (P<0.05) for anthesis date and highly significant (P<0.01) for grain yield, grain moisture, ASI, plant height, and leaf senescence. There was

significant A x B x environment interaction for grain yield. Parent x environment interaction was highly significant for grain yield, ears per plant, and leaf senescence, suggesting different responses among parents at the different environments for these traits. Mean grain yield was 4.08, 3.59, and 4.11 Mg ha^{-1}, for synthetic hybrids, parental synthetics, and checks respectively, across environments (Table 3.6). Mean days to anthesis were shorter for synthetic hybrids (71 d) compared to parental synthetics (72 d) and checks (73 d).

Performance of synthetic hybrids and general combining ability

Means for grain yield and agronomic traits across low N stress, across optimal, and across environments is presented in Table 3.7. The best hybrid was 99SADVIA-# x P502-SRc0-F3 (2.03 Mg ha^{-1}, SCA = 0.15 Mg ha^{-1}) followed by 99SADVLA-# x SYNI137TN-SRF1 (1.99 Mg ha^{-1}, SCA = 0.29 Mg ha^{-1}) across low N stress environments. The best hybrid across optimal environments was 99SADVLA-# x SYNSC-SR-F2 (6.16 Mg ha^{-1}). The third best hybrid across optimal environments (99SADVIB-# x SYNI137TN-SRF1, 6.02 Mg ha^{-1}) also performed well across low N stress environments and was the best hybrid across environments with 4.58 Mg ha^{-1} (Table 3.7). Hybrid 99SADVIA-# x P502-SRc0-F3, the best under low N stress also performed well across environments (4.43 Mg ha^{-1}).

General combining ability effects (GCA) across low N stress environments are presented in Table 3.8. Among the A synthetics, SYNA00F2 had the highest and highly significant GCA effects for grain yield (0.17 Mg ha^{-1}), followed by 99SADVIA-# (0.15 Mg ha^{-1}). This indicated that these two synthetics had good performance under low N stress conditions. Indeed, 99SADVIA-# was parent to two of the best hybrids under low N stress (Table 3.7). Synthetic 99SADVIA-# is composed of stress tolerant CIMMYT lines and this probably partly explains its good performance under low N stress conditions.

Table 3.7. Mean grain yield and agronomic traits of the best five hybrids and checks across environments.

Hybrid†	GY‡	AD	ASI	PH	EPP	SEN	KWT
	Mg ha^{-1}	**d**		**cm**	**no.**	**rating 1-10**	**g**
Across low N stress							
99SADVIA-# x P502-SRc0-F3	2.03	68.54	4.49	159.60	0.85	5.01	21.74
99SADVLA-# x SYNI137TN-SRF1	1.99	71.01	3.96	176.36	0.93	4.82	26.49
99SADVIA-# x SYNTempB-SR-F2	1.97	66.33	4.62	177.43	0.95	5.17	21.02
99SADVIB-# x SYNI137TN-SRF1	1.94	67.78	4.92	180.89	0.83	4.90	24.21
SYNTempA-SR-F2 x P502-SRc0-F3	1.93	65.85	4.76	169.79	0.83	5.07	20.78
LSD(0.05)	**0.45**	**1.83**	**2.35**	**13.49**	**0.12**	**0.50**	**2.62**
Across optimal environments							
99SADVLA-# x SYNSC-SR-F2	6.16	75.64	1.66	240.26	1.07	4.65	29.18
P501-SRc0-F3 x SYNI137TN-SRF1	6.12	72.64	2.19	231.10	1.03	4.33	29.20
99SADVIB-# x SYNI137TN-SRF1	6.02	74.10	1.76	231.73	0.97	4.79	31.84
SYNTempA-SR-F2 x SYNTemB-SR-F2	6.00	69.87	2.55	230.39	1.03	5.19	26.73
99SADVLB-# x SYNI137TN-SRF1	5.93	73.48	1.81	233.48	1.01	4.79	31.17
LSD (0.05)	**0.62**	**1.31**	**1.31**	**11.03**	**0.13**	**0.46**	**2.97**
Across environments							
99SADVIB-# x SYNI137TN-SRF1	4.58	71.18	3.20	212.11	0.91	4.86	27.96
99SADVLA-# x SYNSC-SR-F2	4.55	72.94	3.16	218.66	0.98	4.54	26.20
P501-SRc0-F3 x SYNI137TN-SRF1	4.54	70.94	3.33	205.99	0.97	4.52	28.39
SYNTempA-SR-F2 x SYNTemB-SR-F2	4.52	68.11	3.83	210.32	0.95	5.10	24.50
99SADVLA-# x P502-SRc0-F3	4.43	72.50	2.47	204.46	0.95	4.75	24.89
Checks							
ZM621-FLINT F2	3.32	73.37	4.73	194.39	0.86	4.87	26.26
SC627	4.96	72.06	3.32	216.72	0.91	5.04	27.69
LSD(0.05)	**0.43**	**1.10**	**1.28**	**8.53**	**0.09**	**0.34**	**1.95**

†Means are presented for the best five hybrids based on grain yield.
‡AD, anthesis date; ASI, anthesis silking interval, EPP, ears per plant; GY, grain yield; KWT, 100-kernel weight; PH, plant height; SEN, leaf senescence.

Synthetic SZSYNKITII-F2, SYNN3-SR-F2, and Z97SYNGLS(A)-F3 showed significant negative GCA effects for grain yield (-0.22, -0.12, and -0.11 Mg ha^{-1}, respectively). Among B synthetics, synthetic P502-SRc0-F3 had the highest positive and significant GCA for grain yield (0.14 Mg ha^{-1}) (Table 3.8). This implied good performance of this synthetic under low N stress conditions. Synthetics 9SADVIA-# and P502-SRc0-F3, both showing good GCA effects for yield under low N, produced the best hybrid under low N stress (2.03 Mg ha^{-1}, Table 3.21; SCA = 0.15 Mg ha^{-1}). Synthetics with low GCA effects for grain yield (SYNN3-SR-F2 and SZSYNECU573-F2) produced the lowest hybrid across low N stress environments (0.88 Mg ha^{-1}, Appendix F). This hybrid also had the highest ASI across low N stress environments (10.3 d, Appendix F), possibly arising as a result of the high and positive GCA effect for anthesis date showed by synthetic SZSYNECU573-F2 (2.78 d, Table 3.8). Synthetics SYNTemperateA-SR-F2 and SYNA00F2 had negative and significant GCA effects for anthesis date (-1.73 and -1.37 d, respectively), indicating their potential to produce hybrids that flowered earlier. B synthetic SYNTemperateB-SR-F2 had a significant negative GCA effect for anthesis date. Negative and significant GCA effects for ASI were observed for A synthetic 99SADVIA-#, B synthetics 99SADVLB-#, SYNK64R-SR-F2, and P502-SRc0-F3 (-0.75, -1.09, -1.19, and -0.82 d, respectively) suggesting a shorter ASI for hybrids of these synthetics. Dow et al. (1984) and Edmeades et al. (1993), observed that a shorter ASI indicates increased partitioning of assimilates to the developing ear under stress, implying that these synthetics would be ideal for better ear filling under low N stress environments.

GCA effects for plant height were high, significant, and negative for Z97SYNGLS(A)-F3 (-4.21 cm), SYNI137TN-SRF1 (-4.35 cm), SYNK64R-SR-F2 (-6.68 cm), indicating that these synthetics had good alleles for shorter plant height which is desirable. B synthetic SZSYNECU573-F2 had the highest positive GCA effect for plant height (7.30 cm) showing that this synthetic contributed to increased plant height in the hybrids. Synthetic A SZSYNKITII-F2 and B synthetic SYNI137TN-SRF1 had the highest GCA for 100-kernel weight (1.84 and 2.92 g, respectively), indicating that these synthetics contributed towards heavier kernels under low N stress. GCA estimates for ears per plant were positive and significant for A synthetics P501-SRc0-F2 (0.06 ears per plant) and 99SADVLA-# (0.05 ears per plant), indicating these

Table 3.8. General combining ability effects (GCA) of A and B synthetics for grain yield and agronomic traits across low N stress conditions.

	GY†	AD	ASI	PH	EPP	KWT	GM	SEN
	Mg ha^{-1}	**——— d ———**		**cm**	**no.**	**g**	**g kg^{-1}**	**rating 1-10**
A Synthetics								
99SADVIA-#	0.15**	-0.35	-0.75*	-1.38	0.02	-0.94***	-0.48	0.09
99SADVLA-#	0.10*	1.13***	-0.33	0.86	0.05***	-0.09	-0.19	-0.09
SZSYNKITII-F2	-0.22***	1.65***	0.53	5.37***	-0.08***	1.84***	0.86***	-0.25***
SZSYNUCA-F2	-0.06	2.05***	0.39	3.57*	-0.04**	-1.10***	0.52*	-0.20***
Z97SYNGLS(A)-F3	-0.11*	-0.37	0.18	-4.21**	-0.04**	0.34	0.06	0.12
SYNA00F2	0.17***	-1.37***	-0.47	0.89	0.02	0.38	-0.14	0.09
P501-SRc0-F2	0.08	-0.24	-0.44	-2.52	0.06***	0.27	0.33	-0.15*
SYNN3-SR-F2	-0.12*	-0.65***	-0.18	1.50	-0.03*	0.20	-0.64**	0.29***
SYNTemperateA-SR-F2	0.06	-1.73***	2.57*	-0.60	0.02	-1.78***	-0.66**	0.24***
SYNI137TN-SRF1	-0.05	-0.16	-0.37	-4.35**	0.03*	1.11***	0.40	-0.17**
SE *(g_i)*	**0.05**	**0.19**	**0.34**	**1.51**	**0.01**	**0.27**	**0.24**	**0.06**
B Synthetics								
P502-SRc0-F3	0.14*	0.01	-0.82*	-3.17	0.02	-0.13	-0.05	-0.07
SYNK64R-SR-F2	-0.13*	-0.43	-1.19**	-6.68***	0.00	-1.71***	-0.38*	0.16
SYNSC-SR-F2	-0.05	1.10***	1.97***	1.50	-0.03	0.20	0.37*	-0.23**
SYNTemperateB-SR-F2	0.05	-1.39***	0.17	6.58***	0.00	-0.99	-0.64***	0.14
SYNI137TN-SRF1	0.00	0.79***	0.38	1.97	0.01	2.92***	0.77***	-0.01
99SADVIB-#	0.09	-0.58*	0.07	0.90	0.02	0.04	1.00***	0.05
99SADVLB-#	0.00	0.81***	-1.09**	-0.09	0.02	-0.13	-0.32	0.10
SYNB00-F2	0.07	-1.00***	0.64	-0.92	0.00	0.67*	-0.44*	0.02
SZSYNECU573-F2	-0.34*	2.78***	-0.22	7.30***	-0.13***	1.14***	0.34	-0.17
Z97SYNGLS(B)-F5	0.06	0.41	0.09	-1.82	0.03	0.29	-0.09	0.09
SE *(g_j)*	**0.07**	**0.23**	**0.34**	**1.69**	**0.02**	**0.32**	**0.18**	**0.09**

*,**,*** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.

†AD, anthesis date; ASI, anthesis silking interval, EPP, ears per plant; GM, grain moisture; GY, grain yield; KWT, 100-kernel weight; PH, plant height; SEN, leaf senescence.

Table 3.9. General combining ability effects (GCA) of A and B synthetics for grain yield and agronomic traits across optimal conditions.

	GY†	AD	ASI	PH	EPP	KWT	GM	SEN
	Mg ha^{-1}	**——— d ———**		**cm**	**no.**	**g**	**g kg^{-1}**	**rating 1-10**
A Synthetics								
99SADVIA-#	0.09	-0.46**	-0.31	-7.67***	0.00	0.04	-0.34	0.09
99SADVLA-#	0.28***	1.06***	-0.75***	3.45*	0.00	-0.17	0.10	0.05
SZSYNKITII-F2	-0.06	1.15***	0.55**	17.25***	-0.05***	1.45***	0.83***	-0.16
SZSYNUCA-F2	-0.09	1.36***	0.10	5.42***	0.02	-0.43	0.67***	-0.15
Z97SYNGLS(A)-F3	0.18*	-0.13	0.04	-2.11	0.01	0.01	0.07	-0.21*
SYNA00F2	0.02	-0.18	0.28	-3.25*	0.00	-0.20	0.11	0.05
P501-SRc0-F2	-0.04	-0.48**	0.03	-4.79***	0.04***	0.06	-0.19	-0.21*
SYNN3-SR-F2	-0.34***	-0.25	0.27	-1.95	-0.03**	0.63*	0.02	0.15
SYNTemperateA-SR-F2	-0.14	-1.98***	0.05	-6.06***	0.01	-1.88***	-1.30***	0.34***
SYNI137TN-SRF1	0.14	-0.10	-0.32	-0.35	0.01	0.60*	0.05	0.07
SE *(g_i)*	**0.08**	**0.15**	**0.18**	**1.30**	**0.01**	**0.31**	**0.13**	**0.09**
B Synthetics								
P502-SRc0-F3	0.09	0.28*	-0.19	-4.86**	0.03	0.24	0.03	-0.06
SYNK64R-SR-F2	-0.19*	-0.66***	-0.30	-4.06**	-0.02	-0.70	-0.21	0.10
SYNSC-SR-F2	-0.09	1.02***	0.11	2.25	0.01	0.20	0.21	-0.11
SYNTemperateB-SR-F2	0.13	-1.25***	0.36*	3.11	0.00	-1.32**	-0.59**	0.19*
SYNI137TN-SRF1	0.06	0.68***	0.03	3.94**	-0.01	1.75***	0.63**	-0.15
99SADVIB-#	0.22*	0.30*	-0.36*	0.94	0.00	0.03	0.18	0.00
99SADVLB-#	0.25**	0.54***	-0.45*	2.27	-0.01	0.25	-0.12	0.06
SYNB00-F2	-0.19*	-1.03***	0.42*	-0.47	-0.04*	1.16*	-0.46*	0.11
SZSYNECU573-F2	-0.02	1.64***	0.98***	14.87***	-0.03	1.97***	1.33***	-0.24***
Z97SYNGLS(B)-F5	-0.20*	1.00***	-0.12	-1.54	0.00	0.44	0.06	-0.30***
SE *(g_j)*	**0.09**	**0.14**	**0.18**	**1.48**	**0.02**	**0.41**	**0.19**	**0.08**

*,**,*** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.
†AD, anthesis date; ASI, anthesis silking interval, EPP, ears per plant; GM, grain moisture; GY, grain yield; KWT, 100-kernel weight; PH, plant height; SEN, leaf senescence.

synthetics contribute to increased number of ears under stress. Synthetics SZSYNKITII-F2, Z97SYNGLS(A)-F3, SYNI137TN-SRF1, SYNN3-SR-F2, and SYNSC-SR-F2 contributed to reduced leaf senescence through significant and negative GCA effects for leaf senescence. Synthetic A SYNTemperateA-SR-F2 had the highest negative GCA effect for grain moisture (-0.66 g kg^{-1}) indicating that this synthetic contributes to reduce moisture in the grain.

Estimates for GCA effects across optimal environments are presented in Table 3.9. GCA effects for grain yield ranged from -0.34 Mg ha^{-1} to 0.28 Mg ha^{-1}. Synthetic A 99SADVLA-# and synthetic B 99SADVLB-# had the highest and significant GCA effects for grain yield (0.28 and 0.25 Mg ha^{-1}, respectively). This indicated that these two synthetics contributed good alleles for grain yield under optimal conditions in synthetic hybrids. Synthetics A 99SADVLA-# and B 99SADVLB-# were parents to the best hybrids under optimal conditions (Table 3.7). Synthetic SYNN3-SR-F2 showed the highest negative GCA effect for grain yield (-0.34 Mg ha^{-1}). This synthetic also had significant negative GCA effect for grain yield under low N stress, suggesting that it has poor alleles for grain yield and it was parent to two of the low yielding hybrids under optimal conditions (Appendix F). Synthetic A SYNTemperateA-SR-F2 had the highest negative and significant GCA effect for anthesis date (-1.98 d), followed by B synthetic SYNTemperateB-SR-F2 (-1.98 d) indicating that they possibly have good alleles for early flowering which was evident from their consistent negative GCA effects for anthesis date across low N stress and optimal conditions. Negative and significant GCA effects for ASI was highest for synthetic A 99SADVLA-# (-0.75 d) followed by B synthetic 99SADVLB-# (-0.45 d). This suggests that these synthetics contributed to shorter ASI for hybrids.

GCA effects for plant height were high, significant and negative for synthetics 99SADVIA-# (-7.67 cm), SYNTemperateA-SR-F2 (-6.06 cm), P502-SRc0-F3 (-4.86 cm), P501-SRc0-F2 (-4.79 cm), SYNK64KR-SR-F2 (-4.06 cm), and SYNA00F2 (-3.25 cm), indicating that these synthetics had desirable alleles for reduced plant height. Synthetic A SZSYNKITII-F2 and B synthetic SZSYNECU573-F2 had the highest positive GCA effects for plant height (17.25 and 14.87 cm, respectively). GCA effects for ears per plant was positive and significant for only synthetic A P501-SRc0-F2 (0.04 ears per plant), suggesting this synthetic contributes to increased number of ears under optimal environments. B Synthetics SZSYNECU573-F2 and SYNI137TN-SRF1 had the highest GCA effects for 100-kernel weight (1.97 and 1.75 g, respectively), indicating that these lines contributed towards heavier kernels under optimal environments.

Table 3.10. General combining ability effects (GCA) of A and B synthetic lines for grain yield and agronomic traits across environments.

	GY†	AD	ASI	PH	EPP	KWT	GM	SEN
	Mg ha^{-1}	**d**		**cm**	**no.**	**g**	**g kg^{-1}**	**rating 1-10**
A Lines								
99SADVIA-#	0.12*	-0.41***	-0.54**	-5.13***	0.01	-0.41	-0.39**	0.09
99SADVLA-#	0.21***	1.08***	-0.95***	2.40*	0.02	-0.18	-0.01	-0.03
SZSYNKITII-F2	-0.12*	1.38***	1.19***	12.77***	-0.06***	1.65***	0.85***	-0.21***
SZSYNUCA-F2	-0.08	1.66***	0.13	4.58***	0.00	-0.87***	0.63***	-0.18***
Z97SYNGLS(A)-F3	0.08	-0.23	0.20	-3.00**	-0.01	0.21	0.07	-0.02
SYNA00F2	0.07	-0.72***	0.19	-1.60	0.01	0.10	0.02	0.07
P501-SRc0-F2	0.00	-0.36**	-0.48*	-4.03***	0.05***	0.17	0.00	-0.19***
SYNN3-SR-F2	-0.26***	-0.44***	0.44*	-0.53	-0.03**	0.39	-0.22	0.23***
SYNTemperateA-SR-F2	-0.07	-1.86***	-0.07	-3.88***	0.01	-1.76***	-1.07***	0.28***
SYNI137TN-SRF1	0.07	-0.13	-0.13	-1.98	0.02	0.86***	0.16	-0.07
SE *(g_j)*	**0.05**	**0.11**	**0.19**	**1.08**	**0.01**	**0.23**	**0.14**	**0.05**
B Lines								
P502-SRc0-F3	0.11	0.15	-0.45*	-4.12***	0.02	0.08	-0.01	-0.06
SYNK64R-SR-F2	-0.17**	-0.55***	-0.31	-5.06***	-0.01	-1.25***	-0.27	0.14**
SYNSC-SR-F2	-0.08	1.07***	0.29	1.94	-0.01	0.22	0.27	-0.18***
SYNTemperateB-SR-F2	0.11	-1.32***	0.37*	4.40***	0.00	-1.15***	-0.61***	0.16**
SYNI137TN-SRF1	0.04	0.73***	0.11	3.15**	0.00	2.33***	0.68***	-0.06
99SADVIB-#	0.17**	-0.11	-0.41*	1.18	0.01	0.08	0.47***	0.02
99SADVLB-#	0.16**	0.66***	-0.46*	1.41	0.00	0.06	-0.19	0.09
SYNB00-F2	-0.09	-1.02***	0.15	-0.43	-0.02	0.94***	-0.46	0.07
SZSYNECU573-F2	-0.13*	2.14***	1.70***	11.78***	-0.07***	1.49***	0.98***	-0.18***
Z97SYNGLS(B)-F5	-0.12	0.75***	-0.22	-1.65	0.01	0.38	0.01	-0.08
SE *(g_j)*	**0.06**	**0.14**	**0.18**	**1.08**	**0.01**	**0.20**	**0.14**	**0.05**

*,**,*** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.
†AD, anthesis date; ASI, anthesis silking interval, EPP, ears per plant; GM, grain moisture; GY, grain yield; KWT, 100-kernel weight; PH, plant height; SEN, leaf senescence.

Synthetics Z97SYNGLS(B)-F3 and SZSYNECU573-F2 had the highest negative GCA effects for leaf senescence (-0.30 and -0.24, respectively) and thus they contributed to reduced leaf senescence. Synthetic A SYNTemperateA-SR-F2 had the highest negative GCA effect for grain moisture (-1.30 g kg^{-1}) indicating that this synthetic contributes to reduce moisture in grain.

Across environments, the highest and significant GCA effect for grain yield was observed for synthetic 99SADVLA-# (0.21 Mg ha^{-1}, Table 3.10). The other synthetics showing positive and significant GCA effects across environments were 99SADVIA-# (0.12 Mg ha^{-1}), 99SADVIB-# (0.17 Mg ha^{-1}), and 99SADVLB-# (0.16 Mg ha^{-1}) (Table 3.24). Synthetics 99SADVLA-# and 99SADVIA-# had significant positive GCA effects for grain yield across low N stress environment. Synthetics 99SADVIB-# and 99SADVLB-# had significant positive GCA effects for grain yield across optimal environments, suggesting that this group of synthetics can be a source of favorable alleles for grain yield. These synthetics also exhibited negative and significant GCA effects for ASI across environments (Table 3.10). These synthetics were developed from CIMMYT lines tolerant to stress. Hence, they perform well in stress conditions. Synthetics 99SADVIB-# and 99SADVLA-# were parents to three of the best synthetic hybrids across environments (Table 3.7). Synthetic SYNN3-SR-F2 had the highest negative and significant GCA effect for grain yield (-0.26 Mg ha^{-1}) across environments. This synthetic also showed consistent negative GCA effects for grain yield across low N stress and optimal conditions.

Synthetics SYNTemperateA-SR-F2 and SYNTemperateB-SR-F2 with temperate background had the highest negative GCA for anthesis date across environments (Table 3.10) and these two synthetics showed this negative GCA effects consistently under low N and optimal conditions. Synthetics SZSYNKITII-F2 and SZSYNECU573-F2 that had the highest positive GCA effects for plant height under low N stress and optimal conditions, again showed the highest positive GCA effect for plant height across environments (12.77 and 11.78 cm, respectively). Synthetic P501-SRc0-F2 had the highest and positive GCA effect for ears per plant. For 100-kernel weight, synthetic SYNI137TN-SRF1 had the highest positive GCA effect (2.33 g). The highest significant negative GCA effect for grain moisture was for synthetic SYNTemperateA-SR-F2 (-1.07 g kg^{-1}), showing its potential to contribute to lower kernel moisture. Synthetic SZSYNKITII-F2 had significant negative GCA effect for leaf senescence (-0.21), indicating that this synthetic contributes to delayed leaf senescence and therefore allowing longer grain filling.

Genetic and phenotypic correlations between grain yield and other traits

Genetic and phenotypic correlations across low N stress environments are presented in Table 3.11. Both genetic and phenotypic correlation between grain yield and anthesis date was negative and highly significant, indicating the importance of early flowering for increased grain yield in this set of materials and environments. Plants that flower late give lower yield as a result of an increased anthesis silking interval that leads to aborted kernels. Grain yield and ASI were negatively correlated, showing the importance of shorter ASI for increased grain yield (Table 3.11 and Fig. 3.1). Other studies using different germplasm under stress conditions reported similar results (Bolaños and Edmeades, 1993b; Lafitte and Edmeades, 1995; Bänziger and Lafitte, 1997; Bänziger et al., 2002; Betrán et al., 2003c). Bänziger and Lafitte (1997) noted that a larger ASI indicates that fewer ears reach silking or that more ears reach silking at a later date. The genetic correlation between grain yield and 100-kernel weight was low but negative (-0.13). Lafitte and Edmeades (1995) also reported negative correlation between grain yield and 100-kernel weight in topcrosses evaluated under low N stress. However, Bolaños and Edmeades (1996) reported a positive correlation between grain yield and kernel in inbred progeny evaluated under drought stress. Grain yield showed a strong positive phenotypic correlation with ears per plant (0.50**). Bänziger and Lafitte (1997) indicated that ears per plant reflects the ability of a plant to produce a grain-bearing ear under N stress. Anthesis silking interval showed a negative correlation with ears per plant (Table 3.11 and Fig. 3.2). Bolaños and Edmeades (1993b) and Chapman and Edmeades (1999) reported similar results when working with selections from tropical maize populations under drought conditions. Bänziger and Lafitte (1997) indicated that ASI and ears per plant are related features that reflect the ability of a plant to produce a grain bearing ear under N stress. Kernel weight and leaf senescence were negatively correlated (-0.77**), implying that increased leaf senescence leads to reduce kernel weight.

Genetic and phenotypic correlations across optimal environments are presented in Table 3.12. Grain yield showed a negative and significant correlation with ASI (-0.40*), again underlying the importance of reduced ASI to increased grain yield. Grain yield was also negatively correlated with leaf senescence (-0.30*), indicating that delayed leaf senescence contributes to higher grain yield. Anthesis date showed a negative genetic correlation with ears per plant (-0.25*) and a strong negative genetic correlation with leaf senescence (-0.84**). Chapman and Edmeades (1999) reported also reported a strong correlation between anthesis date and leaf senescence (-0.90) for tropical maize populations evaluated under drought.

Table 3.11. Genetic (upper diagonal) and phenotypic (lower diagonal) correlations between grain yield and agronomic traits across low N stress environments.

	GY†	AD	ASI	PH	EPP	GM	KWT	SEN
Grain yield		-0.55***	-	0.03	-	-0.17	-0.13	0.04
Anthesis date	-0.21**		0.62***	0.12*	-0.46**	0.78***	0.40**	-0.75***
ASI	-0.39**	-0.05		0.47**	-	0.18	0.40*	-0.11
Plant height	0.23	-0.17	-0.08		-0.13	0.25*	0.34*	-0.20
Ears per plant	0.50**	-0.19*	-0.38***	0.11		-0.11	-0.11	0.02
Grain moisture	-0.03	0.20*	0.07	0.09	0.00		0.71***	-0.77***
Kernel weight	0.08	0.09	0.05	0.17*	0.02	0.29**		-0.59**
Leaf senescence	-0.09	-0.39**	0.03	0.07	-0.07	-0.32**	-0.19*	

†AD, anthesis date; ASI, anthesis silking interval, EPP, ears per plant; GM, grain moisture; GY, grain yield; KWT, 100-kernel weight; PH, plant height; SEN, leaf senescence.

Table 3.12. Genetic (upper diagonal) and phenotypic (lower diagonal) correlations between grain yield and agronomic traits across optimal environments.

	GY†	AD	ASI	PH	EPP	GM	KWT	SEN
Grain yield		-0.07	-0.40*	0.31**	0.49*	0.05	0.23*	-0.30*
Anthesis date	-0.11		0.15	0.50**	-0.25*	0.95***	0.71**	-0.84***
ASI	-0.16*	-0.11*		0.62*	-	0.45**	0.30*	-0.01
Plant height	0.27*	-0.01	-0.08		-0.52*	0.75**	0.67**	-0.46**
Ears per plant	0.12*	-0.07	-0.23**	0.10*		-0.41	-0.60*	-0.32*
Grain moisture	0.06	0.24*	0.13*	0.11*	-0.04		0.85***	-0.72***
Kernel weight	0.30**	0.18*	0.03	0.27**	0.05	0.35***		-0.78***
Leaf senescence	-0.20*	-0.35**	-0.07	-0.02	-0.09	-0.38***	-0.29**	

†AD, anthesis date; ASI, anthesis silking interval, EPP, ears per plant; GM, grain moisture; GY, grain yield; KWT, 100-kernel weight; PH, plant height; SEN, leaf senescence.

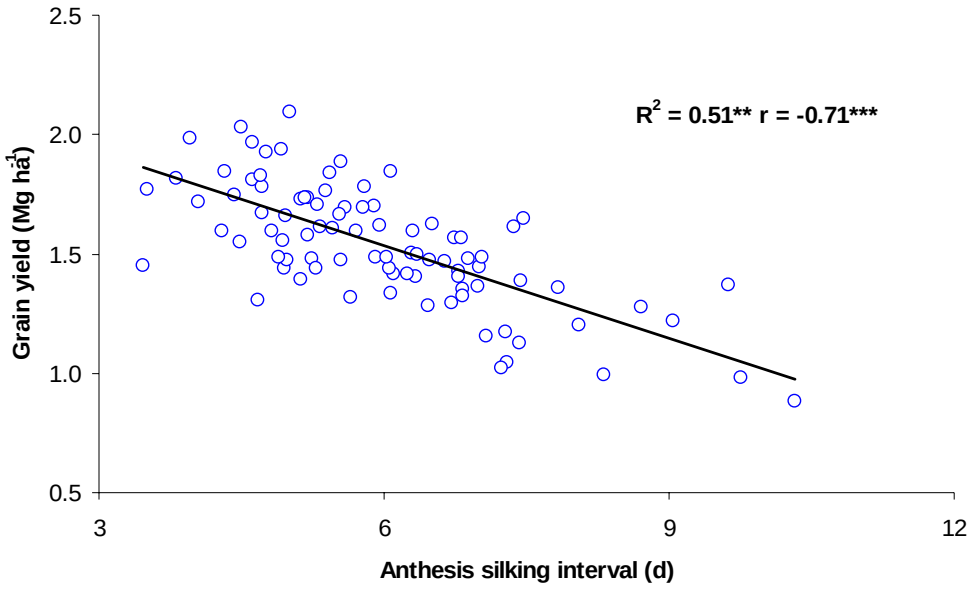

Fig. 3.1. Relationship between anthesis silking interval and grain yield under low N stress.

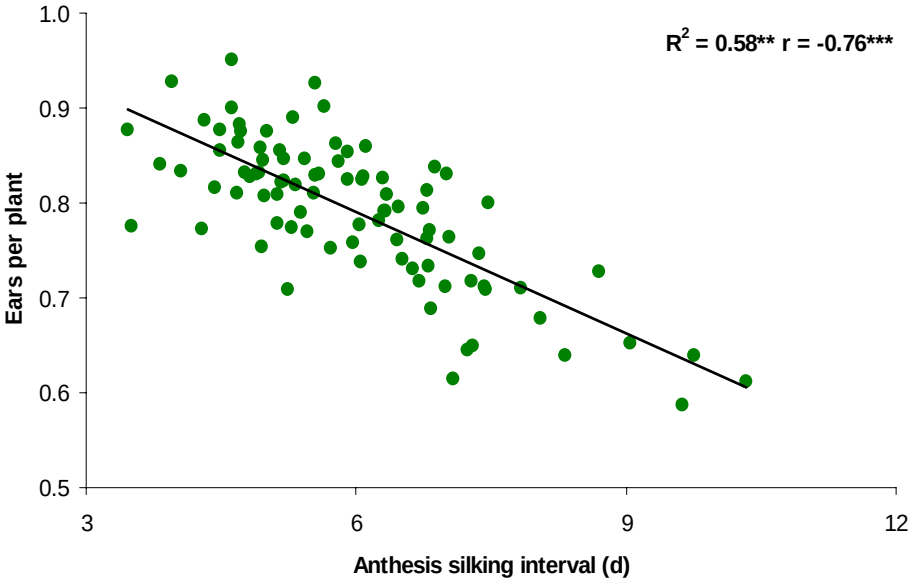

Fig. 3.2. Relationship between anthesis silking interval and ears per plant under low N stress.

Across environments, grain yield was negatively correlated with anthesis date (-0.17*), leaf senescence (-0.29*), and strongly negatively correlated with ASI (-0.59**) (Table 3.13, Fig. 3.3). An increase in anthesis date, ASI, and leaf senescence would lead to reduction in yield as result of reduced grain filling. Bolaños and Edmeades (1996) reported negative genetic correlation with grain yield in S_1 and S_2 progenies evaluated under well-watered and stress environments. Anthesis silking interval showed a negative correlation with ears per plant and leaf senescence (Table 3.13, Fig. 3.4). The relationship indicated a significant reduction in ears per plant as ASI increased (Fig. 3.4). Grain yield showed a positive correlation with kernel weight and a similar result was reported by Bolaños and Edmeades (1996). This suggests that both traits could be improved simultaneously.

Table 3.13. Genetic (upper diagonal) and phenotypic (lower diagonal) correlations between grain yield and agronomic traits across environments.

	GY†	AD	ASI	PH	EPP	GM	KWT	SEN
Grain yield		-0.17*	-0.59**	0.30*	0.69**	-0.01	0.21*	-0.29*
Anthesis date	-0.14**		0.33*	0.42**	-0.36**	0.89***	0.52***	-0.75***
ASI	-0.24**	-0.07		0.57**	-0.94***	0.36**	0.33**	-0.12
Plant height	0.27**	-0.09*	-0.08		-0.36	0.57**	0.54**	-0.38*
Ears per plant	0.21**	-0.14*	-0.33***	0.07		-0.33	-0.25*	-0.07
Grain moisture	0.04	0.21**	0.10	0.11*	-0.03		0.74***	-0.79***
Kernel weight	0.22**	0.13*	0.04	0.23*	0.02	0.31**		-0.65***
Leaf senescence	-0.17*	-0.36***	-0.01	0.02	-0.09	-0.33**	-0.23**	

†AD, anthesis date; ASI, anthesis silking interval, EPP, ears per plant; GM, grain moisture; GY, grain yield; KWT, 100-kernel weight; PH, plant height; SEN, leaf senescence.

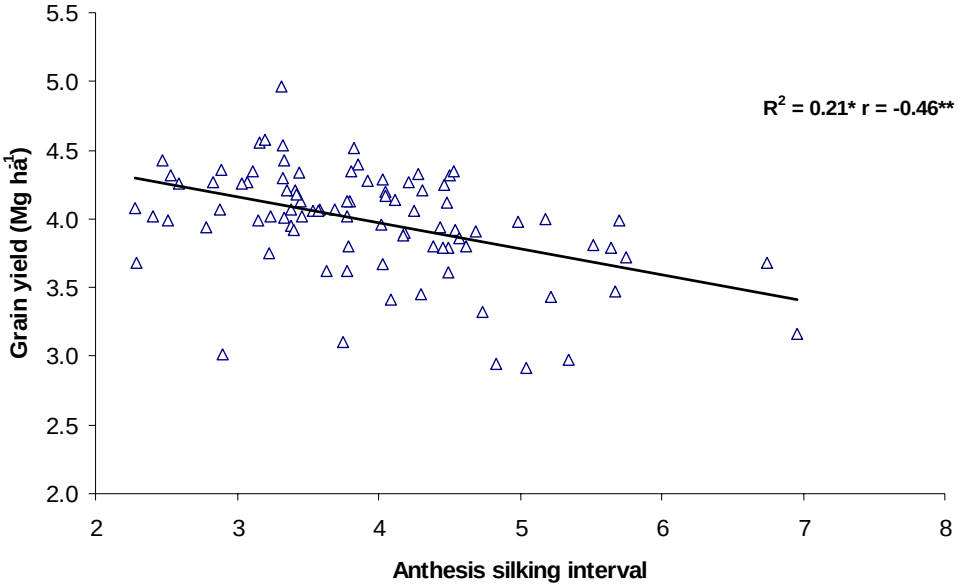

Fig. 3.3. Relationship between anthesis silking interval and grain yield across environments.

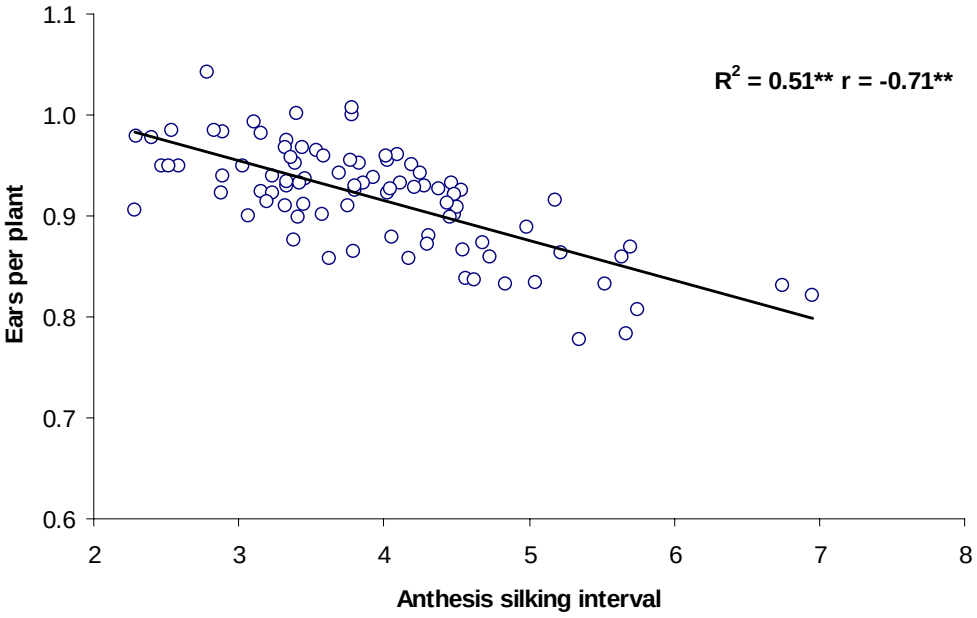

Fig. 3.4. Relationship between anthesis silking interval and ears per plant across environments.

Phenotypic correlations among traits

The phenotypic correlations among traits were visualized using a biplot through singular value decomposition (SVD) of a genotype by trait two-way table (Yan and Tinker, 2005). The traits were centered and standardized before SVD. In the biplot, genotypes are represented by points and traits are represented by vectors. An acute angle between any two vectors indicates a strong positive correlation between them. Trait vectors forming an obtuse angle indicate negative correlation between two traits.

The biplot constructed for low N stressed environments showed that the first two principal components explained a total of 64.7% of the total variation (Fig. 3.5). Grain yield and ears per plant showed a very tight angle between them indicating a strong positive correlation. Grain moisture, 100-kernel weight, and plant height exhibited tight angles which showed high correlation between these traits. Anthesis silking interval had the biggest angle with grain yield and ears per plant, thus showing the negative correlation between ASI and grain yield.

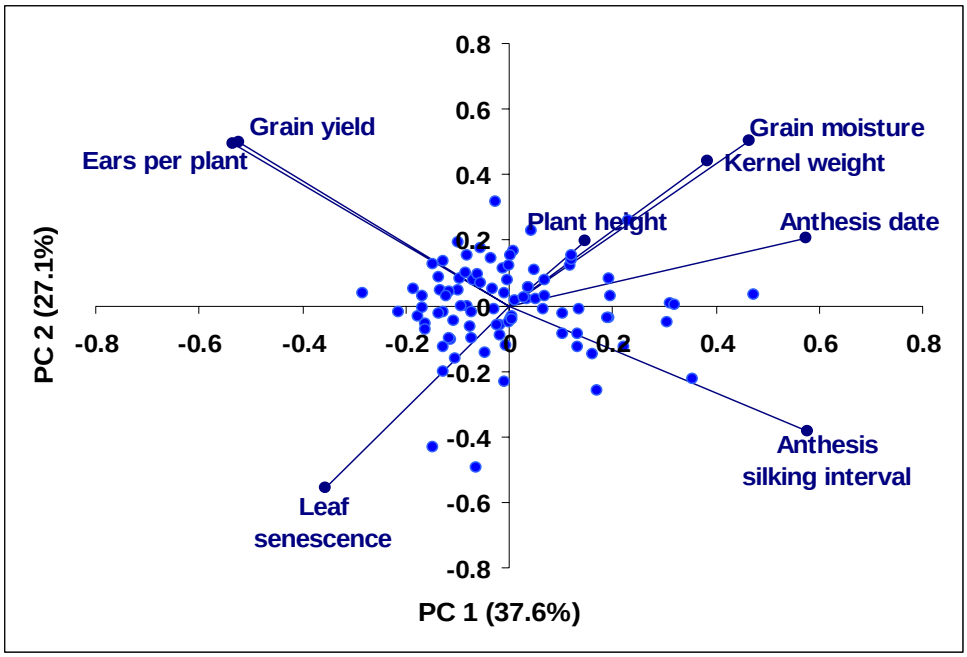

Fig. 3.5. Singular value decomposition biplot showing correlations among traits across low N environments.

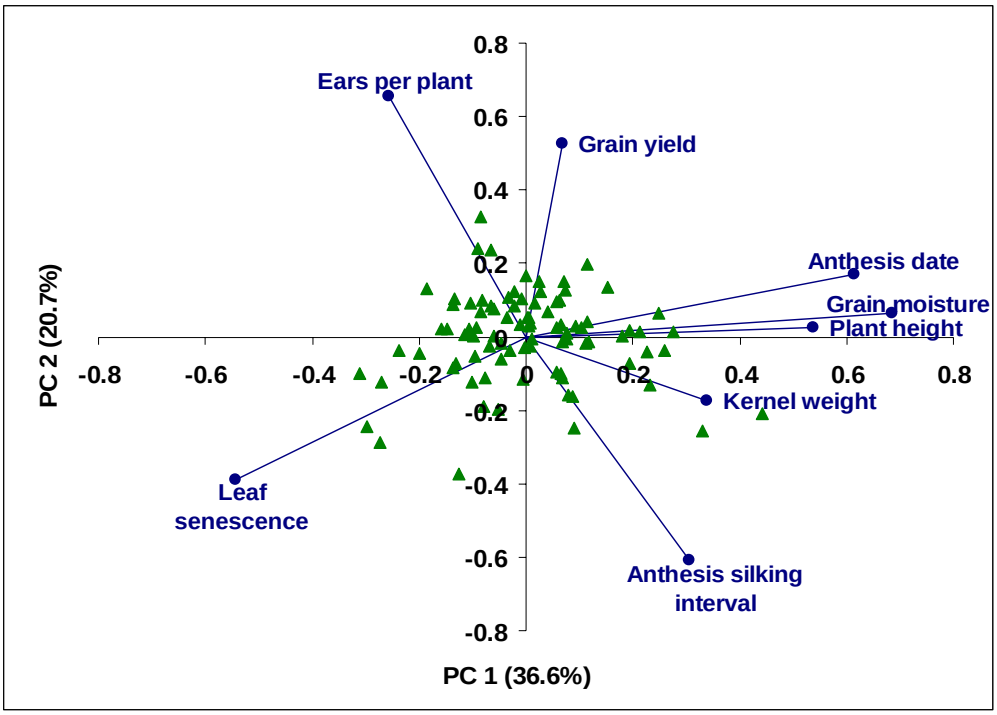

Fig. 3.6. Singular value decomposition biplot showing correlations among traits across optimal environments.

Across optimal environments, the biplot explained 57.3% of the total variation (Fig. 3.6). It showed high correlations between anthesis date, grain moisture, and plant height. Leaf senescence was negatively correlated with anthesis date and grain yield. The biplot constructed with data across environments explained 68.4% of the total variation in this data set (Fig. 3.7). An acute angle between grain yield and ears per plant indicated the strong positive correlation between these traits. Anthesis date, grain moisture, 100-kernel weight, and plant height exhibited tight angles which showed high correlation between these traits. This biplot indicated the weak correlation between leaf senescence and ears per plant, and ASI.

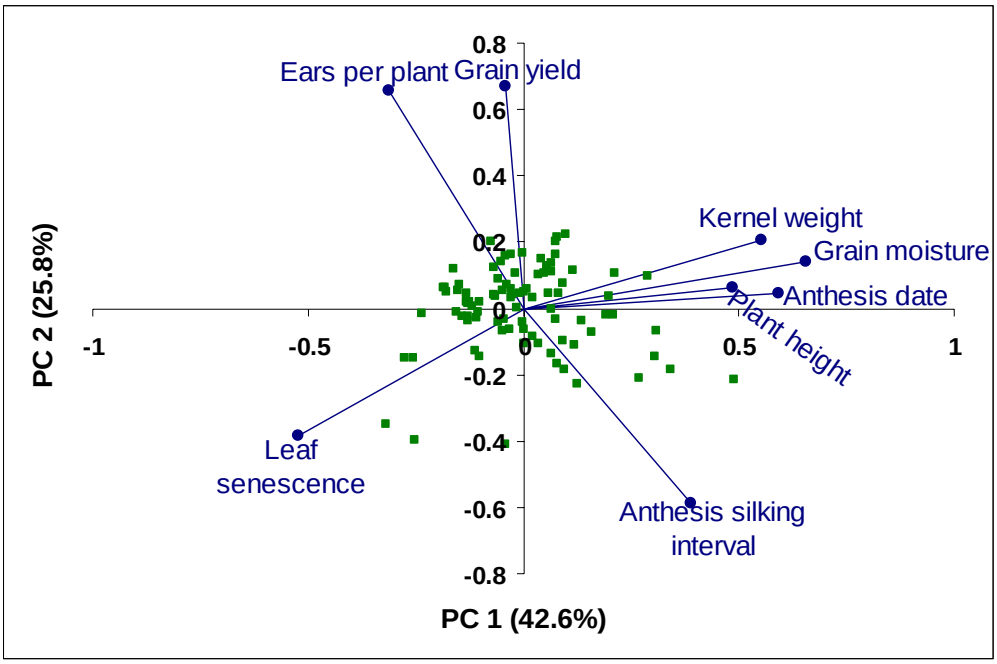

Fig. 3.7. Singular value decomposition biplot showing correlations among traits across environments.

Effect of agronomic traits on grain yield in different environments

An AMMI biplot was constructed to visualize the effect of different traits on grain yield across environments from a two way table of phenotypic correlations with grain yield and environments. The biplot shows traits as vectors and environments as points. The length of a trait vector measures the magnitude of its effect on yield and the cosine of the angle between vectors of traits measures the similarity between them relative to their effects on yield (Yan and Tinker, 2005). The biplot explained 75.6% of the variation (Fig. 3.8) and it showed that most of the traits had a strong effect on grain yield. Plant height had an acute angle with ear height and this indicates that these two traits had a similar effect on yield. The biplot indicated that anthesis silking interval (ASI) had a negative on grain yield. Thus an increase in ASI is associated with reduced yield. Negative correlation between ASI and grain yield has been reported in other studies (Bolaños and Edmeades, 1996; Bänziger and Lafitte, 1997; Betrán et al., 2003c). Also indicated on the biplot is the opposite effect of ears per plant and anthesis silking interval on grain yield. Ears per plant is positively correlated with grain yield. This graphical display of correlations confirms results reported earlier.

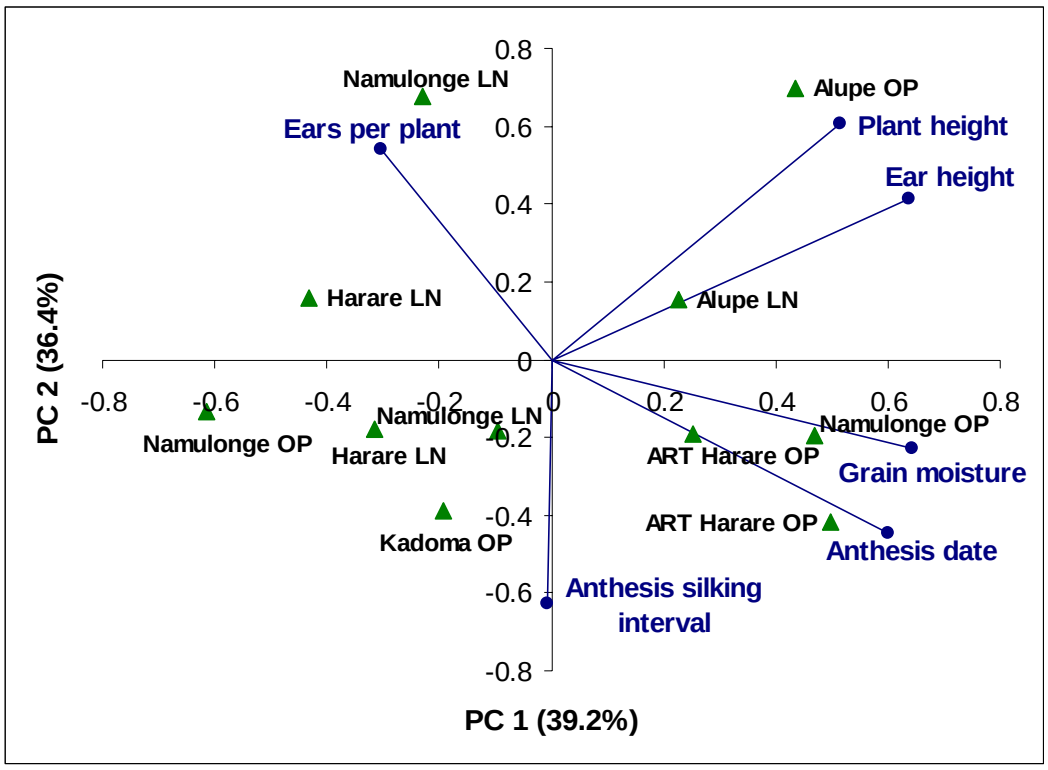

Fig. 3.8. Biplot of first two principal components based on a two-way table of correlation coefficients between agronomic traits and grain yield in each of 11 environments.

Repeatability of traits

Repeatability sets an upper limit to broad sense and narrow sense heritability and can thus provide information on heritability (Falconer and Mackay, 1996). Repeatability across environments is presented in Table 3.14. Repeatability for grain yield was medium across low N stress environments (0.50 ± 0.09) and high across optimal conditions (0.75 ± 0.04). This suggests that actual estimates of heritability for grain yield might be low across low N stress environments. Anthesis silking interval showed medium repeatability across optimal conditions (0.48 ± 0.09) and across low N stress (0.50 ± 0.09). Bolaños and Edmeades (1996) reported broad-sense heritability of 0.60 in S_1 and 0.69 in S_2 progeny for ASI under well-watered environments. Under low N stress, error variance was 34% of total variance while under optimal conditions error variance was 51% of total variance for ASI (Table 3.15), and this might explain the low heritability recorded for ASI across these environments. Plant height, grain moisture, and 100-

kernel weight had relatively high repeatability across environments (Table 3.14). Bolaños and Edmeades (1996) reported high broad-sense heritability estimates for plant height, kernel weight across well-watered and severe stress environments. Repeatability for ears per plant was low across optimal environments (0.21± 0.05), suggesting low heritability values for ears per plant for this trait across environments. This low repeatability could be explained by the high proportion of error variance (63.7%) relative to total variance recorded for ears per plant across optimal environments (Table 3.15). Low repeatability and therefore heritability indicate that likely little progress will be made in improvement of those traits.

Table 3.14. Repeatability (± standard error) for grain yield and agronomic traits across low N stress, optimal and environments.

	Low N	Optimal	Across
Grain yield	0.50 ± 0.09	0.75 ± 0.04	0.69± 0.04
Anthesis date	0.86 ± 0.02	0.91 ± 0.02	0.89 ± 0.02
Anthesis silking interval	0.50 ± 0.09	0.48 ± 0.09	0.55 ± 0.06
Plant height	0.64 ± 0.06	0.82 ± 0.03	0.79 ± 0.03
Ears per plant	0.64 ± 0.06	0.21 ± 0.05	0.47 ± 0.07
Grain moisture	0.65 ± 0.06	0.70 ± 0.05	0.73 ± 0.04
Kernel weight	0.74 ± 0.05	0.68 ± 0.06	0.72 ± 0.04
Leaf senescence	0.57 ± 0.08	0.65 ± 0.07	0.57 ± 0.05

Table 3.15. Variance component estimates for agronomic traits of synthetics across low N stress, optimal, and environments.

Trait	Component					
	Environment (E)	Reps(Env)	Blocks(Rep*E)	Genotype	Genotype x E	Residual
Across Low N						
Grain yield	0.10	0.02	0.02	0.03	0.02	0.25
Anthesis date	30.96	0.18	0.49	2.48	0.11	3.95
Anthesis silking interval	2.85	0.31	0.75	0.91	1.36	6.45
Plant height	769.50	6.95	56.77	37.98	17.10	177.48
Ears per plant	0	0	0	0	0	0.02
Grain moisture	19.17	0.14	0.16	0.56	0.06	2.92
Kernel weight	10.05	0.35	0.71	2.88	0.80	6.46
Leaf senescence	0.78	0.07	0.04	0.05	0.03	0.21
Across Optimal						
Grain yield	6.80	0.04	0.12	0.20	0.19	0.82
Anthesis date	535.27	0.07	0.50	2.12	0.23	2.19
Anthesis silking interval	3.75	0.00	0.27	0.25	0.40	2.38
Plant height	1509.49	10.89	36.29	74.93	18.85	217.72
Ears per plant	0.04	0	0	0	0	0.03
Grain moisture	16.40	0.09	0.34	0.51	0.58	2.88
Kernel weight	54.52	0.03	0.12	2.61	0.62	8.71
Leaf senescence	1.04	0.00	0.05	0.06	0.04	0.12
Across Environments						
Grain yield	7.79	0.03	0.08	0.11	0.15	0.62
Anthesis date	286.36	0.12	0.50	2.24	0.21	2.99
Anthesis silking interval	6.84	0.13	0.50	0.60	0.79	4.22
Plant height	2075.89	9.44	43.35	56.87	21.06	203.25
Ears per plant	0.03	0	0	0	0	0.02
Grain moisture	16.53	0.11	0.28	0.55	0.36	2.90
Kernel weight	35.03	0.22	0.38	2.85	0.65	7.51
Leaf senescence	0.75	0.04	0.04	0.05	0.03	0.17

Heterosis and its relationship to grain yield

Mid-parent and high-parent heterosis for grain yield at each location and across environments are presented in Table 3.16. Average mid-parent heterosis (MPH) ranged from 1.6% at Namulonge B to 37.7% at Namulonge A for low N stress locations. Across low N environments, MPH averaged 23.0%. The high MPH observed for the 1st season at Namulonge could be attributed to the lower yield of the parental synthetics due to drought that hit the crop at this location. The synthetic hybrids performed much better than the parental synthetics, hence the observed high MPH. In the second season, MPH was low because both the parental synthetics and hybrids performed almost equally well. In optimal environments, MPH ranged from 3.2% at Matopos to 50.1% at Alupe. Average MPH across optimal environments was 22.3% and average HPH was 8.4%. The highest average MPH across low N stress was in cross SYNTemperateA-SR-F2 x SYNTemperateB-SR-F2 (71.7%), followed by 99SADVLA-# x SYNI137TN-SR-F1 (57.4 %). The cross SYNTemperateA-SR-F2 x SYNTemperateB-SR-F2 also gave the highest MPH across locations (65.6%, Appendix G). Under optimal conditions, the cross showing the highest average MPH was SYNTemperateA-SR-F2 x SYNTemperateB-SR-F2 (61.6%) followed by SZSYNUCA-F2 x SYNK64R-SR-F2 (59.2%). Vales et al. (2001) evaluated interpopulation crosses obtained from three synthetic populations and recorded MPH ranging from 8.5% to 32.8%.

Average high-parent heterosis (HPH) ranged from -12.7% to 15.2% under low N stress. Under optimal conditions, heterosis ranged from -12.9% to 19.0%. The cross exhibiting the highest average HPH was SYNTemperateA-SR-F2 x SYNTemperateB-SR-F2 (53.8%) under low N stress (Appendix G). The highest average HPH under optimal conditions was found for cross SZSYNUCA-F2 x SYNK64R-SR-F2 (48.1%). Other studies utilizing maize populations have also indicated low high-parent heterosis values. Beck et al. (1990) reported HPH ranging from -11.2 to 9.6% in tropical early and intermediate populations. Crossa et al. (1990) reported HPH values in the range -3.6 to 17.5% in tropical yellow maize populations, while Vasal et al. (1992) reported a range -3.1% to 12.7% in tropical white populations. In temperate maize populations with some exotic germplasm, Crossa et al. (1987), reported HPH in the range 0 to 47%. Mickelson et al. (2001) reported high-parent heterosis for grain yield in variety crosses grown in Mexico and Zimbabwe that ranged from -30 to 52% and they attributed this to the low *per se* yield of the parents used in the crosses.

Table 3.16. Average mid-parent and high-parent heterosis at each location.

Location	Mid-parent heterosis	High-parent heterosis
Low N stress		
Harare A†	23.2	8.8
Harare B	21.7	4.4
Namulonge A	37.7	15.2
Alupe	30.6	9.5
Namulonge B	1.6	-12.7
Across Low N	**23.0**	**5.0**
Optimal environments		
R.A. Harare A	26.4	17.9
ART Farm Harare A	28.1	13.7
Kadoma	13.2	3.6
ART Farm Harare B	21.2	10.5
Namulonge A	24.6	9.5
Alupe	50.1	19.0
R.A. Harare B	24.2	11.9
Matopos	3.2	-12.9
Namulonge B	10.3	2.4
Across Optimal	**22.3**	**8.4**

†A and B refer to 1st and 2nd year

Mid-parent heterosis averaged over hybrid synthetics varied across synthetics (Figs. 3.9, 3.10, and 3.11). Across low N stressed environments, synthetic 99SADVLA had the highest HPH across combinations with 38.43% (Fig. 3.9). Two other synthetics (SYNK64R-SR and 99SADVIB) showed high MPH, suggesting they performed well under low N stress environments. Across optimal conditions, synthetic A SYNA00 had the highest MPH (37.4%) followed by synthetic A 99SADVIA (32.7%) (Fig. 3.10). Across environments, the best synthetics for MPH were 99SADVIA (31.7%) and SYNK64R-SR (31.2%) (Fig. 3.11). Both synthetics had high MPH across low N stress environments and optimal environments.

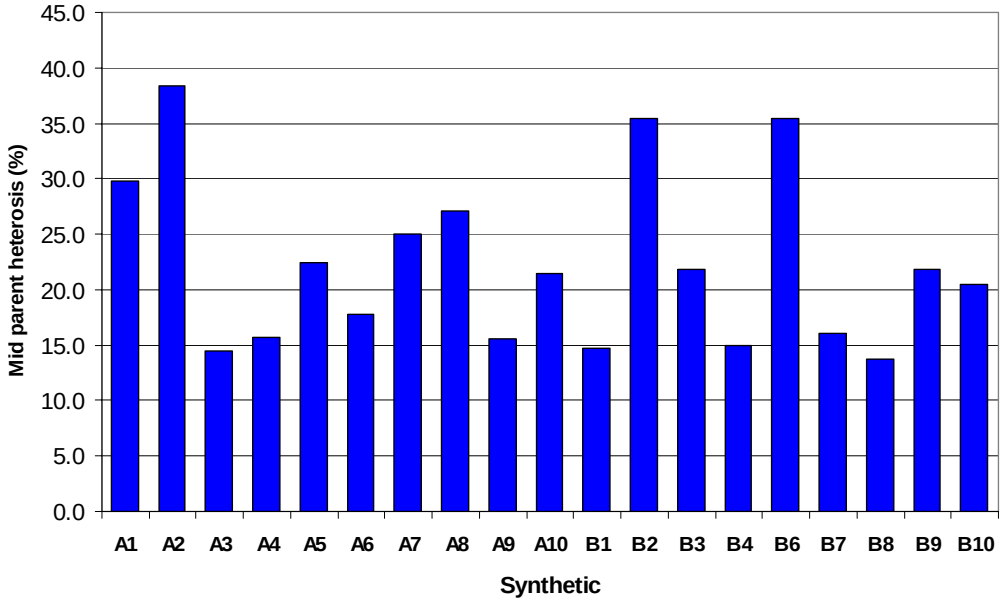

Fig. 3.9. Average mid parent heterosis for 19 synthetics across low N stress environments.

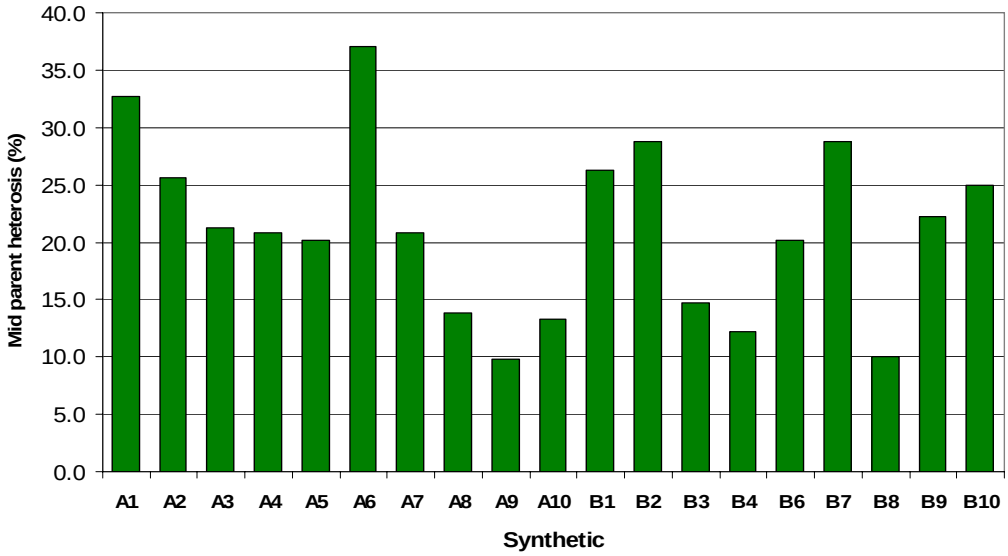

Fig. 3.10. Average mid parent heterosis for 19 synthetics across optimal environments.

[A1=99SADVIA; A2=99SADVLA; A3=SZSYNKITII; A4=SZSYNUCA; 5=Z97SYNGLS(A); A6=SYNA00; A7=P501-SR; A8=SYNN3-SR; A9=SYNTemperateA-SR; A10=SYNI137TN-SR; B1=P502-SR; B2 = SYNK64R-SR; B3=SYNSC-SR; B4=SYNTemperateB-SR; B6=99SADVIB; B7=99SADVLB; B8=SYNB00; B9=SZSYNECU573; B10=Z97SYNGLS(B)].

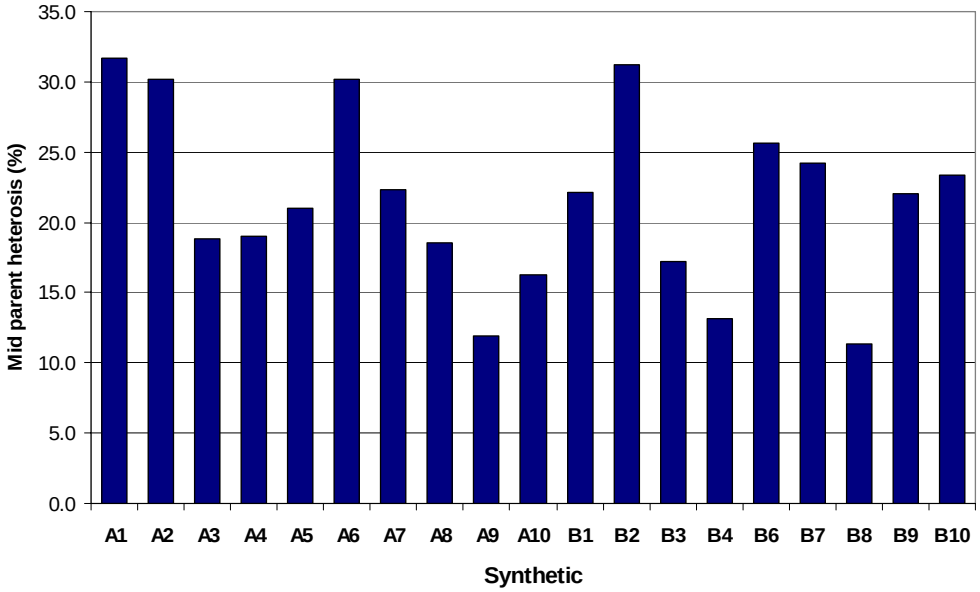

Fig. 3.11. Average mid parent heterosis for 19 synthetics across environments.
[A1=99SADVIA; A2=99SADVLA; A3=SZSYNKITII; A4=SZSYNUCA; 5=Z97SYNGLS(A); A6=SYNA00; A7=P501-SR; A8=SYNN3-SR; A9=SYNTemperateA-SR; A10=SYNI137TN-SR; B1=P502-SR; B2 = SYNK64R-SR; B3=SYNSC-SR; B4=SYNTemperateB-SR; B6=99SADVIB; B7=99SADVLB; B8=SYNB00; B9=SZSYNECU573; B10=Z97SYNGLS(B)].

The relationship between heterosis and grain yield was investigated across environments. The correlation between MPH and grain yield in low N stress was high (R^2 = 0.62, r = 0.79; Fig. 3.12). A significant correlation between grain yield and MPH was observed under optimal conditions (R^2 = 0.44, *r* = 0.67) and also across all environments (R^2 = 0.46, *r* = 0.68). Under low N stress conditions, MPH would be a good predictor of synthetic hybrid performance, as suggested by the strong correlation.

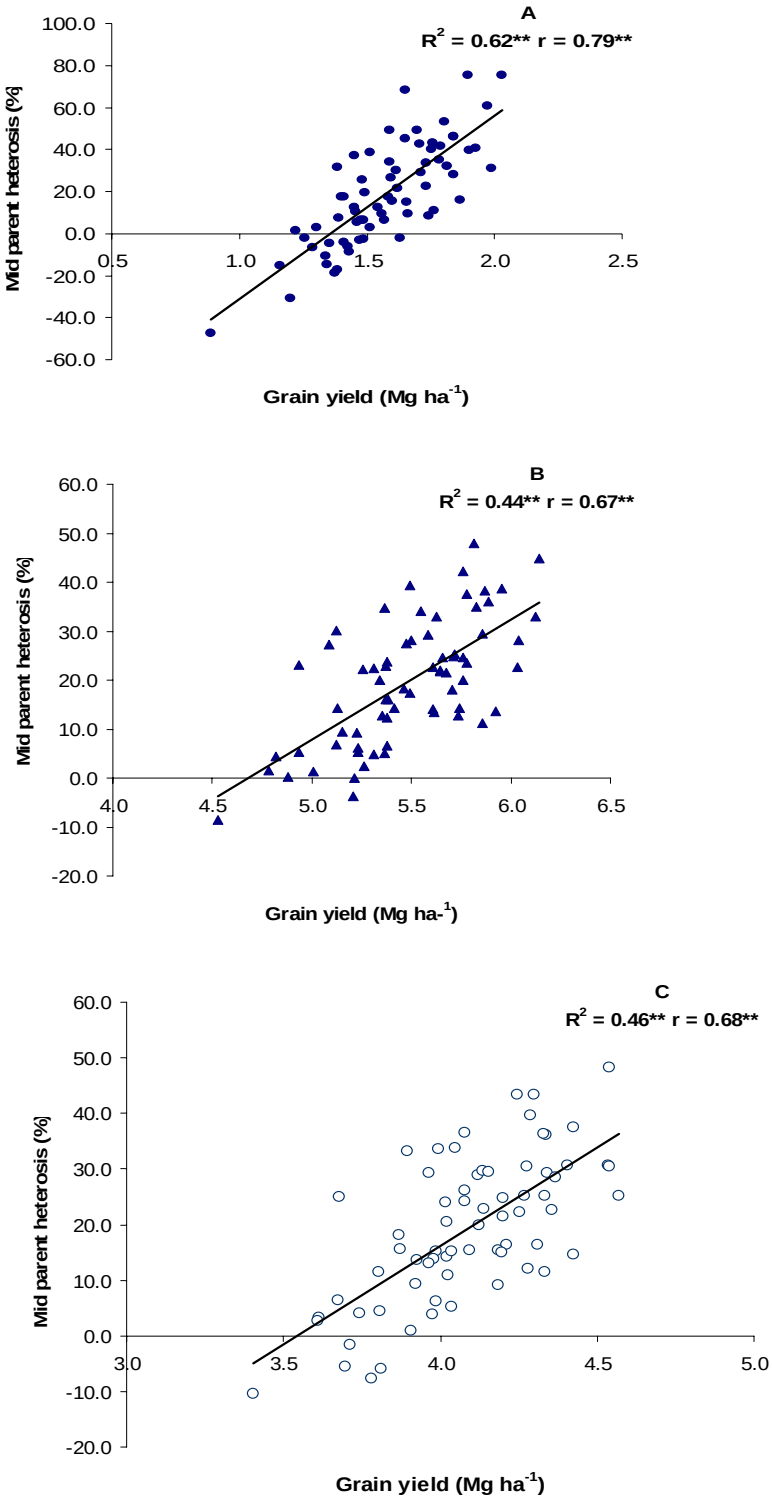

Fig. 3.12. Relationship between grain yield and mid-parent heterosis for synthetics across low N environments (A), optimal environments (B), and across environments (C).

Stability and AMMI analysis

Stability analysis was conducted on average grain yield for all synthetics across all their hybrid combinations. Parental synthetic SYNI137TN-SRF1 had the highest yield across environments (4.34 Mg ha^{-1}, Table 3.17). Stability parameters were variable for the synthetics as measured by the slope, b, and mean squared deviation (Table 3.17). Stability values ranged from 0.82 to 1.19 for parental synthetics. Among the parental synthetics, B synthetic SYNTemperateA-SR-F2 was the most stable (b = 1.01, mean squared deviation = 0.44). Other stable parental synthetics were SZSYNECU573-F2 (b = 1.05, mean squared deviation = 0.41) and SYNN3-SR-F2 (b = 0.98, mean squared deviation = 0.30). These parental synthetics are expected to perform averagely well across environments. The least stable parental synthetic was 99SADVLA-# (b = 0.85, mean squared deviation = 0.41). Check variety SC627 was less stable (b = 1.34, mean squared deviation = 0.34). In hybrid combination, stability values ranged from 0.94 to 1.07 (Table 3.17). Synthetics 99SADVIA-# and P502-SRc0-F3 were the most stable (b = 1.00, mean squared deviation = 0.03; Table 3.17). The narrow range of stability values might indicate that these synthetic hybrids will do well across a range of environments. It has been suggested that more heterozygous varieties and heterogeneous populations are less affected by environmental differences (Allard and Bradshaw, 1964). Synthetics are heterogeneous and this might explain the range of stability values observed in this study.

Additive main effects and multiplicative interaction (AMMI) analysis of adjusted grain yield revealed that the first two principal components explained 28.2% and 18.5% of the total genotype x location sums of squares, respectively (Table 3.18). An AMMI biplot in which genotypes are represented as points and environments are represented by vectors was used to show both genotypes and environments simultaneously. The biplot was generated using the first two principal component scores to visualize the relationship between environments and hybrids. The biplot (Fig. 3.12) showed most of the low N stress locations clustered together and had small angles between them, except Alupe that clustered with R.A. Harare. This implies that the low N stress locations were similar in ranking the hybrids. This might suggest uniformity of N stress at the locations since they mostly clustered together yet they are in geographically different locations. The low N stress sites were mostly separate from the optimal environments implying different ranking of hybrids between optimal and low N stress environments. Locations Matopos, R.A. Harare A, and ART Farm Harare had the longest vectors, suggesting that these environments were the most discriminating for the genotypes. Locations Kadoma and ART Farm

Harare, both optimal environments, had a very tight angle between them implying that they were similar in ranking the synthetic hybrids.

Table 3.17. Mean grain yield (Mg ha^{-1}) for parental synthetics, checks, and synthetic hybrids, and their stability (b).

	Parents and checks			Hybrids		
	Grain yield	b†	σ^2_{di}	Grain yield	b	σ^2_{di}
99SADVIA-#	2.93	0.89	0.30	4.23	1.00	0.03
99SADVLA-#	2.97	0.85	0.41	4.31	1.02	0.07
SZSYNKITII-F2	2.95	0.91	0.31	3.99	1.07	0.09
SZSYNUCA-F2	3.59	0.89	0.33	4.06	1.02	0.14
Z97SYNGLS(A)-F3	3.50	1.14	0.26	4.18	1.06	0.06
SYNA00F2	3.13	0.90	0.62	4.17	1.00	0.07
P501-SRc0-F2	3.80	1.09	0.75	4.17	0.99	0.03
SYNN3-SR-F2	3.88	0.98	0.30	3.82	1.00	0.04
SYNTemperateA-SR-F2	4.27	1.01	0.44	4.01	0.96	0.04
SYNI137TN-SRF1	4.34	1.19	0.53	4.12	0.99	0.05
P502-SRc0-F3	3.05	0.80	0.15	4.21	1.00	0.03
SYNK64R-SR-F2	3.30	0.83	0.55	3.94	0.95	0.08
SYNSC-SR-F2	3.51	0.90	0.28	4.03	1.03	0.05
SYNTemperateB-SR-F2	3.95	0.89	0.53	4.20	1.01	0.04
99SADVIB-#	3.80	1.07	0.51	4.20	0.99	0.11
99SADVLB-#	3.30	1.11	0.32	4.22	0.98	0.16
SYNB00-F2	4.05	1.08	0.46	3.92	0.96	0.12
SZSYNECU573-F2	4.00	1.05	0.41	3.92	1.07	0.06
Z97SYNGLS(B)-F5	4.02	1.15	0.45	3.91	0.94	0.04
ZM621 (Check)	3.31	0.94	0.22			
SC627 (Check)	4.92	1.34	0.34			

†b, slope of the regression; σ^2_{di}, mean square deviation.

Table 3.18. Analysis of variance for the Additive Main Effect and Multiplicative Interaction (AMMI) model for grain yield

Source of variation	df	SS	MS	Pr > F	% SS explained
Genotypes	18	4.98	0.28		
Locations	13	2038.01	156.77		
Genotypes x Locations	234	18.30	0.08		
AMMI Component 1	30	5.15	0.17	0.00	28.20
AMMI Component 2	28	3.40	0.12	0.00	18.50
AMMI Component 3	26	2.05	0.08	0.06	11.20
AMMI Component 4	24	1.97	0.08	0.02	10.77
G x E Residual	126	5.73			
Total	265	2061.30			

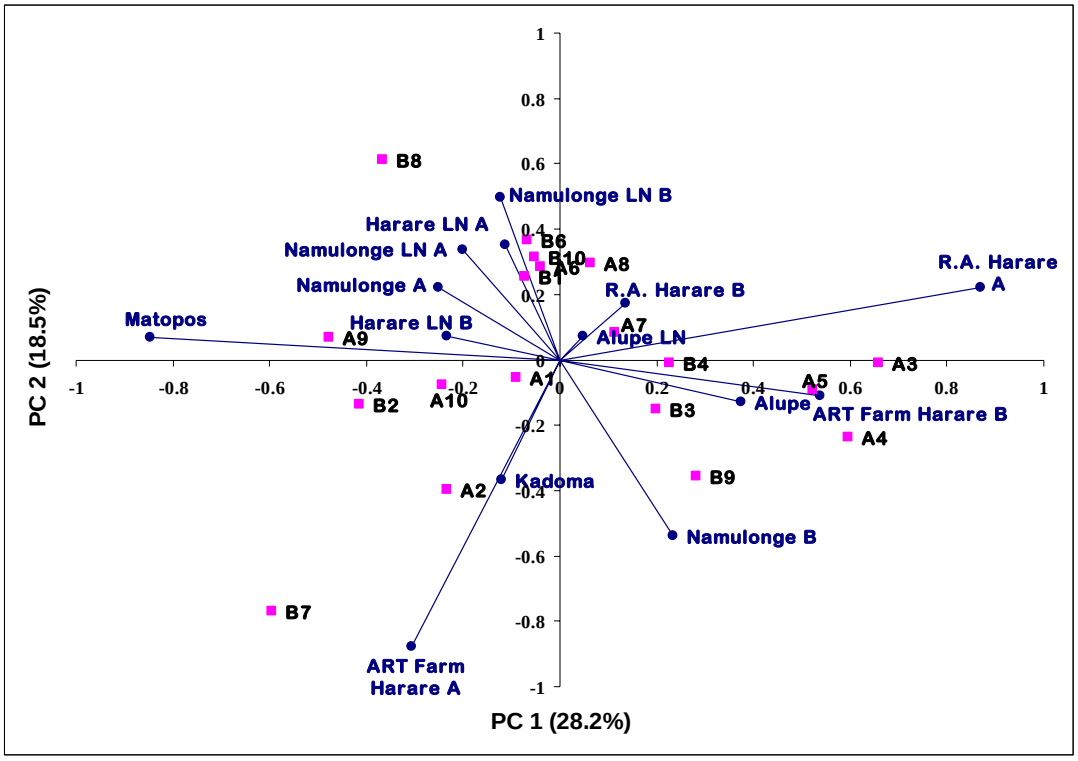

Fig. 3.13. Biplot of first two principal components based on grain yield of 19 synthetic A and B in hybrid combination at 14 environments.

[A1=99SADVIA; A2=99SADVLA; A3=SZSYNKITII; A4=SZSYNUCA; 5=Z97SYNGLS(A); A6=SYNA00; A7=P501-SR; A8=SYNN3-SR; A9=SYNTemperateA-SR; A10=SYNI137TN-SR; B1=P502-SR; B2 = SYNK64R-SR; B3=SYNSC-SR; B4=SYNTemperateB-SR; B6=99SADVIB; B7=99SADVLB; B8=SYNB00; B9=SZSYNECU573; B10=Z97SYNGLS(B)].

CONCLUSIONS

Analysis of variance indicated significant differences between synthetic hybrids, parental synthetics, and checks. Across low N stress environments genotype x environment interaction was not significant for grain yield but significant for anthesis silking interval and kernel weight. Genotype x environment interaction was significant for grain yield across optimal environments and across environments. Analysis of A x B synthetic interaction indicated significant specific combining ability for grain yield across optimal environments, suggesting that there were some superior synthetic hybrid combinations for high grain yield. Significant positive GCA effects for grain yield were observed for A synthetics 99SADVIA and 99SADVLA across low N and optimal conditions. B synthetics 99SADVIB and 99SADVLB also had positive GCA effects. The synthetics showing good GCA effects under low N stress conditions might be considered for developing synthetic hybrids to be used by farmers facing low soil fertility problems. Heterosis for grain yield was observed in some crosses and environmental conditions. The negative genetic correlation between grain yield and anthesis silking interval, and leaf senescence indicated the importance of these two associated traits to increased grain yield. Moderate repeatability was indicated for most traits in low N environments suggesting improvements could be possible under this stress. Most of the synthetics showed good stability and this suggests they have a potential to be used in several countries in the region. It is suggested that those synthetics showing high yield be tested further for potential release.

CHAPTER IV

AGRONOMIC PERFORMANCE AND AFLATOXIN ACCUMULATION IN SINGLE AND THREE-WAY CROSS WHITE MAIZE HYBRIDS

INTRODUCTION

Maize (*Zea mays* L.) grown in the United States is predominantly yellow endosperm maize. However, white maize has played an important role in the history of maize and continues to be a significant U.S. agricultural commodity (Poneleit, 1994). White corn acreage in the U.S. increased from 550,000 acres in 1996 and 1998 to reach 950,000 acres in 2002 (AMRC, 2003). White corn production increased from 66 million bushels in 1995 to 140 million bushels in 2002 but accounts for only 1% of the total U.S. crop of 9.5 billion bushels (AMRC, 2003). Increased production of white corn is attributed to higher acreage and improved yields. White corn production occurs in distinct regions of the U.S. mainly the Corn Belt, Texas Panhandle, southern Texas, and central California. Exports of white corn have increased from 600,000 tons in 1995 to over 1.6 million tons in 2002 (USDA, FAS). White corn utilization has shifted from animal feeding to specialized human food (e.g. tortillas and tortilla chips) and industrial products from dry milling (Poneleit, 1994). This requires high grain quality in addition to increased grain yield. High quality white endosperm corn should have large uniform, dense and nondented or only slightly dented kernels.

Disease-free grain is essential for high quality white corn but maize is affected by the most critical mycotoxin problems. Mycotoxins are fungal metabolites that can contaminate foods and feeds, and exhibit toxic effects in higher organisms that consume contaminated commodities. Therefore, mycotoxin contamination of foods and feeds results in a serious food safety issue and affects the competitiveness of U.S. agriculture in both domestic and world export markets (Cleveland et al., 2003). Mycotoxins that are associated with undesirable consequences include aflatoxins produced by *Aspergillus flavus* Link and *Aspergillus parasiticus* Speare, deoxynivalenol produced by *Fusarium spp.*, and fumonisins produced by *Fusarium verticillioides* Sacc (Sheld) (Munkvold, 2003; Cleveland et al., 2003). Aflatoxins (secondary metabolites produced by the fungus *Aspergillus flavus* Link), are potent liver toxins and carcinogens and are a concern for consumers of maize grain where maize is a major part of the diet (Scott and Zummo, 1988; Duvick, 2001; Cleveland et al., 2003). In the USA, grain with more than 20 ng g^{-1} of

aflatoxin B1 is banned for interstate commerce and grain with more than 300 ng^{-1} of aflatoxin B1 cannot be used as livestock feed. Mycotoxin contamination in maize depends on host susceptibility, environmental conditions favorable for infection, and, in some cases, vector activity (Munkvold, 2003). Aflatoxin development in maize is favored by drought stress (Scott and Zummo, 1988; Payne, 1992; Moreno and Kang, 1999; Naidoo, et al., 2002; Munkvold, 2003) and high temperature (Anderson, 1975; Payne, 1992) and insect damage (Lillehoj et al., 1976).

A number of control measures including cultural practices (Munkvold, 2003), host plant resistance, and biotechnology approaches (Widstrom, 1987) have been tried to reduce aflatoxin contamination in maize. The most effective control method of aflatoxin contamination of maize grain is the use of genetically resistant hybrids (Campbell and White, 1995) but there are no elite inbreds resistant to aflatoxin that can be used directly in commercial hybrids (Betrán et al., 2002). There is need to screen germplasm for possible sources of resistance that can be used in hybrid production and exotic germplasm is potential source of resistance genes to aflatoxin. The objectives of this study were to (i) compare the performance of white single crosses (SC) and three-way crosses (TWC) between exotic (tropical and subtropical) and temperate white lines; (ii) evaluate the SC and TWC hybrids for aflatoxin accumulation; and (iii) estimate combining abilities of the inbred lines for agronomic traits and aflatoxin accumulation.

REVIEW OF LITERATURE

Aflatoxin in maize

Maize (*Zea mays* L.) is a cereal in which a range of mycotoxins have been found throughout the world. One of the most critical mycotoxins is aflatoxin, a secondary metabolite produced by the fungus *Aspergillus flavus* Link. There are more than 10 compounds named as aflatoxins but Aflatoxin B1 is the principal member of the family (Moreno and Kang, 1999). Aflatoxin is reported to occur in many of the maize growing areas in the USA (Widstrom et al., 1978; Lillehoj et al., 1980; Widstrom et al., 1984; Scott and Zummo, 1988) and Africa (Cardwell et al., 2000; Bankole and Adebanjo, 2003), and other countries (Moreno and Kang, 1999). Mycotoxin contamination of foods and feeds results in a serious food and safety issue (Cleveland et al., 2003). Factors that favor aflatoxin growth on maize kernels include drought stress and high temperature (Payne, 1992), nitrogen deficiency (Moreno and Kang, 1999), and insects Lillehoj et al., 1976). Studies have been undertaken to understand the factors promoting aflatoxin accumulation in maize and the genetics of resistance to aflatoxin, and develop methodology for evaluating response to aflatoxin accumulation.

Lillehoj et al., (1980) evaluated commercial and experimental single and three-way cross hybrids for effects of planting date, inoculation, and mechanical damage of developing kernels on aflatoxin accumulation in kernels before harvest. They found no hybrids with complete resistance to aflatoxin and mean toxin levels ranged from 84 ng g^{-1} to 250 ng g^{-1}, with a mean of 154 ng g^{-1}. Lillehoj et al. (1980) indicated that environmental conditions and corn maturity factors interact to yield a differential response to *A. flavus* infection of kernels and subsequent aflatoxin accumulation. Scott and Zummo (1988) determined percentage of kernel infection by aflatoxin for maize inbreds using the pinbar, needle-in-silk-channel, and side-needle inoculation techniques and evaluated maize inbred lines for resistance to *A. flavus*. They reported that resistant inbreds had 5 to 10% infected kernels compared to 10 to 30% infection for susceptible inbreds. Scott and Zummo (1988) reported that the pinbar inoculation method gave higher (36%) kernel infection compared to the needle inoculations. They noted that provided there is a relatively high level of infection and a sufficient number of replications, it should be possible to select for resistance. They concluded that resistance to kernel infection reduces aflatoxin concentration in the grain. Widstrom et al. (1978) evaluated commercial and experimental three-way cross hybrids infested with the corn ear worm for aflatoxin B_1 production. They reported higher aflatoxin levels in

infested hybrids than in noninfested hybrids. No significant differences were detected among commercial hybrids when data was combined over locations. They reported no significant differences for aflatoxin concentration among the three-way testcrosses.

Using a nine-parent diallel, Widstrom et al. (1984) evaluated maize inbreds for total aflatoxin contamination for three years. Widstrom et al. (1984) reported significant GCA and SCA effects but no significant GCA x year and SCA x year interaction. They noted that most of the genetic variability detected among the crosses was attributable to additive effects (GCA) when data were combined and that the GCA effects were not drastically affected by changes in environment but may go undetected when the concentrations of aflatoxin are very low. Darrah et al (1987) evaluated F_1 diallel cross hybrids, inbred lines, and checks to determine genetic control of aflatoxin B_1 production. They found significant GCA mean squares and non significant SCA mean squares for aflatoxin B_1 and reported that GCA sum of squares accounted for 71% of total diallel sums of squares. They found significant GCA effects for insect damage ratings but SCA effects were not significant. Naidoo et al. (2002) studied genetics of resistance to aflatoxin through diallel analysis. They reported significant GCA effects for ear rot rating and aflatoxin concentration. SCA effects were not significant for aflatoxin concentration and ear rot rating. However, they reported significant GCA x environment and SCA x environment interaction for aflatoxin concentration.

Betrán et al. (2002) evaluated aflatoxin accumulation in white and yellow maize inbreds using a diallel. They reported significant differences among inbred GCA effects, among hybrid means, and the SCA effects for both white and yellow maize at two of three locations used. GCA x environment and SCA x environment were significant for aflatoxin concentration for both white and yellow hybrids. In a study using hybrids derived from crosses between selected inbreds and two susceptible inbreds, Campbell and White (1995) evaluated the hybrids for ear rot, kernel infection, and aflatoxin concentration. They reported that genotypes with low ear rot ratings generally had lower aflatoxin concentration. They noted that *Aspergillus* ear rot ratings provided a more accurate estimate of aflatoxin contamination. Windham and Williams (2002) evaluated 18 maize inbreds and advanced breeding lines for three years and reported variable quantities of aflatoxin. A high mean aflatoxin concentration of 3959 ng g^{-1} was reported for 1998. In 1999, the mean aflatoxin concentration was 189 ng g^{-1} for one of the tests and 349 ng g^{-1} for the second test. In 2000 the mean aflatoxin concentration was 1554 ng g^{-1} (Windham and Williams, 2002).

Bhatnagar et al. (2003) reported variation in aflatoxin concentration between white and yellow quality protein maize hybrids at two locations in Texas.

Single- and three-way crosses

A single cross hybrid is produced by crossing two inbred lines. A three-way cross is produced by crossing a single cross hybrid with an inbred line. Seed production of a three-way cross should be superior to the variety cross as the seed would be from a single-cross female parent versus the population (Darrah and Penny, 1975). Production costs favor the three-way cross over single or double crosses (Darrah and Penny, 1975). Seed production from an inbred female parent used for producing a single cross is generally less than that obtained from a single-cross parent used in producing three-way cross. Relative costs of three-way cross production versus the variety cross would depend on the particular lines or populations. Allard and Bradshaw (1964) noted that there are two ways of achieving stability in production. If a hybrid is composed of a number of different genotypes, such as three-way crosses, it could possess population buffering while a hybrid like a single cross composed of members alike, but each member is adapted to a wide range of environments, it possesses individual buffering.

Darrah and Penny (1975) made single crosses and predicted the best three-way crosses based on single cross performance. The three-way crosses were made and evaluated to compare them with single crosses. They noted that most of the three-way crosses had predicted advantages in stalk lodging resistance and ear placement when contrasted to commercial checks and about one-third of the three-way crosses out-yielded the commercial checks. However, they did not find any three-way cross that was significantly better than the variety cross used as a check. The three-way crosses yielded very well and had significantly better stalk lodging resistance. Darrah and Penny (1975) noted that the correlation of observed and predicted yields for the three-way crosses was not significant and concluded that the S_3 x S_3 crosses may have insufficient homozygosity to be of significant value in prediction. Lynch et al. (1973) compared the performance of single cross, three-way cross, and double cross corn hybrids in Canada and found that the average yield of single crosses was significantly greater that the average yield of three-way crosses. In two environments, the yield of three-way crosses was equal to that of the single cross. They found that the three types of crosses responded differently to the yield level of the environment in which they were grown. The single crosses had superior performance in low-yielding environments and had the ability to exploit the higher yielding environments more than

three-way crosses. Lynch et al. (1973) used the parameter *b* used by Eberhart and Russell (1966) to evaluate the stability of the single cross and three-way crosses and found that there was no difference in the average stability of the single cross and three-way crosses over locations and years. They did not find a correlation between a hybrid's average ability to yield and its ability to exploit a high yielding environment or its lack of performance in a poor environment.

Weatherspoon (1970) evaluated the thirty six single, three-way, and double crosses involving nine unrelated inbred lines at two locations. The average yield of the single cross was greater than that for the three-way crosses and the average of the three-way crosses was greater than that of double crosses. Weatherspoon (1970) hypothesized that this relationship could be explained as a result of more complete utilization of both dominance and epistatic effects in single and three-way crosses. He indicated further that single crosses were more sensitive to environmental conditions than three-way crosses. Weatherspoon (1970) found that the mean square for single crosses was twice as big as that of three-way crosses and the crosses x environments mean square for single crosses was about one and half times larger than that for three-way crosses. Eberhart et al. (1964) used single cross and three-way crosses to predict double cross performance in maize. They found significant hybrid by year interactions for both single crosses and three-way crosses with the hybrid by mean square for single crosses being twice as large as that for three-way crosses. They indicated that average yield of three-way crosses was less than the single crosses yields and this was because recombination in the parental single cross of each three-way cross provided an opportunity for the loss of some of the favorable epistatic combinations.

Eberhart and Hallauer (1968) tested the importance of epistasis in single cross, three-way and double-cross hybrids. They indicated that epistatic effects did not give any average superiority of the single cross over three-way or double crosses and in one of the trials there were no yield differences between single cross and three-way crosses. Springfield (1950) in a study carried out using all single, three-way, and double crosses from four maize inbred lines reported that average three-way cross yield was equal to the average single cross yield. Melchinger et al. (1986) compared single and three-way crosses among flint and dent inbred

lines in six environments and found significant variation in mean performance of all hybrids. When averaged across all environments, they observed that the single crosses significantly out-yielded the three-way crosses, had lower ear moisture and significantly lower plant height than the three-way crosses. The average yield potential of the single cross hybrids was 1.2% higher than that of the three-way crosses. Melchinger et al. (1986) indicated that considering the costs and risks of seed production and stability of yields, three-way crosses could have an advantage over single crosses under marginal conditions.

Saleh et al. (2002) compared ten single, four double, and four three-way crosses and measured yield as well as estimating heterosis and heritability. Mid-parent heterosis for grain yield ranged from 306 to 478% while high-parent heterosis ranged from 281 to 398%. Saleh et al. (2002) reported that heterosis for plant height was moderate (17-63%) with days to silking and days to maturity showing negative heterosis. Saleh et al. (2002) concluded from their study that there were no obvious differences in average performance between single, double, and three-way crosses. Tallury and Goodman (1999) evaluated 60 three-way cross hybrids with different percentages of tropical germplasm and reported that 19 hybrids yielded at least 6.8 Mg ha^{-1}, as much as the lowest yielding single cross check hybrid used in their study. Eight of the high yielding hybrids had between 27-44% and another eight had 59-68% tropical germplasm.

MATERIALS AND METHOS

Germplasm and environments

Thirteen inbred lines were used in this study. These included eleven inbred lines of tropical and subtropical origins (CML343, CML311, CML269, CML270, CML176, CML322, CML405, T39, T35, Y21, Tx601W) and two inbred lines of temperate origins (NC340 and Tx130) (Table 4.1). The thirteen inbred lines were crossed following a NC II design with three testers (Tx114, CML78, and Tx110) and their single cross combinations (CML78 x Tx110, Tx114 x CML78, and Tx114xTx110) to generate single (SC) and three-way cross (TWC) hybrids. The resulting 78 SC and TWC hybrids together with five commercial checks (Pioneer Brand hybrids P30G54 and P32H39,Wilson hybrid W1859W, and Asgrow hybrids RX949W and R953W) and seven experimental hybrids were evaluated in 2003 at Castroville, College Station, Corpus Christi, Granger, and Weslaco in Texas (Table 4.2). Standard cultural and agronomic practices were followed at all locations.

Table 4.1. Inbred lines and testers used to form single and three-way cross hybrids.

Inbred line	Pedigree/Origin	Type
CML343	LPSC3-H17-1-2-3-2-1-##-B-B-B	Tropical
CML311	S89500 F2-2-2-2-B*5	Subtropical
CML269	Pob25STEC1HC13-6-1-1-#-BBB-f	Tropical
CML270	Pob29STEC1HC17-4-1-1-2-1-BB-f	Tropical
CML176	(P63-12-2-1/P7-5-1-1)-1-2-B-B	Subtropical
CML322	Recy 89[L/LMBR]17-B-5-3-1-4-B*4	Subtropical
CML405	POSTA SEQC0-S3-12-1-1-B*11	Tropical
NC340	PX105A x (P306A x H5)	Temperate
T35	INIFAP Mexico	Tropical
T39	INIFAP Mexico	Tropical
Tx130	(((Va35/Tx585)/Va35)/Va35)-B-B-B	Temperate
Y21	Pop 21 INIFAP CIMMYT Mexico	Subtropical
Tx601W	Tx601 yellow converted Tuxpan	Subtropical
Testers		
Tx114	((K55/B73)/B73)	Temperate
CML78	G32 C19MH32-1-#2-B-###-3-B	Subtropical
Tx110	(((((Tx61M x Tx6252)Tx6252^{4}-1-B-B-B	Temperate
CML78 x Tx110		
Tx114 x CML78		
Tx114 x Tx110		

Table 4.2. Locations used to evaluate single and three-way cross hybrids.

Location	Latitude	Longitude	Plot size
Castroville, TX	29°17'N	98°52'W	7.9 x 0.91 m
College Station, TX	30°37'N	96°20'N	6.4 x 0.76 m
Corpus Christi, TX	27°48'N	97°23'W	6.7 x 0.97 m
Granger	30°43'N	97°26'W	7.9 x 0.97 m
Weslaco	26°09'N	97°59'W	7.6 x 0.76 m

Field measurements

The experimental field design used was an alpha lattice (Paterson and Williams, 1976) with 2 replications at Castroville, Granger, and Weslaco, and 3 replications at College Station, Corpus Christi, and Weslaco. Measurements on plot basis were recorded on the following agronomic traits: silking date (days from planting to 50% silking), plant height (distance in cm from the ground to the top of tassel), and ear height (distance in cm from the ground to the main ear-bearing node), root lodging (% plants leaning at an angle greater than 30% from the vertical), stalk lodging (% plants with broken stalks at or below the main ear at maturity), grain moisture (g kg^{-1} moisture of grain at harvest), test weight (kg m^{-3}), grain yield (combine harvested or hand harvested grain weight adjusted to 12.5% grain moisture content and expressed in Mg ha^{-1}), grain texture (visual rating from 1 to 5; 1=flint, 5=dent), and kernel integrity (visual rating 1 to 5; 1 = all ears without splits kernels or damage by insects to 5 = most of the ears with splits and/or insect damage) .

Aflatoxin evaluation

Aspergillus flavus isolate NRRL3557 was used to inoculate plants at College Station, Corpus Christi, and Weslaco. A conidial suspension containing 3 x 10^7 conidia of *A. flavus* in 3 mL distilled water was injected 6 to 10 d after midsilk by the silk channel inoculation technique (Zummo and Scott, 1989). Inoculated ears were hand harvested, shelled, and ground. Quantification of aflatoxin was conducted in 50-g subsamples from each plot with monoclonal antibody affinity columns and fluorescence determination by the Vicam Aflatest (Watertown, MA). Aflatoxin concentration was expressed in nanograms per gram (ng g^{-1}). Aflatoxin concentration was log transformed to equalize variance for statistical analysis.

Statistical analyses

Analysis of variance for each environment and adjusted means were compute with the PROC MIXED procedure (SAS, 1997) considering genotypes as fixed effects and reps and blocks within reps as random effects. Combined analyses of variance across locations were computed using PROC GLM in SAS (SAS, 1997). Analysis was done following the line x tester (L x T) analysis (Kempthorne, 1957). Tests of significance for line, tester, and line x tester mean squares were conducted using the pooled error term in the analysis at each environment. In the analysis across environments, tests of significance for line, tester, and line x tester mean squares were conducted using their respective interaction with the environment as the error term. The genotypes sums of squares were partitioned into sources due to hybrids, checks, a contrast between hybrids and checks. The hybrids source was partitioned into variation due to lines, testers, and the line x tester interaction. The tester source of variation was further partitioned into variation due to inbred line testers, single cross testers, and a contrast between inbred line and single cross testers. In L x T analysis, variance due to lines and testers is equivalent to variation due to general combining ability (GCA) effects while variance due to L x T interaction is equivalent to variation due to specific combining ability (SCA) effects. To compare single cross and three-way cross hybrids a new variable, hybrid type comparison (HTC), was computed per replication as HTC = $[TWC_{(1x2)} - (SC_1 + SC_2)/2]$ where SC_1 and SC_2 are the hybrids of one inbred with tester inbreds 1 and 2 and $TWC_{(1x2)}$ is the three-way cross of the same inbred and single cross tester 1x2 in the same replication. The new variable HTC was subject to analysis of variance in a similar way to the other variables.

For grain yield, aflatoxin concentration, and log transformed aflatoxin concentration, at each environment, and for all traits across environments, GCA (*gi* or *gj*) and SCA (*sij*) effects were estimated as follows:

$$g_i = (y_{i\cdot} - y_{\cdot\cdot})$$

$$g_j = (y_{\cdot j} - y_{\cdot\cdot})$$

$$s_{ij} = (y_{ij} - y_{\cdot\cdot} - g_i - g_j)$$

where y_{ij} is the mean of the hybrid of crossing the i^{th} line with the j^{th} tester, $y_{i\cdot}$ is the mean of all hybrids involving the i^{th} line, $y_{\cdot j}$ is the mean of all hybrids involving the j^{th} tester, and $y_{\cdot\cdot}$ is the mean of all hybrids (Sharma, 1998). Standard errors for GCA and SCA effects were calculated following Cox and Frey (1984) and Sharma (1998). Standard error of GCA, $SE_{GCA} = \{MS_{fl}(f-1)/mflr\}^{0.5}$ or $\{MS_{ml}(m-1)/mflr\}^{0.5}$ for lines or testers, respectively. MS_{fl} and MS_{ml} are the

respective line x location and tester x location mean squares, and f, m, l, r, are the number of lines, testers, locations, and replications, respectively. Standard error of SCA, $SE_{SCA} = \{(MS_{fml})(f-1)(m-1)/mflr\}^{0.5}$. Two tailed *t*-tests were used to test the significance of the GCA and SCA effects where $t = GCA/SE_{GCA}$ or SCA/SE_{SCA}, respectively (Singh and Chaudhary, 1977; Sharma, 1998).

Genotypic and phenotypic correlations were calculated between traits for each environment and across environments considering genotypes as random effects. Repeatability was estimated for each trait per environment and across environments assuming genotypes random. Repeatability was calculated as $R = \frac{\sigma^2 g}{\sigma^2 g + \frac{\sigma^2 e}{r}}$ where $\sigma^2 g$ is the genotypic variance, $\sigma^2 e$ is the error variance and r is the number of replications for a single environment. Across environments, repeatability was calculated as $R = \frac{\sigma^2 g}{\sigma^2 g + \frac{\sigma^2 ge}{e} + \frac{\sigma^2 e}{re}}$ where $\sigma^2 g$ is the genotypic variance, $\sigma^2 ge$ is the genotype x environment variance, $\sigma^2 e$ is the error variance, *e* is the number of environment, and *r* is the number of replications for a single environment. Genotypic and phenotypic correlations and repeatability were calculated using SAS (Holland, 2003).

Additive Main Effects and Multiplicative Interaction (AMMI) analysis of grain yield was carried out to assess the relationship among lines and testers. This analysis was carried out using IRRISTAT (IRRI, 1998) and Biplot v1.1 (Dr. E.P. Smith, Virginia Tech; http://www.stat.vt.edu/facstaff/epsmith.html). Stability analysis of hybrids across locations was conducted with joint linear regression method (Eberhart and Russell, 1966) using IRRISTAT (IRRI, 1998) and SAS.

RESULTS AND DISCUSSION

Single location analysis for grain yield and aflatoxin concentration

There were highly significant differences (P<0.001) between genotypes for grain yield at Castroville (CA), Granger (GR), College Station (CS), and Weslaco aflatoxin inoculated (WE-AF) (Table 4.3), indicating that there was variation between hybrids and checks for grain yield at these locations. There was highly significant (P<0.01) variation among lines and testers within hybrids at CA, GR, CS, and WE-AF (Table 4.3). Significant differences among lines and testers indicate presence of significant GCA effects. The lines accounted for 31.5%, 29.1%, 18.3%, 20.61%, and 45% of the variation among hybrids for grain yield at CA, GR, WE, CS, and WE-AF, respectively. Significant differences for SCA effects as measured by line x tester interaction were found at CA, GR, CS, and WE-AF (Table 4.3). Line x tester interaction contributed most of the variation in grain yield at all the sites (50.4% at CA, 62.1% at GR, 73.4% at WE, 65.7% at CS, and 48.5% at WE-AF). The contrast between inbred line testers and single cross testers for grain yield was significant at GR and WE-AF, suggesting that there were differences between the two types of testers at these two locations. No significant difference was detected for the contrast hybrids between checks for grain yield at all locations, suggesting the hybrids and checks were equal in performance for grain yield at these locations.

There were highly significant differences (P<0.01) among genotypes for aflatoxin concentration at CS, WE-AF, and CC (Table 4.4). Highly significant differences (P<0.001) among hybrids for aflatoxin concentration were observed at WE-AF and CC. There was significant (P<0.05) variation between lines and between testers within hybrids at CS and WE-AF, and between lines at CC (Table 4.4) for aflatoxin concentration. Significant differences among lines and testers indicate presence of significant GCA effects for aflatoxin concentration among both lines and testers. The lines accounted for 22.8%, 19.8%, and 35.1% of the variation among hybrids for aflatoxin concentration at CS, WE-AF, and CC, respectively. SCA effects for aflatoxin concentration were significant only at WE (Table 4.4). Line x tester interaction contributed 61.0% at CS, 71.0% at WE-AF, and 59.8% at CC of the variation among hybrid for aflatoxin concentration. The contrast between inbred line testers and single cross testers for aflatoxin was not significant suggesting that there were no differences between the two types of testers overall. No significant difference was detected for the contrast hybrids vs. checks for grain yield at all locations, suggesting the hybrids and checks were similar in response to

Table 4.3. Analysis of variance for grain yield (Mg ha^{-1}) of single- and three-way crosses at five locations.

Source of variation	df†	Mean squares			df	Mean squares	
		Castroville	Granger	Weslaco		College Station	Weslaco-AF
		Mg ha^{-1}				Mg ha^{-1}	
Rep	1	1.24	10.78***	8.62*	2	9.00**	17.43***
Genotypes	89	2.65***	0.87***	2.53*	89	3.30***	1.81***
Hybrids	77	2.35***	0.96***	1.73	77	3.24***	1.77***
Lines	12	4.76***	1.79***	2.03	12	4.26**	5.11***
Testers	5	6.04***	1.29**	2.20	5	7.16***	1.76*
IL Testers	2	14.83***	0.11	2.00	2	16.46***	1.12
SC Testers	2	0.27	0.66	3.08	2	1.40	0.49
IL vs. SC Testers	1	0.02	4.94***	0.87	1	0.10	5.58**
Line x Tester	60	1.56**	0.77***	1.63	60	2.71**	1.10**
Line x IL Testers	24	1.58**	1.16**	1.52	24	2.61*	0.92
Line x SC Testers	24	1.86**	0.55	1.53	24	2.33	1.31**
Line x IL vs. SC Testers	12	0.73	0.41	2.02	12	3.70*	1.05
Checks	11	4.97***	0.31	8.24***	11	3.70*	2.14***
Hybrids vs. Checks	1	0.08	0.41	2.07	1	3.33	1.45
Error		89	0.78	0.30	1.75	178	1.620.68
Mean (overall)		**8.26**	**5.89**	**7.05**		**6.67**	**4.18**
Mean for hybrids		**8.26**	**5.88**	**7.01**		**6.63**	**4.21**
Mean for checks		**8.32**	**6.02**	**7.32**		**6.96**	**3.99**
LSD (0.05)		**1.76**	**1.09**	**2.63**		**2.05**	**1.32**

*,**,*** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.
†df, degrees of freedom, Weslaco-AF, Weslaco *A. flavus* inoculated experiment.

Table 4.4. Analysis of variance for aflatoxin (ng g^{-1}) and log of aflatoxin of single- and three-way crosses at three locations.

Source of variation	College Station			Weslaco			Corpus Christi		
		Mean squares			Mean squares			Mean squares	
	df†	AF‡	LogAF‡	df	AF	LogAF	df	AF	LogAF
		ng g^{-1}			ng g^{-1}			ng g^{-1}	
Rep	2	201258.43***	8.58***	2	14026.70	0.78	2	7599.05	0.09
Genotypes	89	40147.96**	0.41	89	131129.44***	0.57***	89	27761.72***	0.82***
Hybrids	77	32311.37	0.40	77	137967.14***	0.49***	77	31017.50***	0.77***
Lines	12	47304.80*	0.40	12	170346.61***	1.25***	12	69906.81***	2.06***
Testers	5	67227.32*	0.80	5	230302.51**	0.55	5	24166.88	1.50***
IL Testers	2	25178.04	0.69	2	524627.44***	1.17*	2	13733.44	3.03***
SC Testers	2	100959.93*	0.92	2	39870.91	0.17	2	33510.06	0.44
IL vs. SC Testers	1	83860.63	0.80	1	22515.82	0.05	1	26347.39	0.56
Line x Tester	60	25282.67	0.34	60	122511.70***	0.34	60	23810.53	0.45**
Line x IL Testers	24	27953.09	0.38	24	165051.06***	0.36	24	7314.26	0.45
Line x SC Testers	24	31310.70	0.40	24	76344.92	0.38	24	39277.51***	0.38
Line x IL vs. SC Testers	12	7885.75	0.19	12	129766.56*	0.21	12	25869.08	0.59*
Checks	11	93885.67***	0.54	11	77700.45	0.70**	11	6106.69	1.12***
Hybrids vs. Checks	1	39222.53	0.93	1	187525.72	4.67***	1	15271.41	1.40*
Error	164	25575.26	0.37	174	58302.26	0.27	178	14952.03	0.26
Mean (overall)		**140.39**	**61.66**		**215.67**	**97.72**		**60.73**	**21.88**
Mean for hybrids		**135.45**	**60.26**		**226.45**	**60.26**		**63.68**	**23.44**
Mean for Checks		**171.57**	**64.57**		**146.81**	**45.71**		**41.56**	**14.45**
LSD (0.05)		**257.83**	**9.55**		**389.11**	**6.76**		**197.02**	**6.61**

*,**,*** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.
†df, degrees of freedom
‡ AF, aflatoxin; LogAF, logarithm of aflatoxin accumulation.

aflatoxin at all locations (Table 4.4). Analysis of the log transformed aflatoxin concentration showed significant differences between both genotypes and hybrids at WE-AF and CC (Table 4.4). Log transformed aflatoxin also revealed significant differences between hybrids and checks at WE-AF and CC.

Mean grain yield ranged from 6.05 to 10.51 Mg ha^{-1} at CA, the best hybrid being single cross (SC) CML343 x Tx110 followed by three-way cross (TWC) [CML78 x Tx110] x CML343 (10.03 Mg ha^{-1}). At GR, mean grain yield ranged from 4.15 to 7.23 Mg ha^{-1}. The best hybrid at GR was [Tx114 x Tx110] x T39 followed by CML343 x Tx114 (6.78 Mg ha^{-1}). At WE, the range of grain yield was 4.08 to 8.87 Mg ha^{-1}, with the best hybrid being CML343 x CML78. Mean grain yield at CS ranged from 4.58 to 9.11 Mg ha^{-1}, while at WE-AF mean grain yield ranged from 2.59 to 5.99 Mg ha^{-1}. The best hybrids at CS and WE-AF were T39 x Tx110 (9.11 Mg ha^{-1}) and [Tx114 x Tx110] x CML270 (5.99 Mg ha^{-1}), respectively. Average aflatoxin concentration was highest at WE and lowest at CC. Mean aflatoxin concentration at CS ranged from 3.52 to 518.86 ng g^{-1}. The hybrid with the lowest aflatoxin concentration at CS was CML269 x CML78 (3.52 ng g^{-1}) followed by T39 x Tx110 (20.44 ng g^{-1}). Mean aflatoxin concentration ranged from 14.66 to 1226.89 ng g^{-1} at WE. Three-way cross [Tx114 x Tx110] x CML270 had the lowest aflatoxin concentration (14.66 ng g^{-1}), followed by CML269 x CML78 (20.38 ng g^{-1}) at WE. At CC, mean aflatoxin concentration ranged from 1.00 to 806 ng g^{-1}. Single cross CML269 x CML78 had the lowest aflatoxin concentration (1.00 ng g^{-1}), followed by three-way cross [Tx114 x CML78] x CML269 (3.33 ng g^{-1}).

The observed variability in aflatoxin concentration has been reported in other studies (Lillehoj, et al., 1980; Darrah et al., 1987; Scott and Zummo, 1988; Betrán et al., 2002; Betrán and Isakeit, 2004). The range of aflatoxin levels observed at CS and WE were close to those reported by Betrán at al. (2002) at the same location in diallel study using white maize inbred lines. Some of the lines in the study by Betrán et al. (2002) were also used in this study. Betrán et al. (2002) reported mean aflatoxin concentration ranging from 15.5 to 382.8 ng g^{-1} at CS, and 44.3 to 1235.0 ng g^{-1} at WE. Hybrids CML343 x Tx114, CMl269 x Tx114, and CML176 x Tx114 did not significantly differ in aflatoxin concentration in both studies (Betrán et al., 2002).

Table 4.5. Analysis of variance for grain yield and agronomic traits of three-way and single-cross hybrids across locations.

	Grain yield		Plant height		EH†	Grain moisture		Test weight		RL	Stalk lodging	
Source of variation	df	MS	df	MS	MS	df	MS	df	MS	MS	df	MS
		Mg ha^{-1}		cm			g kg^{-1}		kg m^{-3}	%		%
Environments (E)	4	518.28***	2	231396.31***	90181.70***	3	877.04***	2	12057.81***	2897.12***	1	733.45***
Reps(Env)	7	10.50***	4	894.38***	482.93	5	13.60*	3	3.09	180.85***	2	21.63
Genotypes	89	4.33***	89	366.55***	159.66***	89	12.48**	89	15.80***	155.88	89	25.55
Hybrids	77	3.62***	77	391.13***	155.18***	77	7.14***	77	14.50***	90.54	77	23.90
Lines	12	6.72*	12	1031.16***	404.86***	12	24.98*	12	61.97***	180.62	12	51.22
Testers	5	8.21*	5	459.37	141.55	5	7.36*	5	21.48***	140.72	5	71.13
IL Tester	2	18.11*	2	107.61	177.93	2	16.05	2	49.61*	289.06	2	149.04
SC Tester	2	1.11	2	104.81	52.02	2	1.60	2	3.79	6.42	2	9.05
IL vs. SC Tester	1	2.60	1	1871.99***	247.85	1	1.49	1	0.61	112.63*	1	39.48*
Line x Tester	60	2.62***	60	257.44*	106.39*	60	3.51***	60	4.43	68.34	60	14.49
Line x IL Tester	24	2.65**	24	254.63*	129.19*	24	5.49***	24	5.99	106.02	24	27.66
Line x SC Tester	24	2.34*	24	200.53	83.86	24	1.27	24	2.82	21.22	24	4.17
Line x IL vs. SC	12	3.14	12	376.88*	105.83	12	4.03	12	4.52	87.22	12	8.81
Checks	11	9.53***	11	214.75*	205.37	11	40.59	11	13.24***	527.04	11	37.53
Hybrid vs. Checks	1	1.90	1	143.92	1.62	1	115.75***	1	144.46***	1104.23***	1	21.09
Genotype x E	356	1.68***	178	161.23	86.08	267	7.86***	178	2.98***	119.24***	89	24.94***
Hybrids x E	308	1.56***	154	163.09	75.39	231	3.23***	154	3.12***	68.43***	77	22.69***
Lines x E	48	2.78***	24	144.71	85.36	36	9.26***	24	3.15***	115.43***	12	53.86***
Testers x E	20	2.38***	10	236.28	66.63	15	1.98	10	1.46	100.60***	5	36.07***
IL Tester x E	8	3.70***	4	201.55	68.08	6	4.09***	4	2.03	134.14**	2	73.49**
SC Tester x E	8	1.23	4	376.48	49.91	6	0.66	4	0.50	16.90	2	5.20
IL vs. SC Tester x E	4	2.23	2	92.74	117.73	3	0.15	2	2.15	178.21**	1	22.95
Line x Tester x E	240	1.27**	120	160.66	74.13	180	2.12*	120	3.25***	56.34***	60	15.34***
Line x IL Tester x E	96	1.26*	48	145.76	63.66	72	2.56**	48	3.88***	87.00***	24	24.47*
Line x SC Tester x E	96	1.29	48	198.71	83.69	72	1.71	48	2.80***	17.98	24	6.06
Line x IL vs. SC x E	48	1.19	24	365.99*	87.77	36	2.16*	24	2.79**	92.65**	12	15.65*
Checks x E	44	2.52	22	89.57	129.57	33	39.24	22	1.66	399.52***	11	42.88***
Hybrid vs. Checks x E	4	1.36	2	1008.18**	439.16**	3	16.83*	2	6.99***	816.00***	1	0.60
Error‡	623	1.06	356	153.89	81.29	424	5.03	267	1.36	31.67	178	7.72

*,**,*** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.

† degrees of freedom; EH, ear height; MS, mean squares; RL, root lodging. ‡Error degrees of freedom for root lodging is 356.

Table 4.6. Analysis of variance for aflatoxin concentration and agronomic traits of three-way and single-cross hybrids across locations.

	Aflatoxin		LogAF†	Texture		Kernel integrity		Silking date	
Source of variation	df	MS	MS	df	MS	df	MS	df	MS
		ng g^{-1}			**rating 1-5**		**rating 1-5**		**d**
Environments (E)	2	1570258.20***	29.62***	2	0.52*	1	13.70***	1	4730.92***
Reps(E)	6	74294.72*	3.15***	5	0.31	4	0.66	3	1.14
Genotypes	89	96937.02***	0.98***	89	3.66***	89	2.25***	89	5.53***
Hybrids	77	97075.56***	0.88***	77	3.33***	77	2.13***	77	5.46***
Lines	12	164524.18*	2.32**	12	17.67***	12	7.45***	12	20.88**
Testers	5	169458.30	2.08*	5	0.63	5	4.94**	5	2.88
IL Tester	2	331993.99	3.57	2	3.49	2	7.23*	2	6.77
SC Tester	2	84838.28	1.16	2	0.08	2	4.78	2	0.23
IL vs. SC	1	13626.95	0.92	1	0.99*	1	0.69	1	0.38
Line x Tester	60	77236.89**	0.49*	60	0.60***	60	0.84	60	2.59
Line x IL Tester	24	95509.73*	0.49	24	0.90**	24	1.24	24	4.53
Line x SC Tester	24	66728.28*	0.54*	24	0.36*	24	0.58	24	1.31
Line x IL vs. SC Tester	12	61708.44	0.37	12	0.51*	12	0.53	12	1.27
Checks	11	100880.52*	1.46**	11	5.15***	11	2.94***	11	5.55
Hybrid v Checks	1	41135.33	3.28**	1	12.90***	1	4.03**	1	10.83*
Genotypes x E	178	49531.97***	0.39**	178	0.37***	89	0.63**	89	2.56
Hybrids x E	154	50460.26***	0.38**	154	0.39***	77	0.67***	77	2.41
Lines x E	24	60998.78**	0.67***	24	0.68***	12	0.66	12	4.06
Testers x E	10	77142.93**	0.40	10	1.10***	5	0.30	5	3.05
IL Tester x E	4	119752.24**	0.57	4	1.90***	2	0.15	2	2.61
SC Tester x E	4	48128.83	0.26	4	0.60**	2	0.40	2	0.21
IL vs. SC Tester x E	2	59548.45	0.25	2	0.68*	1	0.42	1	10.39*
Line x Tester x E	120	46161.83**	0.32	120	0.27***	60	0.71***	60	2.02
Line x IL Tester x E	48	52430.98**	0.38*	48	0.36***	24	0.68	24	2.41
Line x SC Tester x E	48	37681.14	0.28	48	0.20	24	0.90***	24	1.76
Line x IL vs. SC x E	24	86392.35**	0.31	24	0.26*	12	0.38	12	1.72
Checks x E	22	38502.42	0.42	22	0.28*	11	0.32	11	3.66
Hybrid vs. Checks x E	2	100442.16**	1.86**	2	0.09	1	0.32	1	4.36
Error	516	32946.50	0.30	445	0.16	356	0.38	267	2.34

*,**,*** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.

† df, degrees of freedom; LogAF, logarithm of aflatoxin accumulation; MS, mean squares.

Combined analysis across locations for grain yield and agronomic traits

There were highly significant differences (P<0.001) between genotypes, hybrids, and lines within hybrids for all traits except root and stalk lodging (Table 4.5). Significant GCA effects among lines were observed for grain yield, grain moisture, and test weight across locations. Significant differences for SCA effects were detected for grain yield, plant and ear height, and grain moisture (Table 4.5). Significant differences were detected for the contrast between hybrids and checks for grain moisture, test weight, and root lodging, suggesting that hybrids and checks were different in performance across locations. Genotype x environment interaction was highly significant (P<0.001) for all traits except plant and ear height. It accounted for 15.7% of total variation for grain yield, 26.3% of grain moisture, 2.0% of test weight, 42.3% of root lodging, and 33.4% of stalk lodging (Table 4.5). Hybrids x environment interaction were significant for all traits except plant and ear height. This indicated that hybrids responded differently at the varying environments for grain yield, grain moisture, test weight, stalk and root lodging, but some of them reacted similarly for plant and ear height. SCA x environment interaction was significant for all traits except plant and ear height.

An AMMI analysis showed that the first two principal components explained 82.8% of the total genotype x location sums of squares (Fig 4.1). A biplot constructed using adjusted grain yield showed differential performance of the inbred lines across locations. Locations College Station, Weslaco-AF, and Castroville, were the most discriminating as shown by their long vectors. Locations College Station and Weslaco were similar in ranking the hybrids as shown by the acute angle and similar orientation. Inbred lines CML176, CML405, Tx601W performed particularly well at Castroville. Inbred lines CML343, NC340, Y21, and T39 performed averagely well at Castroville, Weslaco, and College Station (Fig. 4.1).

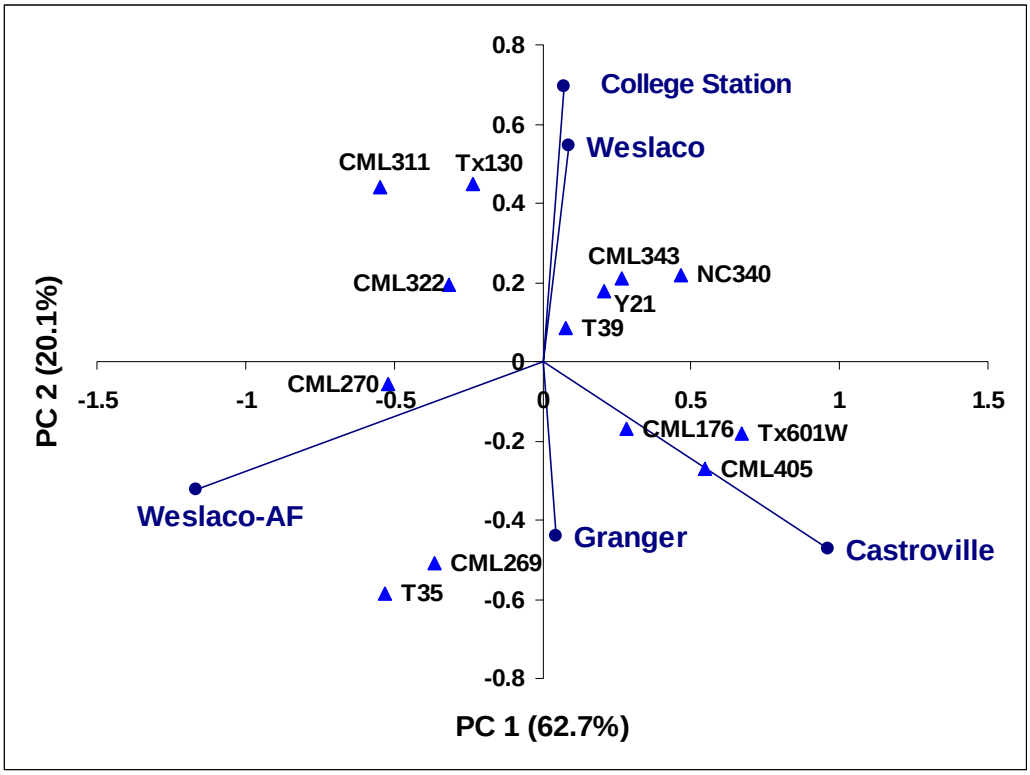

Fig. 4.1. Biplot of first two principal components for grain yield of 13 maize inbred lines in single- and three-way crosses at 5 environments.

Combined analysis for aflatoxin and other agronomic traits

There were significant differences ($P<0.05$) between environments for all traits (Table 4.6). There were highly significant differences ($P<0.001$) between genotypes, hybrids, and lines within hybrids for all traits. Significant GCA effects ($P<0.05$) among lines were observed for aflatoxin concentration, log transformed aflatoxin concentration, grain texture, kernel integrity, and silking date, and among testers for log transformed aflatoxin concentration and kernel integrity across locations. SCA effects were significant for aflatoxin concentration, log transformed aflatoxin concentration, and grain texture (Table 4.6). Genotype x environment interaction was highly significant ($P<0.001$) for aflatoxin concentration, log transformed aflatoxin concentration, grain texture, and kernel integrity and accounted for 23.0% of total variation for aflatoxin concentration (Table 4.6).

Hybrids x environment interaction was significant for aflatoxin concentration, grain texture, and kernel integrity. This indicated that hybrids responded differently to aflatoxin at the different environments. SCA x environment interaction was significant for aflatoxin concentration, texture, and kernel integrity. Significant genotype x environment interaction in aflatoxin studies has been reported in other studies by Darrah et al. (1987) and Betrán et al. (2002). Darrah et al. (1987) indicated that repeatability of genotypic response to aflatoxin concentration within and among environments was very unpredictable. AMMI analysis indicated that 92.8% of the total genotype x environment sums of squares was explained by the first two principal components (Fig. 4.2). The genotype x environment interaction was visualized on a biplot using aflatoxin concentration. The biplot showed that there were differences in response of inbred lines to aflatoxin in different locations. College Station and Corpus Christi were similar in ranking the hybrids for aflatoxin concentration as shown by the acute angle and similar orientation of the vectors. Inbred lines Tx130 had high aflatoxin concentration at College Station and Corpus Christi. Inbred lines NC340, CML405, and Tx601W accumulated more aflatoxin at Weslaco.

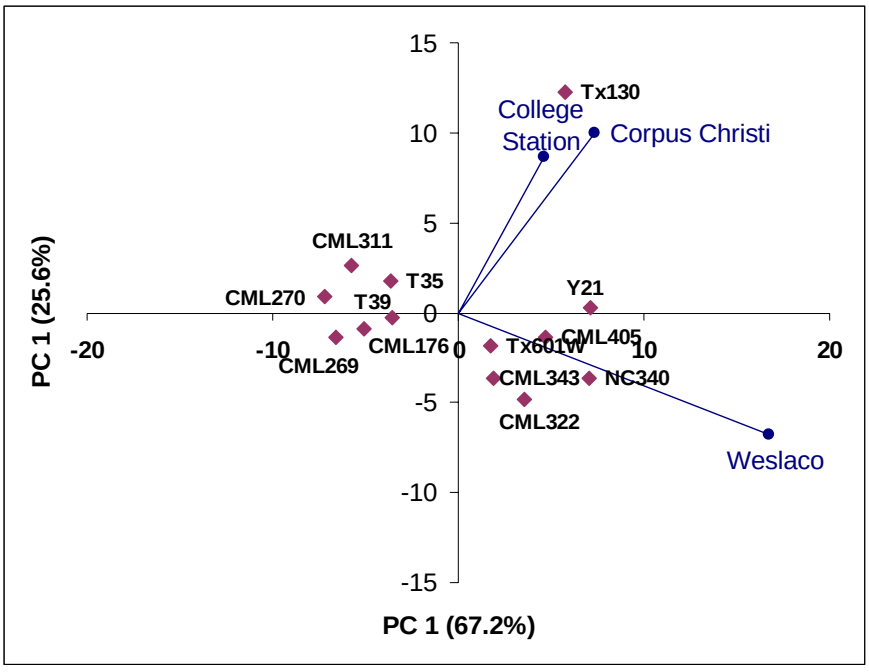

Fig. 4.2. Biplot of first two principal components for aflatoxin concentration of 13 maize inbred lines in single- and three-way crosses at 3 environments.

Table 4.7. Grain yield (Mg ha^{-1}) of white maize lines with inbred and single-cross testers across locations.

		Single cross hybrids			Three-way cross hybrids		
Line	Mean	Tx114	CML78	Tx110	CML78 x Tx110	Tx114 x CML78	Tx114 x Tx110
CML343	**6.77**	6.67	6.52	7.41	7.18	6.70	6.15
CML311	**6.62**	6.96	6.24	7.28	5.53	7.36	6.33
CML269	**6.21**	6.25	5.92	6.08	5.66	6.50	6.82
CML270	**6.54**	6.64	5.80	6.62	6.34	6.79	7.02
CML176	**6.42**	5.99	6.29	6.03	6.56	6.88	6.78
CML322	**6.39**	5.59	6.78	6.34	6.28	6.95	6.40
CML405	**6.19**	6.43	5.66	6.41	6.56	5.73	6.38
NC340	**6.11**	6.50	5.52	6.98	5.49	5.96	6.21
T35	**5.97**	6.33	5.51	6.91	5.40	5.86	5.80
T39	**6.71**	5.69	5.84	7.66	7.24	7.13	6.69
Tx130	**5.84**	5.60	5.69	5.70	6.33	5.66	6.06
Y21	**6.47**	6.17	5.53	7.04	6.72	6.50	6.84
Tx601W	**6.87**	6.81	6.60	6.75	7.19	6.58	7.17
Mean		**6.28**	**6.01**	**6.71**	**6.35**	**6.51**	**6.51**
		Mean (SC†) =	**6.33**		**Mean (TWC) =**	**6.45**	
LSD(0.05) lines =	**0.44**						
LSD(0.05) hybrids =	**0.79**						

†SC = Single-cross; TWC = three-way cross.

Performance and aflatoxin accumulation across locations

Mean grain yield and aflatoxin concentration across locations is presented in Tables 4.7 and 4.8. Tropical inbred line Tx601W had the highest overall yield (6.87 Mg ha^{-1}) in crosses with all testers followed by CML343 (6.77 Mg ha^{-1}), T39 (6.71 Mg ha^{-1}), and CML311 (6.62 Mg ha^{-1}). Among testers, Tx110 had the highest yielding hybrids (6.71 Mg ha^{-1}) followed by Tx114 x CML78 and Tx114 x Tx110 (6.51 Mg ha^{-1}). The highest yielding single cross was T39 x Tx110 (7.66 Mg ha^{-1}) while the highest yield three-way cross was [Tx114 x CML78] x CML311 (7.36 Mg ha^{-1}). Additive Main Effects and Multiplicative Interaction (AMMI) analysis of grain yield was used to assess the relationship among inbreds and testers using the adjusted means, and a biplot was constructed to visualize the relationship. Inbred line testers Tx110, Tx114, and CML78 had different response in combination with exotic lines (Fig. 4.3). The exotic inbreds were positioned across, suggesting variable specific combining ability with the testers. Inbred line CML311 combined well with Tx114 while CML322 combined well with Tx114 x Tx110.

Table 4.8. Aflatoxin accumulation (ng g^{-1}) of white maize lines with inbred and single-cross testers across locations.

Line	Mean	Single cross hybrids			Three-way cross hybrids		
		Tx114	CML78	Tx110	CML78 x Tx110	Tx114 x CML78	Tx114x Tx110
CML343	144.67	200.24	72.35	222.98	118.89	111.56	133.78
CML311	96.19	74.32	80.92	113.07	86.00	72.33	152.00
CML269	67.20	117.36	12.49	54.72	48.28	87.39	79.56
CML270	72.44	44.57	42.75	65.28	79.67	158.67	54.89
CML176	85.02	153.16	28.11	57.87	85.00	48.56	142.22
CML322	152.44	168.89	74.63	268.10	186.27	133.00	95.44
CML405	176.69	163.26	116.22	400.61	47.22	94.67	246.78
NC340	192.99	125.65	132.09	201.48	452.38	209.09	74.56
T35	109.16	123.30	58.55	171.31	93.97	37.78	177.33
T39	105.11	139.89	117.70	45.46	42.44	144.44	141.44
Tx130	243.22	344.19	72.99	119.93	154.11	263.00	506.11
Y21	215.34	99.92	56.00	594.09	81.33	177.00	287.67
Tx601W	161.33	48.20	145.64	119.30	215.78	229.92	212.78
Mean		**137.23**	**78.08**	**185.63**	**126.95**	**135.65**	**177.27**
	Mean (SC†) =		**134.55**	**Mean (TWC) =147.78**			
LSD(0.05) lines	**=**	**155.12**					
LSD(0.05) hybrids	**=**	**163.60**					

†SC = Single-cross; TWC = three-way cross.

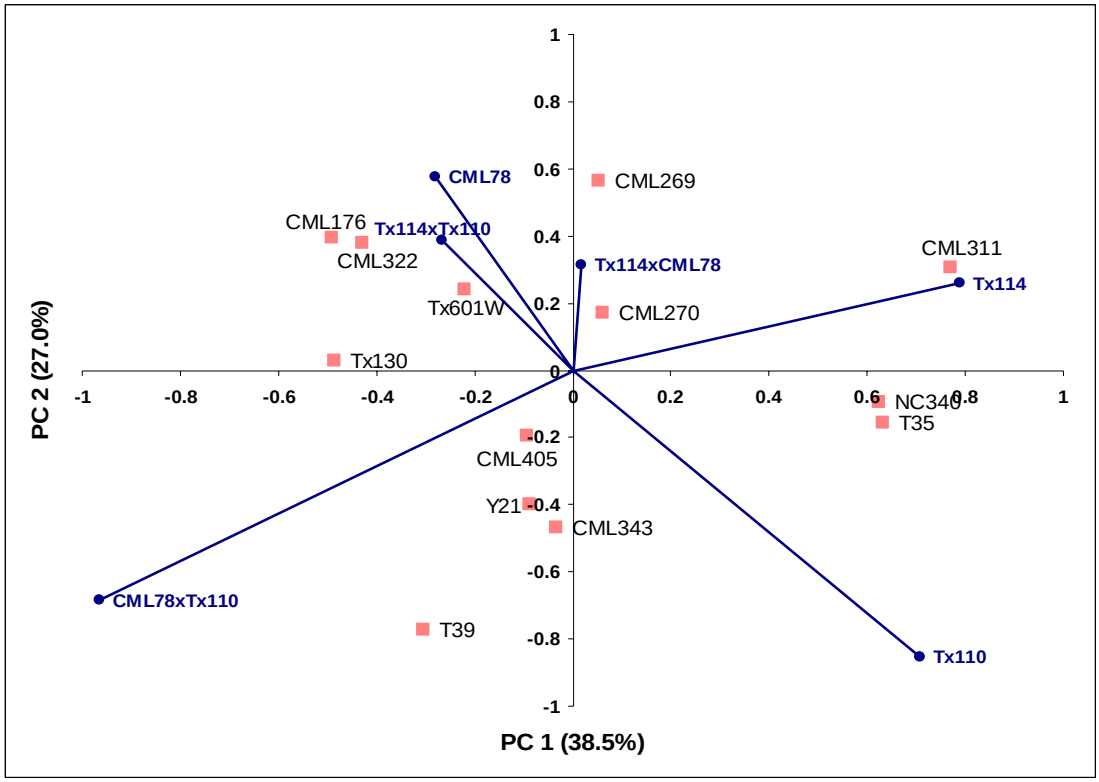

Fig. 4.3. Biplot for grain yield of hybrids between exotic lines and testers across locations.

The inbred line with the lowest amount of aflatoxin concentration in crosses with all testers across locations was CML269 (67.20 ng g^{-1}) followed by CML270 (72.44 ng g^{-1}) (Table 4.8). Among testers, CML78 had the least amount of aflatoxin (78.08 ng g^{-1}). Single cross hybrids CML269 x CML78 and CML176 x CML78 had the lowest aflatoxin concentration (12.49 and 28.11 ng g^{-1}, respectively).

Comparison of three-way and single-cross performance

There were highly significant differences (P<0.001) for grain yield (Table 4.9) and significant differences (P<0.05) for grain texture among hybrids (Table 4.10). Partition of variation among hybrids showed highly significant differences (P<0.01) among lines for grain yield. This indicated that whether a three-way cross (TWC) performs better than the average of the two single crosses (SC) was mostly dependent on the inbred line. Variation in lines

Table 4.9. Analysis of variance for grain yield, aflatoxin, and agronomic traits of three-way and single-cross hybrid type comparison across locations.

Source of variation	df†	Mean squares GY‡	df	Mean squares AF	Mean squares LogAF	df	Mean squares PH	Mean squares EH	df	Mean squares GM
		Mg ha^{-1}		**ng g^{-1}**			**cm**			**g kg^{-1}**
Environment (E)	4	3.56	2	124894.61	0.76	2	11.98	315.13	3	0.76
Reps(E)	7	2.67	6	69514.14	0.42	4	287.77	609.06***	5	8.47*
Hybrids	37	4.03***	37	91149.63	0.60	37	499.59	158.57	37	3.94
Line	12	6.07**	12	94880.51	1.03*	12	905.66*	253.53	12	6.82
Tester	2	3.96	2	18207.70	0.04	2	614.49	8.08	2	6.78
Line x Tester	23	2.32	23	33545.28	0.53	23	383.82	129.09	23	2.11
Hybrids x E	148	1.90*	74	60952.50	0.40	74	325.39	120.42	111	2.92
Line x E	48	2.26*	24	76278.93	0.42	24	338.55	177.00	36	4.24**
Tester x E	8	2.19	4	59995.19	0.89	4	137.00	61.92	6	1.34
Line x Tester x E	92	1.63	46	27692.19	0.34	46	268.45	97.74	69	3.01
Error	259	1.48	212	47936.39	0.46	148	319.80	123.87	175	2.64

*,**,*** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.
†df, degrees of freedom
‡AF, aflatoxin; EH, ear height, GM, grain moisture; GY, grain yield; LogAF, logarithm of aflatoxin accumulation; PH, plant height.

contributed 48.8% of the total sum of squares among hybrids for grain yield. Hybrid x environment interaction was significant ($P<0.05$) for grain yield (Table 4.9). Hybrid x environment interaction was highly significant ($P<0.01$) for grain texture, root lodging, and kernel integrity, and significant ($P<0.05$) for test weight and stalk lodging (Table 4.10). This indicates differences in performance between TWC and SC for grain yield, texture, test weight, kernel integrity, and root and stalk lodging varied between environments. Variation due to line x environment interaction was significant for grain yield (Table 4.9) and grain texture, test weight, root lodging, and stalk lodging (Table 4.10), suggesting that the lines contributed to variation among hybrids in varying proportions in the different environments.

Inbred line Tx601W in crosses with SC testers produced, on average, lower yielding TWC than SC (-0.97 Mg ha^{-1}) (Table 4.11). Inbred lines T35 (0.65 Mg ha^{-1}) had higher yielding TWC on average (Table 4.11). Inbred lines CML176, T39, Tx130, and Y21 produced higher yielding TWC hybrids with all the testers (Table 4.11; Fig. 4.4). Single cross tester CML78 x Tx110 on average produced lower yielding TWC (-0.28 Mg ha^{-1}) while Tx114 x CML78 produced higher yielding TWC (0.27 Mg ha^{-1}). Inbred line CML405 had TWC with lower aflatoxin than the SC (Table 4.11, Fig. 4.5). Among testers SC tester CML78 x Tx110 had TWC hybrids with lower aflatoxin (Fig. 4.5). Weatherspoon (1970) reported average yield superiority of SC over TWC. In a study involving SC, double cross (DC), and TWC hybrids, Lynch et al. (1973) reported that average yield of SC hybrids was significantly greater than the average of TWC hybrids although there was no difference in average stability of the different types of hybrids. Average yield potential of SC hybrids was 1.2% higher than that of TWC hybrids of flint and dent inbred lines (Melchinger et al., 1986). For forage yield in maize, Melchinger et al. (1987) reported SC hybrids to have 3.4% higher dry matter yield of grain than TWC hybrids. In tropical maize, Saleh et al. (2002) did not find differences in average performance between single and three-way crosses.

Table 4.10. Analysis of variance for agronomic traits of three-way and single-cross hybrid type comparison across locations.

	Texture		Test weight		Silking date		Root lodging		Stalk lodging		Kernel integrity	
Source of variation	df†	MS‡	df	MS	df	MS	df	MS	df	MS	df	MS
		rating 1-5		**Kg m^{-3}**		**d**		**%**		**%**		**rating 1-5**
Environment (E)	2	0.68*	2	2.74	1	16.46*	2	410.92***	1	27.59	1	0.86
Reps(E)	5	0.21	3	7.05	3	8.01*	4	6.73	2	6.53	4	0.72
Hybrids	37	0.81*	37	8.08	37	2.39	37	88.57	37	13.33	37	1.09
Line	12	0.84	12	13.50	12	2.14	12	165.77	12	20.66	12	1.19
Tester	2	0.22	2	2.35	2	2.49	2	36.63	2	6.69	2	2.38
Line x Tester	23	0.68**	23	5.92	23	2.38	23	37.89	23	10.13*	23	0.86
Hybrids x E	74	0.51***	74	7.97*	37	2.57	74	73.66***	37	14.07*	37	1.30***
Line x E	24	0.54**	24	10.89*	12	3.43	24	135.35***	12	33.87***	12	0.94
Tester x E	4	1.22**	4	4.69	2	0.48	4	57.58	2	1.98	2	2.71*
Line x Tester x E	46	0.28	46	6.56	23	1.18	46	38.43	23	4.81	23	0.75
Error	185	0.21	111	5.56	111	2.57	148	38.98	74	7.69	148	0.45

*,**,*** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.
†df, degrees of freedom
‡AF, aflatoxin; EH, ear height, GM, grain moisture; GY, grain yield; LogAF, logarithm of aflatoxin accumulation; PH, plant height.

Table 4.11. Comparison of three-way crosses and single-cross mean performance [TWC – (SC1+SC2)/2] for grain yield and aflatoxin concentration across environments.

	Grain yield				Aflatoxin			
Line	Mean	CML78 x Tx110	Tx114 x CML78	Tx114 x Tx110	Mean	CML78 x Tx110	Tx114 x CML78	Tx114 x Tx110
	t ha^{-1}				**ng g^{-1}**			
CML343	-0.23	0.14	-0.16	-0.68	-40.59	-31.39	-24.22	-66.15
CML311	-0.39	-1.10	0.80	-0.89	5.82	-45.47	31.03	31.91
CML269	0.18	-0.29	0.42	0.42	20.51	22.07	28.19	11.25
CML270	0.30	-0.04	0.27	0.67	62.72	6.20	147.20	34.78
CML176	0.60	0.69	0.65	0.45	18.52	50.11	1.03	4.41
CML322	0.29	-0.41	0.57	0.71	5.62	115.83	4.53	-103.49
CML405	0.01	0.32	-0.57	0.27	-110.90	-178.30	-82.89	-71.52
NC340	-0.57	-1.05	-0.34	-0.32	91.91	189.53	16.34	69.85
T35	-0.60	-0.75	-0.42	-0.64	-36.44	-74.24	-60.30	25.21
T39	0.65	0.51	1.16	0.28	14.78	-19.47	67.36	-3.56
Tx130	0.43	0.68	0.21	0.39	103.40	90.28	39.61	180.31
Y21	0.54	0.59	0.85	0.18	-62.94	-161.05	66.36	-94.12
Tx601W	-0.97	-2.92	0.15	0.24	72.08	-39.35	162.85	136.94
Mean		**-0.28**	**0.27**	**0.06**		**-6.13**	**30.55**	**11.99**
LSD (0.05) hybrids		**0.98**				**LSD (0.05) hybrids**	**203.42**	

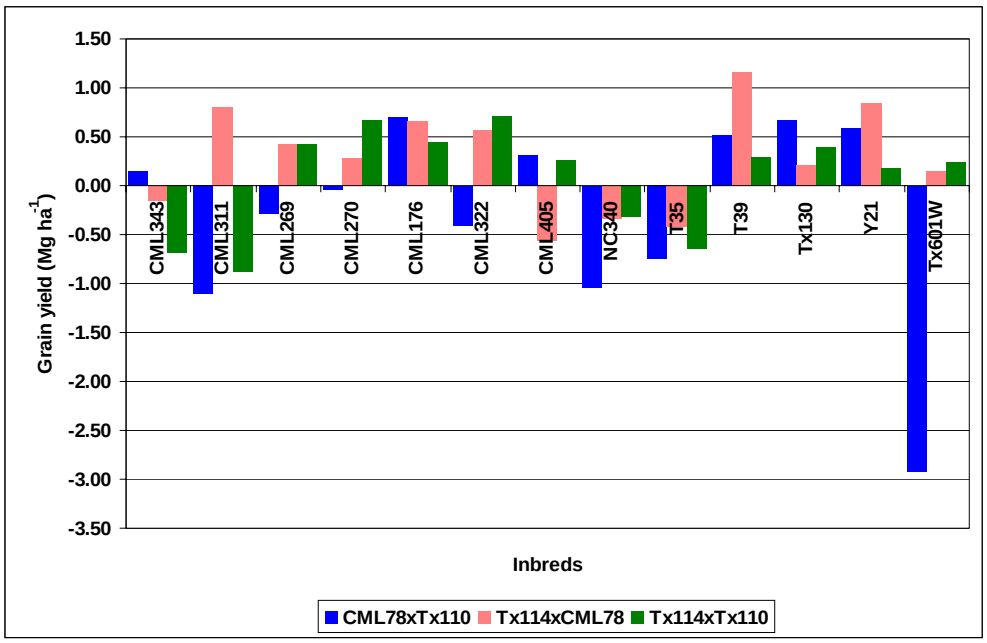

Fig. 4.4. Relative performance of SC and TWC (TWC-SC) for grain yield across locations.

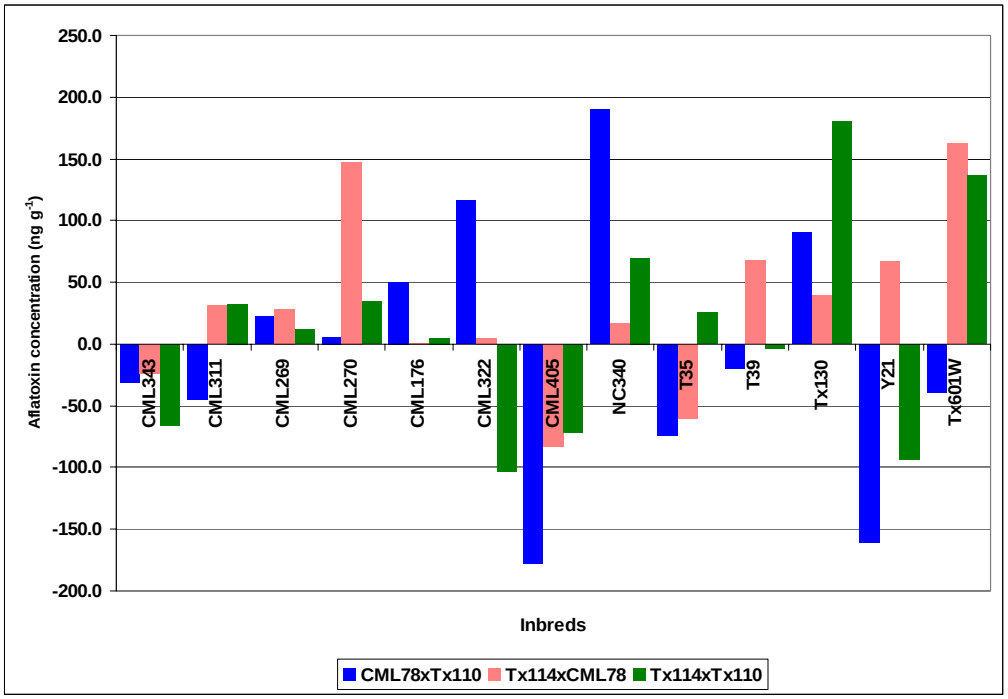

Fig. 4.5. Relative performance of SC and TWC (TWC-SC) for aflatoxin concentration across locations.

Additive Main Effects and Multiplicative Interaction (AMMI) analysis was used to assess how the inbreds related with the SC testers, and a biplot was constructed to visualize the relationship. Inbred line testers Tx130, combined well with [CML78 x Tx110] to produce higher yielding TWC compared to the SC but NC340 and T35 produced lower yielding TWC with the same tester (Fig. 4.6). Inbred lines Y21 and T39 combined with all the testers to produce higher yielding TWC, but some lines produced mostly lower yielding TWC with these testers (Fig. 4.6). This supports the results of the analysis of variance that indicated significant variation among lines for the comparison between TWC and SC for grain yield.

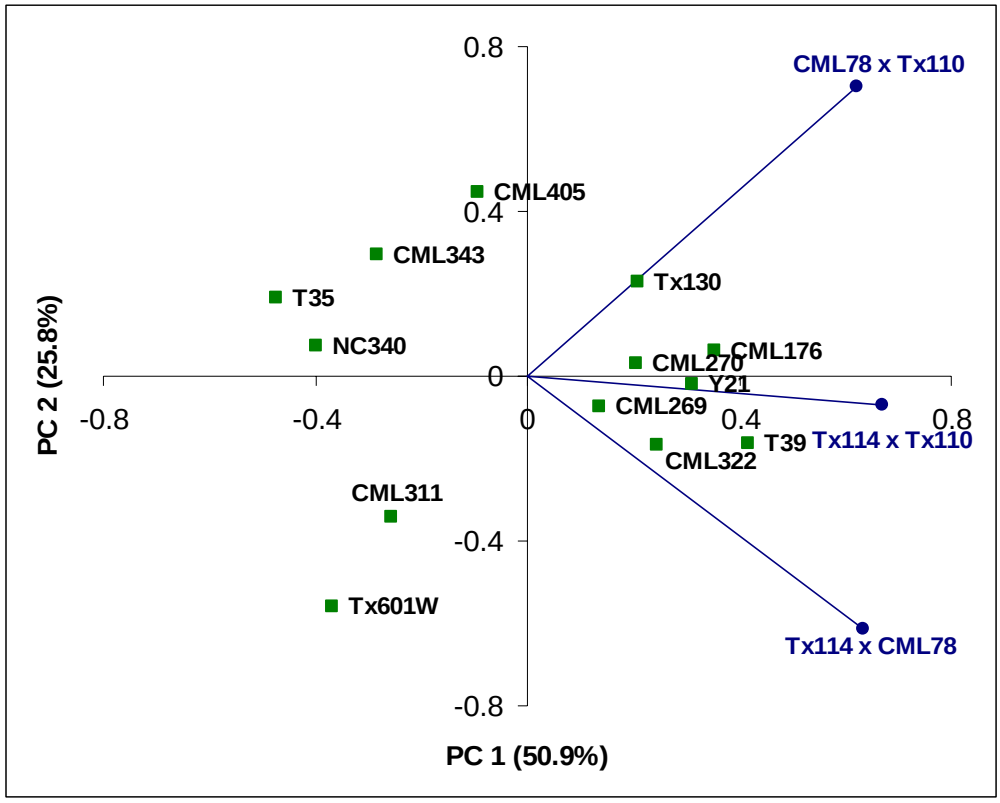

Fig. 4.6. Biplot showing inbred relationship with SC testers for grain yield.

General combining ability for grain yield, aflatoxin accumulation and agronomic traits

General combining ability effects varied across locations. Inbred line Tx601W had the highest positive GCA effect for grain yield at CA (1.27 Mg ha^{-1}) followed by CML343 (0.65 Mg ha^{-1}) (Table 4.12). Inbred line T39 had the best GCA effect for grain yield at CS and GR (0.63 and 0.55 Mg ha^{-1}, respectively) while CML270 had the best GCA at WE-AF (0.77 Mg ha^{-1}). Among testers, Tx110 had the highest positive GCA effect for grain yield at CA (0.74 Mg ha^{-1}), WE (0.37 Mg ha^{-1}), and CS (0.73 Mg ha^{-1}) (Table 4.12). Positive GCA effect indicates that both the inbred lines and testers contributed good alleles for grain yield. Inbred lines with good GCA effect for aflatoxin resistance were CML269 (-68.27 ng g^{-1}) at CA, CML270 (-125.60 ng g^{-1}) at WE-AF, and CML176 (-44.72 ng g^{-1}) at CC (Table 4.12). Inbred line tester CML78 had the best GCA for aflatoxin resistance at CS (-47.63 ng g^{-1}), WE-AF (-125.60 ng g^{-1}), and CC (-28.22 ng g^{-1}). These inbred lines and testers with good GCA effect for aflatoxin resistance contributed to reduce aflatoxin concentration in the hybrids. Inbred line CML176 had consistently good GCA effect for aflatoxin resistance at all three locations, and this agreed with results reported by Betrán et al. (2002), who also reported CML176 to have good GCA effect for aflatoxin resistance at the same three locations. However, the results in this study for inbred lines CML269, CML322, and Tx114 differed from those reported by Betrán et al. (2002). Whereas in this study CML269 had a good GCA effect for aflatoxin resistance at all locations, in the study by Betrán et al. (2002), it had a positive GCA effect at CS. In this study, Tx114 showed good GCA effect for aflatoxin resistance at CS and CC but was reported to have positive GCA effect at all locations (Betrán et al, 2002). These differences could be as a result of significant GCA x environment interaction as some lines and testers showed positive GCA effect at one location and negative GCA effect at another location (Table 4.12).

Across locations, inbred lines Tx601W and CML343 had positive and significant GCA effects for grain yield (0.45 and 0.39 Mg ha^{-1}, respectively) (Table 4.13). Inbred line NC340 had the highest negative GCA effect for grain moisture. The smallest GCA effect for plant height, ear height, and silking date was detected for inbred line CML322. Thus, inbred line CML322 contributed alleles for shorter plant height, low ear placement, and earlier flowering. Among testers, Tx110 had the best GCA for grain yield (0.33 Mg ha^{-1}). Inbred lines CML269 (-72.22 ng g^{-1}) and CML270 (-67.04 ng g^{-1}) had the best GCA effect for aflatoxin resistance among the lines. Among testers, CML78 had the best GCA effect (-67.72 ng g^{-1}) for aflatoxin resistance across locations.

Table 4.12. General combining ability effects (GCA) of inbred lines and testers for grain yield and aflatoxin at five locations.

	Grain yield					Aflatoxin			Antilog Aflatoxin		
	CA†	GR	WE	CS	WE-AF	CS	WE-AF	CC	CS	WE-AF	CC
	Mg ha^{-1}					**ng g^{-1}**					
Inbred lines											
CML343	0.67**	0.20	0.51	0.60*	0.07	-3.17	59.69	-38.72	3.02	48.66	-29.57
CML311	-0.46	-0.06	0.38	0.50	0.72***	17.92	-111.18*	-34.61	-17.34	-86.89	-24.71
CML269	-0.18	-0.11	-0.45	-0.59*	0.46*	-68.27*	-102.59	-41.00	-56.03	-77.83	-34.06
CML270	-0.28	0.01	0.18	-0.08	0.77***	-26.02	-125.60*	-44.22	-5.10	-94.46	-24.22
CML176	0.33	0.32*	0.32	-0.29	-0.30	-33.23	-77.89	-44.72	-23.81	-111.07	-33.59
CML322	-0.31	-0.23	0.02	0.13	0.33	-43.53	91.99	-6.89	-34.48	85.75	-12.45
CML405	0.51*	0.00	-0.60	-0.04	-0.73***	4.32	88.14	24.33	18.00	-11.52	18.97
NC340	0.26	-0.59***	0.38	-0.44	-0.76***	-44.30	139.91*	52.39	-22.02	148.51	15.65
T35	-0.69**	-0.10	-0.79**	-0.87**	0.32	-13.27	-73.31	0.33	-8.13	-64.97	11.70
T39	0.26	0.55***	0.12	0.63*	0.10	-8.59	-55.50	-37.72	3.68	-25.84	-25.31
Tx130	-1.04***	-0.63***	-0.37	-0.22	-0.49**	116.43**	13.54	178.11***	74.28	15.13	121.65
Y21	0.09	0.31*	0.03	0.41	-0.33	82.55*	122.10*	15.83	64.41	138.55	27.33
Tx601W	1.27***	0.48**	0.41	0.39	-0.23	28.73	46.05	-34.64	9.80	59.97	-17.13
S.E (g_i)	**0.25**	**0.15**	**0.37**	**0.30**	**0.19**	**36.22**	**54.68**	**27.69**	-	-	-
Testers											
Tx114	0.17	-0.24*	0.00	-0.33	-0.02	-18.43	23.94	-13.56	8.28	0.28	-4.57
CML78	-0.91***	-0.13	-0.20	-0.51**	-0.38**	-47.63*	-122.32***	-28.22	-38.37	-87.45	-19.00
Tx110	0.74***	-0.22*	0.37	0.73***	0.00	3.31	129.28***	7.75	-9.25	100.35	18.61
CML78xTx110	-0.21	0.16	-0.39	-0.12	0.04	-46.68*	-11.97	0.86	-35.01	-9.10	-12.32
Tx114xCML78	0.15	0.43***	-0.10	-0.07	0.25*	47.81*	-44.96	-11.79	43.15	-15.06	-9.10
Tx114xTx110	-0.02	0.00	0.27	0.26	0.09	54.37*	15.70	42.85*	25.55	3.56	23.97
S.E (g_j)	**0.16**	**0.10**	**0.24**	**0.19**	**0.12**	**23.38**	**35.30**	**17.87**	-	-	-

*,**,*** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.

†CA, Castroville; CC, Corpus Christi; CS, College Station; WE, Weslaco; WE-AF, Weslaco *A. flavus* inoculated.

Table 4.13. General combining ability effects (GCA) of inbred lines and testers for grain yield, aflatoxin, and agronomic traits across locations.

	GY†	GM	AF	LogAF	PH	EH	TW	RL	SL	SD	TXT	KI
	Mg ha^{-1}	**g kg^{-1}**	**ng g^{-1}**		**cm**		**kg m^{-3}**	**%**		**d**	**rating 1-5**	
Inbred lines												
CML343	0.39*	-0.04	3.85	-10.57***	2.62*	-0.80	-1.34***	-0.44	-0.99	1.44***	0.20*	-0.15
CML311	0.24	0.02	-42.59	-24.72***	2.11*	4.63***	-0.74*	-1.78	-1.21	-0.23	-0.43***	-0.23*
CML269	-0.17	0.98*	-72.22*	-46.23***	2.17*	2.11	0.97***	0.67	2.26*	-0.60	-0.80***	-0.62***
CML270	0.16	0.43	-67.04*	-30.97***	-2.39*	2.72	1.55***	-0.05	2.80**	-0.96**	-0.96***	-0.77***
CML176	0.05	0.56	-54.54	-43.55***	4.36***	0.86	1.71***	3.65*	1.89	0.43	-0.65***	-0.36**
CML322	0.01	-0.16	13.47	-1.91***	-9.15***	-7.08***	-0.44	-1.29	-0.44	-1.29**	-0.26*	-0.08
CML405	-0.18	-0.22	37.24	9.86***	-1.20	-0.62	-2.45***	-2.46	-0.98	1.10**	0.81**	0.07
NC340	-0.28	-1.39***	57.94	18.66***	-2.34*	-3.09*	-0.76**	-1.07	0.76	-0.24	0.57**	0.49***
T35	-0.41*	0.70	-29.27	-6.45***	-1.78	-3.57*	0.67*	0.53	-0.62	-0.84*	-0.04	0.29*
T39	0.33	0.64	-35.22	-13.01***	10.58***	4.00**	0.57*	3.58*	-0.50	0.68	-0.22*	-0.03
Tx130	-0.54**	-1.03*	103.25**	77.30***	-3.80*	-1.99	1.75***	2.03	-1.17	-0.69	0.74***	0.81***
Y21	0.09	-0.05	76.18*	63.71***	-2.71	-0.22	-0.87**	-2.26	-1.14	0.28	0.89***	0.59***
Tx601W	0.45*	-0.66	13.42	11.82***	8.81***	4.60***	-0.93**	-1.66	-0.99	1.39***	0.23*	0.01
S.E *(g_i)*	**0.19**	**0.40**	**32.29**	**0.29**	**1.80**	**1.38**	**0.28**	**1.68**	**1.44**	**0.36**	**0.11**	**0.13**
Testers												
Tx114	-0.10	0.30*	-1.70	0.97***	-0.88	0.03	0.55***	1.03	0.61	-0.28	0.01	-0.03
CML78	-0.44***	0.24*	-67.72**	-36.21***	-3.30	-1.62	0.17	2.04*	2.04*	0.45*	-0.14	-0.42***
Tx110	0.33**	-0.39**	47.02*	21.01***	-1.90	-0.27	-0.96***	-1.64	-1.23	0.06	0.06	0.26***
CML78xTx110	-0.10	-0.22	-17.56	-17.21***	2.75	0.06	-0.01	-0.10	-0.48	-0.06	-0.04	0.02
Tx114xCML78	0.13	-0.03	-3.76	7.27***	2.76	0.17	0.20	-0.44	-0.13	-0.12	0.09	-0.17**
Tx114xTx110	0.13	0.09	37.17	20.08***	0.53	1.50	0.06	-0.80	-0.70	-0.03	0.08	0.31***
S.E *(g_j)*	**0.12**	**0.12**	**23.44**	**0.13**	**1.48**	**0.79**	**0.13**	**0.97**	**0.76**	**0.20**	**0.09**	**0.06**

*,**,*** Indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively.

†AF, aflatoxin; EH, ear height; GM, grain moisture; GY, grain yield; KI, kernel integrity; LogAF, logarithm of aflatoxin accumulation; PH, plant height; RL, root lodging; SD, silking date; SL, stalk lodging; TW, test weight; TXT, texture.

Table 4.14. Specific combining ability (SCA) effects for aflatoxin concentration (ng g^{-1}) across locations.

	Single cross hybrids			Three-way cross hybrids		
	Tx114	CML78	Tx110	CML78xTx110	Tx114xCML78	Tx114xTx110
CML343	56.97	-3.49	33.96	-6.97	-27.75	-46.16
CML311	-21.45	50.62	-32.32	10.21	-21.04	20.55
CML269	51.91	16.38	-60.44	-3.91	27.02	-24.38
CML270	-27.31	34.72	-57.93	25.65	90.32	-58.89
CML176	67.51	10.51	-76.20	17.25	-31.56	19.05
CML322	17.48	-14.15	68.93	44.17	-15.72	-94.16
CML405	-15.67	10.24	175.96**	-112.40	-79.94	28.37
NC340	-72.18	0.65	-42.99	266.78***	13.98	-159.68*
T35	14.51	14.48	15.31	1.14	-67.10	28.21
T39	37.35	81.57	-106.06	-44.60	39.10	-0.80
Tx130	102.47	-102.70	-169.95**	-69.66	21.22	225.18***
Y21	-114.34	-89.88	331.92***	-118.72	-36.32	33.90
Tx601W	-101.73		-84.67		83.34	24.35
SE (*ij*) =	**62.81**					

Specific combining ability for aflatoxin concentration across locations

Specific combining ability for aflatoxin concentration is presented in Table 4.14. Among the SC, the cross that showed significant specific combining ability for reduced aflatoxin concentration was Tx130 x Tx110 (-169.95 ng g^{-1}). Other crosses showing high specific combining ability for lower aflatoxin concentration were Y21 x Tx114 (-114.34 ng g^{-1}), Tx130 x Tx110 (-106.06 ng g^{-1}), and Tx130 x CML78 (-102.70 ng g^{-1}). Crosses CML405 x Tx110 and Y21 x Tx110 showed high specific combining ability for increased aflatoxin concentration (Table 4.14). Among TWC, the cross [Tx114 x Tx110] x NC340 showed high specific combining ability for reduced aflatoxin concentration (-159.68 ng g^{-1}). Crosses [CML78 x Tx110] x NC340 and [Tx114 x Tx110] x Tx130 had high specific combining ability for increased aflatoxin concentration (Table 4.14).

Repeatability of traits

Repeatability for grain yield was varied across environments (Table 4.15). Repeatability for grain yield was high at CA (0.71 ± 0.06), GR (0.73 ± 0.06), and WE-AF (0.68 ± 0.06), medium at CS (0.52 ± 0.09), and low at WE (0.31 ± 0.14). Aflatoxin concentration had medium repeatability at CS, WE-AF, and CC (Table 4.14). Grain moisture had high repeatability at CA and GR, but very low repeatability at WE and CS. Grain texture, test weight, and kernel integrity had high repeatability at all locations. Differences between repeatability estimates for the same trait measured at different locations were probably due to larger error variances at some of the locations, leading to lower repeatability estimates. Across locations, grain yield, grain moisture, plant height, ear height, silking date, root and stalk lodging had low repeatability (Table 4.15). This suggests that actual estimates of heritability for these traits will be low. These low repeatability values also indicate the strong environmental influence on these traits. A study by Saleh et al. (2002) with tropical maize single, double, and three-way cross hybrids reported moderate heritability for grain yield (41%), low heritability for plant height (25.8%) and ear height (33.0%).

Genotypic and phenotypic correlation among traits

Correlations between grain yield, aflatoxin, and other traits across locations are presented in Table 4.16. Grain yield had a positive genetic correlation (0.37*) with plant height and negative genetic correlation with root lodging (-0.50*) and stalk lodging (-0.67*). Grain yield had a positive low non-significant genetic correlation (0.27) and very low negative phenotypic correlation with aflatoxin concentration (Table 4.15). Aflatoxin had a positive genetic correlation with grain texture (0.83**) and kernel integrity (0.92**) (Table 4.16). Betrán et al. (2002) reported positive phenotypic correlation coefficient between aflatoxin and grain texture at CS and CC but a negative correlation at WE in white maize inbreds. A negative phenotypic correlation between grain yield and aflatoxin concentration has also been reported in other studies (Betrán et al., 2002; Betrán and Isakeit, 2004).

Table 4.15. Repeatability on mean basis for grain yield, aflatoxin, and other agronomic traits at each location and across locations.

Trait	Castroville	Granger	Weslaco	College Station	Weslaco-AF†	Corpus Christi	Across
Grain yield	0.71 ± 0.06	0.73 ± 0.06	0.31 ± 0.14	0.52 ± 0.09	0.68± 0.06	-	0.32± 0.06
Aflatoxin	-	-	-	0.41 ± 0.11	0.56 ± 0.08	0.46 ± 0.10	0.50 ± 0.09
LogAF	-	-	-	0.13 ± 0.17	0.54 ± 0.09	0.70 ± 0.06	0.61 ± 0.07
Texture	-	-	-	0.89 ± 0.03	0.94 ± 0.01	0.89 ± 0.02	0.83 ± 0.03
Grain moisture	0.94 ± 0.03	0.88 ± 0.03	0.05 ± 0.20	0.19 ± 0.16	-	-	0.15 ± 0.06
Test weight	0.91 ± 0.02	0.87 ± 0.03	0.85 ± 0.04	-	-	-	0.83 ± 0.03
Plant height	0.59 ± 0.09	0.51 ± 0.11	-	0.41 ± 0.11	-	-	0.32 ± 0.07
Ear height	0.34 ± 0.15	0.29 ± 0.16	-	0.50 ± 0.10	-	-	0.27 ± 0.07
Root lodging	0.71 ± 0.06	-	0.14 ± 0.19	0.18 ± 0.15	-	-	0.14 ± 0.11
Stalk lodging	0.76 ± 0.05	0.45 ± 0.13	-	-	-	-	0.05 ± 0.21
Kernel integrity	-	-	0.73 ± 0.05	-	-	0.74 ± 0.05	0.73 ± 0.06
Silking date	-	-	0.58 ± 0.09	-	0.55 ± 0.08	-	0.39 ± 0.09

†*A. flavus* inoculated experiment

Table 4.16. Genetic (upper diagonal) and phenotypic correlations (below diagonal) between grain yield and agronomic traits across environments.

	GY†	PH	EH	SD	RL	SL	GM	TWT	TXT	KI	AF	LogAF
GY		0.37*	0.10	0.06	-0.50*	-0.67*	-0.26	-0.20*	0.13	0.15	0.27	0.37
PH	0.10		0.61**	0.52**	0.78*	0.49	0.03	0.05	0.00	-0.06	-0.14	-
EH	-0.02	0.53**		0.54**	0.91*	0.55	0.34	0.11	-0.48*	-0.47	-	-
SD	-0.09	0.10	0.09		0.32*	-	0.48*	-0.44*	0.02	-0.29	-	-
RL	-0.21*	-0.02	0.04	0.75*		-	-	0.86*	-0.64*	0.64	-	-
SL	-0.09	0.03	-0.02	-0.08	-0.08		0.77	-	-	-	-	-
GM	0.28	-0.09	0.02	0.00	0.12	-0.06		0.39*	-0.97*	-0.94	-	-
TWT	0.06	0.06	0.10	-0.09	0.08	0.18	-0.04		-0.51**	-	-	-
TXT	-0.04	0.06	-0.11	0.00	-0.38*	-0.21*	-0.20	-0.29*		0.88	0.83**	0.90**
KI	-0.17	-0.02	-0.10	-0.13	-0.09	-0.16	-0.16	-	0.59		0.92**	0.91**
AF	-0.03	0.00	-	-	-	-0.24	-	-	0.23	0.38**		0.90**
LogAF	0.00	-	-	-	-	-	-	-	0.33	0.46	0.72**	

†AF, aflatoxin; EH, ear height; GM, grain moisture; GY, grain yield; KI, kernel integrity; LogAF, logarithm of aflatoxin accumulation; PH, plant height; RL, root lodging; SD, silking date; SL, stalk lodging; TW, test weight; TXT, grain texture.

Through singular value decomposition (SVD) of a genotype by trait two-way table, phenotypic correlations among traits were visualized using a biplot. The first two principal components explained 53.0% of the total variation (Fig. 4.7). Aflatoxin concentration, grain texture, and log aflatoxin concentration were positively correlated. Grain moisture, and root lodging were highly correlated and both showed negative correlation with grain yield and aflatoxin concentration. Plant height had a tight angle with ear height and silking date, showing positive correlation between these traits.

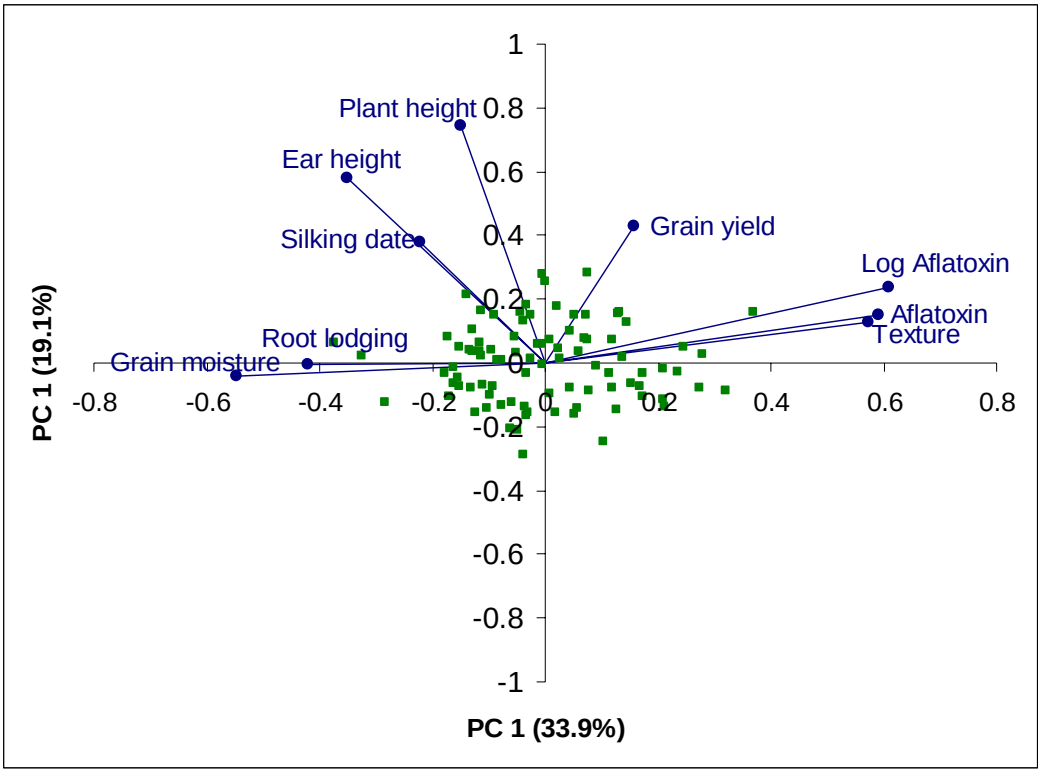

Fig. 4.7. Single value decomposition biplot showing correlations among traits across locations.

Stability of grain yield and aflatoxin

Stability analysis revealed that inbred line T39 was the most stable (b = 1.01) for grain yield (Table 4.17). This inbred line had good yield and was the third highest yielding line (6.71 Mg ha^{-1}) in crosses with all testers across locations. Inbred lines CML343 (b = 1.15) and Y21 (b = 1.09) also showed good stability parameters. Stability of aflatoxin was estimated using the antilogarithm of the logarithmic mean. Most of the lines did not show good stability parameters for aflatoxin concentration. Lines CML270 and CML269 that had good GCA effects for aflatoxin concentration exhibited a very small slope (Table 4.17). Inbred line T39 had slope b = 1.02, but a relatively high mean squared deviation and it showed consistently negative GCA effects for aflatoxin concentration at all locations and across environments. This line could be considered as stable for lower aflatoxin concentration. Although inbred line Y21 had good stability parameters, it showed positive GCA effects for aflatoxin concentration. Stability of aflatoxin concentration reported here should be taken with caution because of the few locations used in the study. To get more indicative results would require testing at more locations and probably over seasons.

Table 4.17. Stability of grain yield and aflatoxin concentration of 13 inbred lines.

	Grain Yield		Aflatoxin	
	b†	σ^2_{di}	b	σ^2_{di}
CML343	1.15	0.01	1.80	27.11
CML311	0.77	0.15	0.46	430.13
CML269	0.80	0.11	0.58	0.76
CML270	0.76	0.05	0.32	519.38
CML176	1.13	0.10	0.22	488.01
CML322	0.87	0.05	2.12	820.00
CML405	1.23	0.16	1.19	15.03
NC340	1.28	0.11	1.82	3063.85
T35	0.70	0.09	0.37	37.55
T39	1.01	0.08	1.02	108.32
Tx130	0.90	0.11	0.45	9.68
Y21	1.09	0.08	1.02	17.41
Tx601W	1.32	0.05	1.63	2.11

† b, slope of regression; σ^2_{di}, mean squared deviation.

CONCLUSIONS

Single and three-way cross hybrids of white maize were compared for agronomic performance and aflatoxin accumulation. Significant differences between hybrids for grain yield and aflatoxin accumulation were observed. Lines and line x tester interaction contributed most of the variation among hybrids. The difference in performance between TWC and SC was dependent more on the line than the SC tester. Significant GCA and SCA effects for grain yield, aflatoxin, and other agronomic traits were observed at individual locations and across locations. Inbred lines CML343, Tx601W, and Tx110 showed significant and positive GCA effects for grain yield suggesting they contributed good alleles for yield. Significant GCA effects for lower aflatoxin concentration were observed in lines CML269, CML270, and CML78 across locations. It should thus be possible to use some of the tropical lines for improvement of the temperate lines for aflatoxin resistance. These lines might be useful for hybrid production since a number of experimental hybrids gave good yields. Three-way cross hybrids may have an advantage of genetic heterogeneity that could lead to yield stability and could thus be an option. Three-way cross hybrids may be advantageous over single-cross hybrids in terms of costs for production of hybrid seed. In many parts of developing world where the seed industry is not well established production of TWC hybrid seed could be more sustainable than SC hybrid seed.

CHAPTER V

SUMMARY AND CONCLUSIONS

STUDY 1: COMBINING ABILITY, HETEROSIS, AND GENETIC DIVERSITY IN TROPICAL MAIZE INBREDS UNDER STRESS AND NON STRESS CONDITIONS

Fifteen maize inbred lines of tropical and subtropical origin were crossed in a diallel mating design to produce 105 hybrids that were grown in four well-watered, two low N stress, and two drought stress environments in three countries. Inbred lines *per se* were also planted in separate experiments adjacent to the hybrids. A set of 80 RFLP, 32 SSR and six AFLP primers were used to genotype the inbred lines. Significant GCA x environment interaction was significant for grain yield and other traits suggesting that GCA effects associated with parents were not consistent over locations. Inbred lines CML254, CML258, CML341, and CML343 had consistently positive GCA effects for grain yield across low N, drought stress, well-watered conditions, and across locations. The best hybrids were P501 x CML247 across low N stress and CML258 x CML343 across drought stress and across environments. Inbred lines CML339, CML341, and SPLC7-F had good GCA effects for reduced anthesis silking interval (ASI) across stresses. ASI and ears per plant were negatively correlated in both hybrids and inbreds showing the importance of a small ASI for reduced barrenness. The high correlation between grain yield in hybrids and inbreds under low N stress should allow for prediction of hybrid performance based on inbred line performance under low N stress. Additive genetic effects were more important for grain yield under drought and well-watered conditions. Non-additive genetic effects seem to be more important under low N stress conditions for ears per plant in these inbred lines. Repeatability was low for grain yield under stress conditions due to high error variance. Pattern analysis showed that similar stress environments clustered together, suggesting that stresses imposed were uniform. Additive Main Effect and Multiplicative Interaction (AMMI) analysis showed that some environments explained more of the genotype x environment variation than others. Molecular marker genetic distance was positively correlated with specific combining ability and grain yield but the predictive value was not strong. It is possible to identify good hybrids and flow of germplasm between programs is possible. Inbred lines CML258, CML339, CML341, CML343 that showed positive GCA effects for grain yield and negative GCA for ASI

across stress conditions could be used in production of hybrids, especially three-way cross hybrids for the low soil fertility and drought prone areas. Three-way cross hybrids are suggested because of the reduced cost of seed production.

STUDY 2: PERFORMANCE OF SYNTHETIC MAIZE HYBRIDS UNDER LOW NITROGEN STRESS AND OPTIMAL CONDITIONS

Nineteen synthetics with a range of stress tolerance were crossed in a North Carolina design II to generate 68 synthetic hybrids. Together with the parents and two checks, the hybrids were evaluated at 3 locations under low N stress environments and 4 locations under optimal conditions in three countries. Significant differences between synthetic hybrids, parental synthetics, and checks were observed. Genotype x environment interaction was not significant for grain yield across low N stress but significant across optimal conditions and across environments. Specific combining ability for grain yield was observed across optimal environments, suggesting that there were some superior synthetic hybrid combinations. Positive and significant GCA effects for grain yield were observed for A synthetics 99SADVIA and 99SADVLA across low N and optimal conditions. Also, B synthetics 99SADVIB and 99SADVLB had positive GCA effects for grain yield. The best hybrids were 99SADVIA-# x P502-SRc0-F3 across low N stress conditions, 99SADVLA-# x SYNSC-SR-F2 across optimal conditions, and 99SADVIB-# x SYNI137TN-SRF1 across environments. Heterosis for grain yield was observed and was highly correlated with grain yield across environments suggesting that it could be used to predict good hybrids. The negative genetic correlation between grain yield and anthesis silking interval, and leaf senescence indicated the importance of these two associated traits to increased grain yield. Moderate repeatability was indicated for most traits in low N environments suggesting improvements could be possible under this stress. The synthetics showing good GCA effects under low N stress conditions might be considered for developing synthetic hybrids to be used by farmers facing low soil fertility problems. Most of the synthetics showed good stability across environments, suggesting there is a potential for these synthetic hybrids be used in several countries in the eastern and southern Africa region. Synthetics 99SADVIA, 99SADVLA, 99SADVIB, 99SADVLB, SYNTemperateB-SR-F2,

SYNTemperateA-SR-F2, P502-SRc0-F3 had high yield and showed good stability and it is suggested that these be tested further for possible production of synthetic hybrids.

STUDY 3: AGRONOMIC PERFORMANCE AND AFLATOXIN ACCUMULATION IN SINGLE AND THREE-WAY CROSS WHITE MAIZE HYBRIDS

Thirteen white maize inbred lines of tropical, subtropical, and temperate origins were crossed with three inbred line testers and their single cross testers in a North Carolina design II to generate 78 single cross (SC) and three-way cross (TWC) hybrids. The SC and TWC white maize hybrids were evaluated for agronomic performance and aflatoxin accumulation. Significant differences between hybrids were observed, with lines and line x tester interaction contributing most of the variation among hybrids. Significant GCA and SCA effects for grain yield and aflatoxin were observed at individual locations and across locations. Inbred lines CML343, Tx601W, and Tx110 showed positive GCA effects for grain yield. Significant GCA effects for lower aflatoxin concentration were observed in lines CML269, CML270, and CML78 across locations. These lines also had lower aflatoxin concentration in hybrids and these tropical lines could be potential candidates for incorporation of aflatoxin resistance in maize germplasm. These inbred lines could also be used in production of three-way cross hybrids after further tests. No definite pattern was evident in performance of SC and TWC. The difference in performance between TWC and SC was dependent more on the line than the SC tester. Three-way cross hybrids may have an advantage of genetic heterogeneity that could lead to yield stability and could thus be an option. Three-way cross hybrids may be advantageous over single cross hybrids in terms of costs for production of hybrid seed, especially in the eastern and southern Africa region where the seed industry is not well established and farmers do not readily buy hybrid seed.

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APPENDIX A

MEAN GRAIN YIELD (MG HA^{-1}) FOR 105 DIALLEL CROSS HYBRIDS ACROSS ENVIRONMENTS

Hybrid	Cross	Across Drought Stress	Across Low N Stress	Across Well-watered	Across Environments
1	P502 x P501	2.61	1.49	4.45	3.25
2	P502 x CML78	3.45	1.41	4.02	3.18
3	P502 x CML321	2.50	1.60	3.91	3.01
4	P502 x CML311	3.61	1.57	3.88	3.26
5	P502 x CML202	2.80	1.88	4.31	3.25
6	P502 x CML206	2.84	1.91	4.37	3.41
7	P502 x CML216	3.16	1.32	4.18	3.28
8	P502 x CML247	2.93	1.11	3.77	2.91
9	P502 x CML254	2.79	1.46	4.55	3.39
10	P502 x CML258	3.05	1.64	4.39	3.35
11	P502 x CML339	3.50	1.83	4.88	3.76
12	P502 x CML341	3.68	1.90	4.53	3.68
13	P502 x SPLC7-F	2.69	1.52	3.77	2.93
14	P502 x CML343	3.70	1.86	4.75	3.74
15	P501 x CML78	2.81	1.52	3.97	3.10
16	P501 x CML321	3.09	1.60	4.17	3.29
17	P501 x CML311	3.19	2.24	4.03	3.39
18	P501 x CML202	3.54	1.76	4.89	3.77
19	P501 x CML206	2.45	1.82	3.98	3.03
20	P501 x CML216	1.89	1.16	3.91	2.73
21	P501 x CML247	1.90	3.85	3.82	3.36
22	P501 x CML254	3.04	2.19	4.45	3.58
23	P501 x CML258	3.04	1.26	4.25	3.16
24	P501 x CML339	2.83	2.56	4.06	3.36
25	P501 x CML341	3.71	2.15	4.58	3.76
26	P501 x SPLC7-F	2.69	1.93	3.88	3.10
27	P501 x CML343	4.01	2.24	4.71	3.94
28	CML78 x CML321	2.49	1.57	4.14	3.05
29	CML78 x CML311	3.19	1.92	4.10	3.28
30	CML78 x CML202	2.13	1.19	3.95	2.78
31	CML78 x CML206	2.50	1.15	4.30	3.14
32	CML78 x CML216	3.18	1.81	3.91	3.23
33	CML78 x CML247	2.27	1.47	3.60	2.74
34	CML78 x CML254	3.62	2.22	4.21	3.55
35	CML78 x CML258	3.73	2.28	3.25	3.16
36	CML78 x CML339	3.99	1.70	5.24	4.01
37	CML78 x CML341	2.41	1.34	5.15	3.55
38	CML78 x SPLC7-F	2.88	1.94	5.34	3.91
39	CML78 x CML343	3.62	2.06	3.78	3.31

40	CML321 x CML311	4.33	1.29	4.98	3.92
41	CML321 x CML202	2.44	1.72	4.66	3.41
42	CML321 x CML206	2.22	1.93	3.72	2.92
43	CML321 x CML216	2.25	1.32	4.01	2.88
44	CML321 x CML247	1.89	1.23	3.45	2.51
45	CML321 x CML254	2.90	1.78	3.81	3.13
46	CML321 x CML258	2.37	1.69	4.88	3.74
47	CML321 x CML339	3.56	1.37	4.41	3.18
48	CML321 x CML341	3.26	1.65	4.69	3.63
49	CML321 x SPLC7-F	2.68	1.91	3.88	3.22
50	CML321 x CML343	3.44	1.53	4.23	3.18
51	CML311 x CML202	3.36	2.17	3.60	3.16
52	CML311 x CML206	3.99	0.93	3.65	2.90
53	CML311 x CML216	3.56	1.21	4.50	3.56
54	CML311 x CML247	2.77	0.91	3.19	2.66
55	CML311 x CML254	3.66	1.86	4.24	3.33
56	CML311 x CML258	2.44	0.97	3.78	3.07
57	CML311 x CML339	3.96	1.50	4.53	3.26
58	CML311 x CML341	2.33	1.77	4.66	3.81
59	CML311 x SPLC7-F	4.22	1.17	3.18	2.49
60	CML311 x CML343	1.49	2.01	3.92	3.49
61	CML202 x CML206	1.95	0.96	3.40	2.29
62	CML202 x CML216	1.81	1.14	3.81	2.62
63	CML202 x CML247	2.95	1.18	3.47	2.47
64	CML202 x CML254	3.52	2.20	3.93	3.24
65	CML202 x CML258	2.94	1.53	5.24	3.85
66	CML202 x CML339	2.35	1.54	5.15	3.63
67	CML202 x CML341	1.97	2.14	4.37	3.28
68	CML202 x SPLC7-F	2.78	1.75	3.25	2.51
69	CML202 x CML343	1.52	1.54	5.28	3.74
70	CML206 x CML216	2.28	1.51	3.61	2.56
71	CML206 x CML247	2.27	0.92	3.71	2.65
72	CML206 x CML254	3.71	1.70	4.46	3.21
73	CML206 x CML258	2.10	1.41	4.10	3.36
74	CML206 x CML339	2.35	1.30	5.33	3.49
75	CML206 x CML341	1.69	2.14	4.78	3.49
76	CML206 x SPLC7-F	2.45	0.91	3.65	2.43
77	CML206 x CML343	2.81	1.54	4.07	3.01
78	CML216 x CML247	2.67	1.12	3.84	2.87
79	CML216 x CML254	4.18	2.38	4.82	3.68
80	CML216 x CML258	3.12	1.55	4.99	3.91
81	CML216 x CML339	3.22	1.56	4.79	3.61
82	CML216 x CML341	3.55	1.56	5.35	3.85
83	CML216 x SPLC7-F	3.16	1.38	3.96	3.20
84	CML216 x CML343	3.10	1.60	4.53	3.47
85	CML247 x CML254	3.24	1.56	3.89	3.02
86	CML247 x CML258	1.48	1.45	4.53	3.48
87	CML247 x CML339	2.48	1.39	4.36	2.89
88	CML247 x CML341	2.17	2.10	3.80	2.99

89	CML247 x SPLC7-F	2.56	1.58	3.45	2.67
90	CML247 x CML343	2.59	1.31	4.02	2.89
91	CML254 x CML258	3.88	1.87	4.21	3.26
92	CML254 x CML339	3.37	1.60	4.69	3.77
93	CML254 x CML341	3.14	1.60	4.33	3.39
94	CML254 x SPLC7-F	4.19	1.85	3.63	2.98
95	CML254 x CML343	4.31	2.68	4.77	3.85
96	CML258 x CML339	2.65	1.29	5.01	3.88
97	CML258 x CML341	4.53	1.88	4.74	3.90
98	CML258 x SPLC7-F	2.34	1.54	4.27	3.21
99	CML258 x CML343	2.11	2.54	4.48	4.03
100	CML339 x CML341	2.12	1.74	4.19	3.16
101	CML339 x SPLC7-F	2.23	1.57	4.36	3.18
102	CML339 x CML343	2.42	1.74	5.03	3.47
103	CML341 x SPLC7-F	3.02	1.35	3.91	2.82
104	CML341 x CML343	2.61	1.65	3.70	2.87
105	SPLC7-F x CML343	3.45	1.65	3.82	3.10

APPENDIX B

SPECIFIC COMBINING ABILITY EFFECTS (MG HA^{-1}) FOR GRAIN YIELD ACROSS ENVIRONMENTS

Hybrid	Cross	Across Drought Stress	Across Low N Stress	Across Well-watered	Across Environments
1	P502 x P501	-0.48	-0.47	0.22	-0.15
2	P502 x CML78	0.15	-0.22	-0.29	-0.21
3	P502 x CML321	-0.43	0.08	-0.33	-0.26
4	P502 x CML311	0.02	0.08	-0.15	-0.03
5	P502 x CML202	0.10	0.42	0.02	0.12
6	P502 x CML206	0.23	0.47	0.26	0.30
7	P502 x CML216	0.04	-0.13	-0.12	-0.02
8	P502 x CML247	0.39	-0.22	0.00	0.10
9	P502 x CML254	-0.49	-0.30	0.25	-0.04
10	P502 x CML258	-0.63	-0.17	-0.16	-0.32
11	P502 x CML339	0.52	0.28	0.06	0.17
12	P502 x CML341	0.42	0.24	-0.02	0.20
13	P502 x SPLC7-F	-0.10	-0.09	-0.10	-0.10
14	P502 x CML343	0.26	0.04	0.35	0.24
15	P501 x CML78	-0.20	-0.58*	-0.24	-0.30
16	P501 x CML321	0.29	-0.24	-0.02	-0.02
17	P501 x CML311	-0.23	0.41	0.01	0.03
18	P501 x CML202	1.00*	-0.25	0.70	0.59**
19	P501 x CML206	0.19	0.03	-0.08	0.01
20	P501 x CML216	-1.13*	-0.67*	-0.42	-0.66**
21	P501 x CML247	-0.62	0.19	0.14	0.02
22	P501 x CML254	0.08	-0.10	0.15	0.07
23	P501 x CML258	-0.64	1.02*	-0.25	-0.07
24	P501 x CML339	-0.02	0.65*	-0.68*	-0.20
25	P501 x CML341	0.76	0.06	0.07	0.24
26	P501 x SPLC7-F	0.08	0.03	0.03	0.04
27	P501 x CML343	0.91*	-0.09	0.37	0.39
28	CML78 x CML321	-0.53	0.10	0.00	-0.09
29	CML78 x CML311	-0.40	0.24	0.15	0.01
30	CML78 x CML202	-0.68	-0.39	-0.28	-0.40*
31	CML78 x CML206	-0.13	-0.34	0.26	0.09
32	CML78 x CML216	0.72	0.25	-0.31	0.09
33	CML78 x CML247	-0.22	0.20	-0.12	-0.08
34	CML78 x CML254	0.53	0.30	-0.08	0.14
35	CML78 x CML258	0.03	0.28	-1.21***	-0.50*
36	CML78 x CML339	0.97*	0.02	0.56	0.55**
37	CML78 x CML341	-0.74	-0.29	0.65*	0.05
38	CML78 x SPLC7-F	0.29	0.28	1.51***	0.89***
39	CML78 x CML343	0.21	0.16	-0.61	-0.25
40	CML321 x CML311	0.89*	-0.21	0.99**	0.66**
41	CML321 x CML202	-0.10	0.20	0.47	0.31

42	CML321 x CML206	0.16	0.56*	-0.27	0.07
43	CML321 x CML216	-0.48	-0.01	-0.25	-0.31
44	CML321 x CML247	-0.43	0.01	-0.22	-0.22
45	CML321 x CML254	-0.01	-0.17	-0.64	-0.35
46	CML321 x CML258	-0.16	-0.19	0.41	0.12
47	CML321 x CML339	-0.31	-0.19	-0.30	-0.26
48	CML321 x CML341	0.59	-0.04	0.24	0.25
49	CML321 x SPLC7-F	0.91*	0.35	-0.01	0.29
50	CML321 x CML343	-0.39	-0.25	-0.06	-0.19
51	CML311 x CML202	0.28	0.62*	-0.41	0.01
52	CML311 x CML206	0.57	-0.19	-0.17	0.04
53	CML311 x CML216	0.51	0.04	0.36	0.30
54	CML311 x CML247	0.61	-0.34	-0.27	-0.08
55	CML311 x CML254	-0.75	0.02	0.22	-0.06
56	CML311 x CML258	-0.49	-0.71*	-0.44	-0.52*
57	CML311 x CML339	-0.87*	-0.03	-0.02	-0.26
58	CML311 x CML341	0.26	-0.09	0.42	0.30
59	CML311 x SPLC7-F	-0.84*	-0.15	-0.44	-0.44*
60	CML311 x CML343	0.42	0.29	-0.25	0.05
61	CML202 x CML206	-0.31	-0.40	-0.66*	-0.53**
62	CML202 x CML216	-0.65	-0.33	-0.56	-0.56**
63	CML202 x CML247	-0.32	-0.20	-0.31	-0.23
64	CML202 x CML254	0.27	0.24	-0.31	0.00
65	CML202 x CML258	0.25	-0.13	0.80*	0.39
66	CML202 x CML339	0.47	-0.03	0.34	0.26
67	CML202 x CML341	-0.31	0.20	-0.10	-0.10
68	CML202 x SPLC7-F	-0.21	0.33	-0.59	-0.27
69	CML202 x CML343	0.20	-0.30	0.89**	0.43*
70	CML206 x CML216	-0.84	0.27	-0.53	-0.41*
71	CML206 x CML247	0.35	-0.22	0.04	0.02
72	CML206 x CML254	-0.10	-0.09	0.37	0.13
73	CML206 x CML258	0.57	-0.05	-0.13	0.09
74	CML206 x CML339	0.00	-0.08	0.72*	0.28
75	CML206 x CML341	-0.07	0.56	0.44	0.38
76	CML206 x SPLC7-F	-0.33	-0.44	-0.05	-0.27
77	CML206 x CML343	-0.29	-0.10	-0.18	-0.21
78	CML216 x CML247	0.46	-0.03	-0.04	0.04
79	CML216 x CML254	-0.42	0.61*	0.50	0.32
80	CML216 x CML258	0.47	-0.03	0.48	0.34
81	CML216 x CML339	0.15	0.17	-0.06	0.10
82	CML216 x CML341	0.28	-0.23	0.77*	0.39
83	CML216 x SPLC7-F	1.01*	0.14	0.05	0.31
84	CML216 x CML343	-0.13	-0.06	0.13	0.07
85	CML247 x CML254	0.52	-0.16	0.04	0.07
86	CML247 x CML258	0.19	0.12	0.65*	0.45*
87	CML247 x CML339	-0.66	-0.02	0.11	-0.14
88	CML247 x CML341	-0.11	0.56*	-0.22	-0.02
89	CML247 x SPLC7-F	-0.05	0.38	0.10	0.19
90	CML247 x CML343	-0.11	-0.28	0.10	-0.11

91	CML254 x CML258	-1.05*	-0.08	-0.25	-0.38
92	CML254 x CML339	0.95*	-0.44	-0.04	0.15
93	CML254 x CML341	0.15	-0.31	-0.24	-0.20
94	CML254 x SPLC7-F	0.44	-0.10	-0.30	-0.12
95	CML254 x CML343	-0.13	0.57*	0.33	0.26
96	CML258 x CML339	0.78	-0.22	0.01	0.14
97	CML258 x CML341	0.59	-0.16	-0.03	0.06
98	CML258 x SPLC7-F	-0.67	-0.22	0.22	-0.08
99	CML258 x CML343	0.76	0.53	-0.09	0.30
100	CML339 x CML341	-0.64	0.01	-0.85**	-0.57**
101	CML339 x SPLC7-F	-0.28	-0.05	-0.02	-0.04
102	CML339 x CML343	-1.08*	-0.08	0.19	-0.18
103	CML341 x SPLC7-F	-0.96	-0.36	-0.24	-0.35
104	CML341 x CML343	0.41	0.26	0.19	0.27
105	SPLC7-F x CML343	0.14	-0.19	-0.22	-0.11

*,** Indicates significance at 0.05 and 0.01 probability levels, respectively

APPENDIX C

GENETIC DISTANCE (NEI AND LI) BETWEEN 15 INBRED LINES IN DIALLEL CALCULATED USING ALL MARKER DATA

	P502	P501	CML78	CML321	CML311	CML202	CML206	CML216	CML247	CML254	CML258	CML339	CML341	SPLC7-F
P502														
P501	0.50													
CML78	0.58	0.51												
CML321	0.54	0.52	0.58											
CML311	0.57	0.58	0.52	0.58										
CML202	0.52	0.57	0.58	0.55	0.54									
CML206	0.57	0.56	0.57	0.55	0.54	0.50								
CML216	0.54	0.59	0.59	0.60	0.57	0.45	0.57							
CML247	0.46	0.56	0.57	0.55	0.57	0.55	0.59	0.52						
CML254	0.60	0.58	0.58	0.59	0.59	0.57	0.59	0.63	0.58					
CML258	0.58	0.58	0.60	0.57	0.61	0.60	0.56	0.62	0.57	0.52				
CML339	0.57	0.58	0.58	0.62	0.54	0.61	0.58	0.61	0.63	0.61	0.59			
CML341	0.56	0.59	0.54	0.61	0.53	0.57	0.60	0.60	0.57	0.54	0.59	0.58		
SPLC7-F	0.60	0.58	0.57	0.58	0.58	0.59	0.56	0.59	0.60	0.54	0.56	0.56	0.60	
CML343	0.57	0.57	0.53	0.55	0.53	0.57	0.57	0.56	0.55	0.58	0.56	0.54	0.50	0.57

APPENDIX D

GENETIC DISTANCE (MODIFIED ROGER'S) BETWEEN 15 INBRED LINES IN DIALLEL CALCULATED USING ALL MARKER DATA

	P502	P501	CML78	CML321	CML311	CML202	CML206	CML216	CML247	CML254	CML258	CML339	CML341	SPLC7-F
P502														
P501	0.61													
CML78	0.64	0.61												
CML321	0.62	0.62	0.64											
CML311	0.64	0.65	0.61	0.64										
CML202	0.62	0.65	0.64	0.64	0.63									
CML206	0.64	0.64	0.64	0.64	0.63	0.62								
CML216	0.63	0.65	0.65	0.65	0.64	0.59	0.65							
CML247	0.59	0.65	0.64	0.64	0.64	0.64	0.66	0.63						
CML254	0.65	0.65	0.64	0.65	0.65	0.64	0.65	0.67	0.65					
CML258	0.65	0.66	0.66	0.64	0.66	0.66	0.65	0.67	0.65	0.62				
CML339	0.64	0.65	0.64	0.67	0.63	0.67	0.66	0.67	0.68	0.66	0.66			
CML341	0.64	0.66	0.63	0.66	0.63	0.65	0.66	0.67	0.66	0.63	0.66	0.66		
SPLC7-F	0.66	0.66	0.65	0.65	0.65	0.66	0.65	0.66	0.67	0.64	0.65	0.65	0.67	
CML343	0.64	0.65	0.62	0.64	0.63	0.65	0.65	0.65	0.64	0.65	0.65	0.64	0.62	0.65

APPENDIX E

MID PARENT HETEROSIS (MPH) AND HIGH PARENT HETEROSIS (HPH) FOR GRAIN YIELD OF 105 DIALLEL CROSS HYBRIDS AT FOUR ENVIRONMENTS

	ZBWW†		ZBLN		PRLN		ZBSS	
Cross	***MPH***	***HPH***	***MPH***	***HPH***	***MPH***	***HPH***	***MPH***	***HPH***
	%							
P502 x P501	62.9	43.9	61.1	15.5	90.3	88.2	186.5	160.8
P502 x CML78	83.4	30.9	206.8	190.9	78.3	38.1	359.9	276.6
P502 x CML321	160.4	97.2	360.0	231.4	67.0	53.7	313.0	270.2
P502 x CML311	14.1	-3.5	272.4	219.4	107.2	49.8	484.2	361.9
P502 x CML202	86.9	77.5	360.8	326.0	129.5	71.8	276.4	240.5
P502 x CML206	90.4	86.7	248.6	192.1	48.0	10.7	307.5	219.3
P502 x CML216	44.9	24.3	236.6	165.7	82.9	18.0	399.2	255.4
P502 x CML247	163.3	110.7	145.4	92.5	91.4	43.3	362.7	262.5
P502 x CML254	142.5	61.2	155.3	144.2	80.0	64.0	186.5	182.2
P502 x CML258	67.1	50.3	310.1	257.6	41.3	22.8	191.1	181.1
P502 x CML339	75.9	51.7	477.9	308.2	55.8	47.4	453.1	307.3
P502 x CML341	131.1	117.8	292.5	286.9	117.7	104.2	452.3	347.9
P502 x SPLC7-F	104.7	33.4	189.3	187.9	64.6	55.8	391.1	223.8
P502 x CML343	133.5	111.7	237.7	187.6	64.7	45.9	322.1	313.4
P501 x CML78	129.6	78.8	78.2	23.8	104.7	59.2	284.0	192.5
P501 x CML321	233.4	178.6	157.3	53.3	70.7	58.1	235.5	176.9
P501 x CML311	93.6	83.9	242.1	124.1	133.0	69.0	354.5	235.7
P501 x CML202	154.5	114.9	151.0	71.8	51.9	14.1	309.7	240.9
P501 x CML206	109.2	81.6	107.6	70.5	95.2	46.7	183.7	107.9
P501 x CML216	70.6	32.1	57.4	-1.6	85.9	20.2	99.1	34.2
P501 x CML247	238.3	201.8	198.4	86.0	78.9	34.4	73.8	27.3
P501 x CML254	176.4	97.6	169.7	99.0	56.1	41.1	200.4	169.8
P501 x CML258	102.4	63.2	31.6	-13.0	892.4	767.1	133.6	119.8
P501 x CML339	163.9	156.8	338.5	158.5	95.2	86.0	272.4	158.5
P501 x CML341	97.8	84.5	158.2	83.5	141.3	127.7	337.3	230.3
P501 x SPLC7-F	127.5	58.7	152.5	81.6	84.5	75.7	261.1	127.8
P501 x CML343	122.6	116.2	155.2	106.4	71.6	52.9	298.1	269.5
CML78 x CML321	302.3	268.4	408.1	279.0	160.8	112.0	274.9	238.2
CML78 x CML311	212.3	152.8	382.7	334.0	211.7	185.3	457.7	433.1
CML78 x CML202	90.7	32.0	190.8	183.2	140.2	131.2	221.5	187.5
CML78 x CML206	201.8	112.9	79.2	43.8	148.1	138.8	358.2	332.9
CML78 x CML216	86.2	21.6	436.8	341.8	187.1	122.0	912.6	742.9
CML78 x CML247	183.6	142.7	357.5	274.0	167.8	157.8	303.7	281.3
CML78 x CML254	317.2	269.2	380.3	336.6	107.7	50.8	437.1	345.0
CML78 x CML258	89.5	27.1	502.5	451.3	103.4	78.6	425.3	318.6
CML78 x CML339	246.0	174.9	442.8	296.3	110.7	69.3	718.6	612.9
CML78 x CML341	124.5	66.5	182.7	171.7	159.6	112.9	333.4	328.1
CML78 x SPLC7-F	258.0	206.0	345.1	320.0	93.9	57.0	615.1	436.1
CML78 x CML343	128.2	74.1	290.0	217.8	137.5	102.7	350.0	262.5

CML321 x CML311	395.9	332.7	309.1	230.6	131.8	74.5	647.4	547.7
CML321 x CML202	266.9	168.2	462.4	327.3	152.1	97.3	235.0	231.7
CML321 x CML206	203.3	126.6	342.9	187.4	117.6	70.3	331.5	270.0
CML321 x CML216	85.9	27.2	477.3	408.5	113.7	41.6	363.4	255.6
CML321 x CML247	263.4	237.3	433.6	373.6	75.7	37.6	263.3	211.6
CML321 x CML254	447.6	349.1	311.4	188.5	79.0	51.6	293.1	257.2
CML321 x CML258	283.5	170.5	482.9	364.2	46.0	34.8	304.0	251.1
CML321 x CML339	206.7	162.1	492.5	473.4	92.7	86.1	322.4	237.2
CML321 x CML341	354.5	259.3	366.3	239.0	87.2	85.0	483.6	420.8
CML321 x SPLC7-F	332.0	243.3	425.7	277.6	119.2	113.5	596.0	387.8
CML321 x CML343	243.6	180.5	296.1	159.5	1.2	-4.6	263.6	220.0
CML311 x CML202	102.2	63.8	526.1	476.8	199.9	188.3	447.6	370.5
CML311 x CML206	110.0	74.7	64.9	22.3	269.2	247.6	553.4	545.4
CML311 x CML216	91.2	42.9	296.2	258.4	341.0	260.2	853.2	724.1
CML311 x CML247	141.0	125.4	178.1	149.6	108.1	96.8	583.2	574.9
CML311 x CML254	276.9	178.4	339.6	263.4	60.9	9.9	364.3	271.2
CML311 x CML258	69.7	31.6	90.9	87.2	191.9	135.8	447.0	321.5
CML311 x CML339	191.7	184.6	412.0	303.6	151.6	87.7	370.0	326.2
CML311 x CML341	140.3	113.8	278.0	228.2	106.1	56.8	571.5	549.5
CML311 x SPLC7-F	173.8	97.0	178.1	137.6	158.2	94.2	499.4	363.9
CML311 x CML343	140.3	122.1	333.7	225.9	128.6	79.9	503.9	370.2
CML202 x CML206	83.2	77.2	90.2	49.7	66.2	68.5	189.5	146.2
CML202 x CML216	52.6	37.1	247.1	191.9	108.5	67.6	274.3	185.2
CML202 x CML247	156.9	97.8	229.5	175.1	109.7	112.6	143.5	107.1
CML202 x CML254	132.1	50.4	360.5	308.8	106.6	45.5	286.5	254.4
CML202 x CML258	177.1	161.7	337.2	310.1	144.7	106.3	322.4	270.3
CML202 x CML339	109.5	73.0	453.5	311.2	76.6	36.8	411.8	305.4
CML202 x CML341	120.9	98.3	402.0	370.4	44.0	13.9	284.5	240.0
CML202 x SPLC7-F	127.7	44.9	318.2	285.0	167.7	109.1	325.6	196.6
CML202 x CML343	173.7	136.9	174.7	119.3	136.2	93.8	284.9	241.7
CML206 x CML216	10.6	-3.5	243.3	138.9	134.2	84.4	212.4	173.0
CML206 x CML247	194.0	131.9	73.1	19.8	106.8	105.4	221.8	221.8
CML206 x CML254	209.9	104.0	155.3	122.2	70.7	20.3	181.9	123.4
CML206 x CML258	142.7	122.3	200.0	125.4	104.0	72.0	412.4	291.4
CML206 x CML339	271.7	215.5	186.6	83.3	85.8	44.0	328.9	293.3
CML206 x CML341	113.0	97.1	286.6	220.2	102.2	59.8	338.7	319.3
CML206 x SPLC7-F	89.5	22.3	48.1	24.6	45.3	13.5	340.2	243.7
CML206 x CML343	117.7	93.9	142.7	138.0	62.6	33.4	216.0	143.9
CML216 x CML247	99.3	42.6	327.9	324.2	143.2	92.3	577.9	492.3
CML216 x CML254	200.2	85.5	563.4	407.0	53.3	-5.1	273.4	168.2
CML216 x CML258	66.7	58.0	404.5	348.6	166.3	87.0	473.6	300.0
CML216 x CML339	77.5	68.2	624.9	520.7	101.7	33.1	524.6	492.2
CML216 x CML341	108.6	70.4	253.9	182.4	101.9	35.7	708.3	579.6
CML216 x SPLC7-F	69.1	2.9	233.5	162.3	251.0	133.5	1118.7	967.2
CML216 x CML343	83.9	45.5	263.7	155.8	112.8	46.3	301.8	182.5
CML247 x CML254	386.8	276.8	190.7	120.9	134.7	65.3	320.1	232.8
CML247 x CML258	258.5	165.3	313.6	264.9	269.4	211.4	409.0	288.9
CML247 x CML339	248.7	218.7	452.6	376.7	83.1	41.8	175.3	152.4
CML247 x CML341	207.3	158.0	449.8	335.9	156.2	102.5	355.5	335.4

CML247 x SPLC7-F	250.1	163.4	307.8	218.8	178.1	117.2	328.0	234.2
CML247 x CML343	225.1	182.7	151.3	75.9	125.6	85.0	256.7	175.4
CML254 x CML258	228.7	107.6	417.7	334.6	0.0	-19.6	262.5	244.9
CML254 x CML339	395.1	259.9	235.0	130.6	74.6	51.6	553.7	386.1
CML254 x CML341	199.3	105.3	193.2	176.6	95.8	68.6	379.0	293.0
CML254 x SPLC7-F	287.4	272.1	237.2	224.1	63.9	42.2	421.9	246.6
CML254 x CML343	452.2	287.9	372.5	318.1	95.3	59.8	240.3	228.4
CML258 x CML339	230.0	160.7	413.0	298.7	125.8	105.2	525.8	350.7
CML258 x CML341	151.9	115.0	343.6	291.7	69.9	57.9	469.2	349.4
CML258 x SPLC7-F	116.3	34.4	267.5	219.1	75.5	60.8	345.7	188.9
CML258 x CML343	110.4	73.6	445.1	315.1	113.3	108.0	412.2	404.8
CML339 x CML341	178.7	153.6	421.4	271.4	76.3	73.6	349.6	295.7
CML339 x SPLC7-F	246.1	145.4	319.0	195.1	86.1	85.1	441.6	353.2
CML339 x CML343	259.4	240.0	311.0	165.1	71.9	59.5	129.3	66.6
CML341 x SPLC7-F	133.9	57.0	176.2	170.9	82.3	81.0	417.4	291.1
CML341 x CML343	60.0	53.5	196.6	149.6	93.1	83.2	236.7	168.7
SPLC7-F x CML343	101.3	38.2	177.0	136.8	87.4	75.3	369.5	206.4

† PRLN, Poza Rica Low N; ZBLN, Harare Low N; ZBSS, Chiredzi drought stress; ZBWW, Harare well-watered.

APPENDIX F

MEAN GRAIN YIELD (MG HA^{-1}) AND ANTHESIS SILKING INTERVAL (D) OF SYNTHETIC HYBRIDS ACROSS ENVIRONMENTS

Cross	Grain yield			Anthesis silking interval		
	Low N	Optimal	Across	Low N	Optimal	Across
	Mg ha^{-1}			d		
[99SADVIA-#/[SYNI137TN-SR]F1]	1.48	5.61	4.13	6.9	1.8	4.1
[99SADVIA-#/SYNK64R-SR-F2]	1.77	5.36	4.08	3.5	1.3	2.3
[99SADVIA-#/SYNTemperateB-SR-F2]	1.97	5.65	4.34	4.6	2.4	3.4
[99SADVIA-#/SYNSC-SR-F2]	1.48	5.72	4.21	5.2	1.9	3.4
[99SADVIA-#/P502-SRc0-F3]	2.03	5.64	4.35	4.5	2.0	3.1
[99SADVLA-#/[SYNI137TN-SR]F1]	1.99	5.62	4.32	4.0	1.3	2.5
[99SADVLA-#/SYNK64R-SR-F2]	1.39	5.56	4.06	5.1	1.0	2.9
[99SADVLA-#/SYNTemperateB-SR-F2]	1.60	5.75	4.27	4.8	1.6	3.1
[99SADVLA-#/SYNSC-SR-F2]	1.66	6.16	4.55	5.0	1.7	3.2
[99SADVLA-#/P502-SRc0-F3]	1.82	5.88	4.43	3.8	1.3	2.5
[SZSYNKITII-F2/[SYNI137TN-SR]F1]	1.44	5.61	4.11	7.0	2.4	4.5
[SZSYNKITII-F2/SYNK64R-SR-F2]	1.17	5.45	3.92	7.3	2.3	4.5
[SZSYNKITII-F2/SYNTemperateB-SR-F2]	1.28	5.49	3.99	8.7	3.2	5.7
[SZSYNKITII-F2/SYNSC-SR-F2]	1.37	5.02	3.72	9.6	2.5	5.7
[SZSYNKITII-F2/P502-SRc0-F3]	1.60	5.66	4.21	5.7	3.2	4.3
[SZSYNUCA-F2/SYNK64R-SR-F2]	1.55	5.78	4.26	4.5	1.8	3.0
[SZSYNUCA-F2/[SYNI137TN-SR]F1]	1.39	5.42	3.98	7.4	2.9	5.0
[SZSYNUCA-F2/SYNTemperateB-SR-F2]	1.62	5.75	4.28	6.0	2.2	3.9
[SZSYNUCA-F2/SYNSC-SR-F2]	1.47	4.78	3.61	6.6	2.8	4.5
[SZSYNUCA-F2/P502-SRc0-F3]	1.61	5.34	4.00	5.5	1.5	3.3
[Z97SYNGLS(A)-F3/[SYNI137TN-SR]F1]	1.61	5.40	4.06	5.3	2.0	3.5
[Z97SYNGLS(A)-F3/SYNK64R-SR-F2]	1.36	5.74	4.19	7.0	1.6	4.1
[Z97SYNGLS(A)-F3/SYNTemperateB-SR-F2]	1.43	5.81	4.25	6.8	2.6	4.5
[Z97SYNGLS(A)-F3/SYNSC-SR-F2]	1.57	5.86	4.32	6.7	2.6	4.5
[Z97SYNGLS(A)-F3/P502-SRc0-F3]	1.44	5.62	4.13	4.9	2.2	3.4
[SYNA00F2/[SYNI137TN-SR]F1]	1.84	5.70	4.32	6.1	2.8	4.3
[SYNA00F2/SYNK64R-SR-F2]	1.70	5.13	3.90	5.9	2.7	4.2
[SYNA00F2/SYNTemperateB-SR-F2]	1.76	5.34	4.07	5.4	2.1	3.6
[SYNA00F2/SYNSC-SR-F2]	1.78	5.45	4.13	5.8	2.1	3.8
[SYNA00F2/P502-SRc0-F3]	1.69	5.91	4.40	5.6	2.4	3.9
[P501-SRc0-F3/[SYNI137TN-SR]F1]	1.67	6.12	4.54	4.7	2.2	3.3
[P501-SRc0-F3/SYNK64R-SR-F2]	1.45	4.93	3.68	3.5	1.3	2.3
[SYNSC-SR-F2/P501-SRc0-F3]	1.67	5.74	4.29	5.5	2.7	4.0
[P501-SRc0-F3/SYNTemperateB-SR-F2]	1.73	5.36	4.05	5.2	3.5	4.3
[P501-SRc0-F3/P502-SRc0-F3]	1.81	5.11	3.94	4.6	1.3	2.8
[SYNN3-SR-F2/[SYNI137TN-SR]F1]	1.35	5.24	3.86	6.8	2.7	4.6
[SYNTemperateB-SR-F2/SYNN3-SR-F2]	1.65	5.29	4.00	7.5	3.3	5.2
[SYNN3-SR-F2/SYNK64R-SR-F2]	1.44	4.83	3.62	5.3	2.3	3.6
[SYNN3-SR-F2/SYNSC-SR-F2]	1.40	4.53	3.41	6.3	2.2	4.1
[SYNN3-SR-F2/P502-SRc0-F3]	1.50	5.93	4.35	6.3	1.7	3.8
[SYNTemperateA-SR-F2/[SYNI137TN-SR]F1]	1.58	5.38	4.02	5.2	1.6	3.2

[SYNTemperateA-SR-F2/SYNK64R-SR-F2]	1.41	4.94	3.67	6.3	2.2	4.0
[SYNTemperateA-SR-F2/SYNTempB-SR-F2]	1.84	6.00	4.52	5.4	2.5	3.8
[SYNTemperateA-SR-F2/SYNSC-SR-F2]	1.49	5.35	3.96	5.9	2.5	4.0
[SYNTemperateA-SR-F2/P502-SRc0-F3]	1.93	5.08	3.95	4.8	2.2	3.4
[[SYNI137TN-SR]F1bulk/SYNK64R-SR-F2]	1.32	5.53	4.02	5.6	2.2	3.8
[[SYNI137TN-SR]F1bulk/SYNTempB-SR-F2]	1.49	5.80	4.27	7.0	1.9	4.2
[[SYNI137TN-SR]F1bulk/SYNSC-SR-F2]	1.50	5.50	4.07	6.3	1.5	3.7
[[SYNI137TN-SR]F1bulk/P502-SRc0-F3]	1.85	5.77	4.36	4.3	1.7	2.9
[Z97SYNGLS(B)-F5/P501-SRc0-F3]	1.89	5.37	4.13	5.5	2.3	3.8
[99SADVIB-#/P501-SRc0-F3]	1.78	5.66	4.27	4.7	1.3	2.8
[99SADVLB-#/P501-SRc0-F3]	1.70	5.62	4.21	5.8	1.4	3.4
[SYNB00-F2/P501-SRc0-F3]	1.83	5.25	4.02	4.7	2.4	3.5
[SZSYNECU573-F2/P501-SRc0-F3]	1.60	5.87	4.35	6.3	3.1	4.5
[Z97SYNGLS(B)-F5/SYNN3-SR-F2]	1.28	5.34	3.88	6.5	2.2	4.2
[99SADVIB-#/SYNN3-SR-F2]	1.41	5.12	3.80	6.8	2.4	4.4
[99SADVLB-#/SYNN3-SR-F2]	1.33	5.74	4.17	6.1	2.4	4.0
[SYNB00-F2/SYNN3-SR-F2]	1.42	5.10	3.79	6.1	3.2	4.5
[SZSYNECU573-F2/SYNN3-SR-F2]	0.88	5.23	3.68	10.3	3.8	6.7
[Z97SYNGLS(B)-F5/SYNTemperateA-SR-F2]	1.55	5.23	3.92	4.9	2.1	3.4
[99SADVIB-#/SYNTemperateA-SR-F2]	1.48	5.69	4.18	5.0	2.1	3.4
[99SADVLB-#/SYNTemperateA-SR-F2]	1.49	5.38	3.99	4.9	1.7	3.2
[SYNB00-F2/SYNTemperateA-SR-F2]	1.73	5.36	4.06	5.1	2.3	3.6
[SZSYNECU573-F2/SYNTemperateA-SR-F2]	1.20	5.25	3.81	8.1	3.3	5.5
[Z97SYNGLS(B)-F5/[SYNI137TN-SR]F1]	1.74	4.89	3.75	5.2	1.6	3.2
[99SADVIB-#/[SYNI137TN-SR]F1]	1.94	6.02	4.58	4.9	1.8	3.2
[99SADVLB-#/[SYNI137TN-SR]F1]	1.74	5.93	4.43	5.2	1.8	3.3
[SYNB00-F2/[SYNI137TN-SR]F1]	1.57	5.20	3.91	6.8	2.9	4.7
[SZSYNECU573-F2/[SYNI137TN-SR]F1]	1.22	5.21	3.79	9.0	2.8	5.6
[SYNI137TN-SR]F2	1.13	3.90	2.92	7.4	3.1	5.0
[SYNTemperateA-SR]F2	1.16	3.97	2.95	7.1	3.0	4.8
[SYNN3-SR]F2	0.99	4.11	2.98	8.3	2.9	5.3
[P501-SRc0]F2	1.71	4.68	3.62	5.3	2.5	3.8
[SZSYNKITII]F2	1.04	4.81	3.47	7.3	4.3	5.7
[SZSYNUCA]F2	1.44	4.03	3.11	6.1	1.8	3.7
[Z97SYNGLS(A)]F3	1.02	5.34	3.80	7.2	2.5	4.6
[SYNA00]F2	1.62	5.00	3.80	6.5	1.5	3.8
[99SADVIA]F2	1.72	5.68	4.26	4.1	1.4	2.6
[99SADVLA]F2	1.47	5.85	4.29	5.5	1.5	3.3
[SYNK64-SR]F2	1.31	3.96	3.01	4.7	1.4	2.9
[SYNTemperateB-SR]F2	1.36	4.57	3.43	7.8	3.0	5.2
[SYNSC-SR]F2	1.47	4.55	3.45	6.5	2.4	4.3
[P502-SRc0]F2	1.75	5.23	3.99	4.4	0.9	2.5
[Z97SYNGLS(B)]F5	1.32	5.16	3.79	6.8	2.5	4.5
[SZSYNECU]F2	0.98	4.40	3.16	9.8	4.6	7.0
[SYNB00]F2	1.61	5.25	3.94	7.4	2.0	4.4
[99SADVIB]F2	1.60	5.38	4.02	4.3	0.8	2.4
[99SADVLB]F2	1.49	5.50	4.07	6.0	1.2	3.4
ZM621-FLINT F2	1.29	4.43	3.32	6.7	3.1	4.7
SC627	2.09	6.56	4.96	5.0	1.9	3.3

APPENDIX G

AVERAGE MID PARENT HETEROSIS (MPH) AND HIGH PARENT HETEROSIS (HPH) FOR GRAIN YIELD OF SYNTHETIC HYBRIDS ACROSS ENVIRONMENTS

Synthetic Hybrid	Mid-parent heterosis			High-parent heterosis		
	Optimal	Low N	Across	Low N	Optimal	Across
	%					
[SYNTemperateB-SR-F2/SYNN3-SR-F2]	32.8	33.5	33.2	14.7	16.6	15.9
[SYNSC-SR-F2/P501-SRc0-F3]	11.6	21.0	17.2	-2.1	15.3	9.1
[Z97SYNGLS(B)-F5/[SYNI137TN-SR]F1]	49.5	15.6	29.1	33.2	0.6	12.2
[Z97SYNGLS(B)-F5/SYNTemperateA-SR-F2]	49.6	16.1	29.5	19.1	0.0	6.8
[Z97SYNGLS(B)-F5/SYNN3-SR-F2]	11.1	32.0	23.6	-1.6	12.7	7.6
[Z97SYNGLS(B)-F5/P501-SRc0-F3]	31.8	17.2	23.0	16.3	11.5	13.2
[SZSYNECU573-F2/[SYNI137TN-SR]F1]	15.8	26.6	22.3	-0.8	10.3	6.4
[SZSYNECU573-F2/SYNTemperateA-SR-F2]	28.9	24.3	26.1	14.0	9.9	11.4
[SZSYNECU573-F2/SYNN3-SR-F2]	-4.6	31.8	17.3	-12.9	9.8	1.7
[SZSYNECU573-F2/P501-SRc0-F3]	24.0	32.5	29.1	-5.0	9.8	4.5
[SYNB00-F2/[SYNI137TN-SR]F1]	8.4	13.0	11.2	-6.2	-3.9	-4.7
[SYNB00-F2/SYNTemperateA-SR-F2]	35.0	15.4	23.2	1.8	-1.5	-0.3
[SYNB00-F2/SYNN3-SR-F2]	4.6	9.4	7.5	-14.3	-7.3	-9.8
[SYNB00-F2/P501-SRc0-F3]	6.9	2.3	4.1	-2.4	-4.3	-3.6
[99SADVIB-#/[SYNI137TN-SR]F1]	49.7	40.8	44.3	27.1	19.4	22.1
[99SADVIB-#/SYNTemperateA-SR-F2]	18.1	23.0	21.1	-14.5	8.2	0.1
[99SADVIB-#/SYNN3-SR-F2]	10.3	10.4	10.4	-9.8	-4.7	-6.5
[99SADVIB-#/P501-SRc0-F3]	8.9	14.8	12.4	-2.7	2.3	0.5
[99SADVLB-#/[SYNI137TN-SR]F1]	35.7	35.4	35.5	16.5	16.3	16.4
[99SADVLB-#/SYNTemperateA-SR-F2]	20.6	17.4	18.7	-5.8	-1.6	-3.1
[99SADVLB-#/SYNN3-SR-F2]	15.7	26.6	22.3	-4.5	10.0	4.8
[99SADVLB-#/P501-SRc0-F3]	9.8	20.5	16.2	2.2	8.5	6.2
[[SYNI137TN-SR]F1bulk/SYNK64R-SR-F2]	11.6	44.4	31.3	1.1	31.6	20.7
[[SYNI137TN-SR]F1bulk/SYNTemperateB-SR-F2]	26.7	50.1	40.7	6.9	33.4	23.9
[[SYNI137TN-SR]F1bulk/SYNSC-SR-F2]	22.5	41.4	33.8	11.1	23.1	18.8
[[SYNI137TN-SR]F1bulk/P502-SRc0-F3]	32.6	23.6	27.2	12.5	4.5	7.4
[SYNTemperateA-SR-F2/[SYNI137TN-SR]F1]	52.2	38.5	44.0	23.2	28.5	26.6
[SYNTemperateA-SR-F2/SYNK64R-SR-F2]	25.9	25.9	25.9	6.0	13.8	11.0
[SYNTemperateA-SR-F2/SYNTemperateB-SR-F2]	71.7	61.6	65.6	53.8	42.3	46.4
[SYNTemperateA-SR-F2/SYNSC-SR-F2]	48.9	22.7	33.1	25.5	10.0	15.5
[SYNTemperateA-SR-F2/P502-SRc0-F3]	33.4	11.2	20.1	-5.1	-4.4	-4.6
[SYNN3-SR-F2/[SYNI137TN-SR]F1]	19.1	28.6	24.8	4.4	17.5	12.8
[SYNN3-SR-F2/SYNK64R-SR-F2]	21.8	19.8	20.6	9.0	12.7	11.4
[SYNN3-SR-F2/SYNSC-SR-F2]	20.5	0.3	8.3	16.4	-10.5	-0.9
[SYNN3-SR-F2/P502-SRc0-F3]	13.0	20.2	17.3	-11.1	4.6	-1.0
[P501-SRc0-F3/[SYNI137TN-SR]F1]	24.3	53.8	42.0	5.7	35.2	24.7
[P501-SRc0-F3/SYNK64R-SR-F2]	-0.5	15.1	8.9	-12.1	8.1	0.9

[P501-SRc0-F3/SYNTemperateB-SR-F2]	32.7	20.3	25.3	9.7	12.4	11.4
[P501-SRc0-F3/P502-SRc0-F3]	7.9	10.3	9.4	-2.7	0.0	-1.0
[SZSYNKITII-F2/[SYNI137TN-SR]F1]	36.9	39.0	38.2	18.3	20.8	19.9
[SZSYNKITII-F2/SYNK64R-SR-F2]	7.4	32.5	22.5	-11.6	22.5	10.3
[SZSYNKITII-F2/SYNTemperateB-SR-F2]	25.6	19.1	21.7	-0.8	7.1	4.3
[SZSYNKITII-F2/SYNSC-SR-F2]	25.7	0.4	10.5	7.3	-10.2	-4.0
[SZSYNKITII-F2/P502-SRc0-F3]	16.6	10.0	12.6	-11.7	-2.3	-5.7
[SZSYNUCA-F2/SYNK64R-SR-F2]	24.7	59.2	45.4	15.9	48.1	36.6
[SZSYNUCA-F2/[SYNI137TN-SR]F1]	7.2	54.3	35.5	-6.5	38.8	22.6
[SZSYNUCA-F2/SYNTemperateB-SR-F2]	43.7	45.4	44.7	26.4	32.6	30.4
[SZSYNUCA-F2/SYNSC-SR-F2]	11.4	7.7	9.2	-6.3	-1.5	-3.2
[SZSYNUCA-F2/P502-SRc0-F3]	1.8	18.5	11.8	-13.5	3.9	-2.3
[Z97SYNGLS(A)-F3/[SYNI137TN-SR]F1]	47.1	19.9	30.8	49.7	2.7	19.5
[Z97SYNGLS(A)-F3/SYNK64R-SR-F2]	13.1	31.4	24.1	3.8	13.3	9.9
[Z97SYNGLS(A)-F3/SYNTemperateB-SR-F2]	27.4	24.2	25.5	6.6	10.3	9.0
[Z97SYNGLS(A)-F3/SYNSC-SR-F2]	32.5	17.6	23.6	17.7	10.3	12.9
[Z97SYNGLS(A)-F3/P502-SRc0-F3]	4.9	10.8	8.4	-15.0	3.0	-3.4
[SYNA00F2/[SYNI137TN-SR]F1]	35.4	27.9	30.9	20.0	9.0	12.9
[SYNA00F2/SYNK64R-SR-F2]	26.4	13.4	18.6	15.7	2.5	7.2
[SYNA00F2/SYNTemperateB-SR-F2]	44.0	9.0	23.0	23.7	-3.6	6.2
[SYNA00F2/SYNSC-SR-F2]	31.3	9.6	18.3	17.3	-0.1	6.1
[SYNA00F2/P502-SRc0-F3]	-1.7	9.1	4.8	-17.7	-1.2	-7.1
[99SADVIA-#/[SYNI137TN-SR]F1]	5.3	19.1	13.6	-13.1	-2.2	-6.1
[99SADVIA-#/SYNK64R-SR-F2]	19.8	10.0	13.9	1.8	-6.9	-3.8
[99SADVIA-#/SYNTemperateB-SR-F2]	35.8	9.2	19.9	12.4	-3.8	2.0
[99SADVIA-#/SYNSC-SR-F2]	-1.6	9.3	4.9	-16.9	-1.9	-7.3
[99SADVIA-#/P502-SRc0-F3]	18.3	1.7	8.3	7.1	-4.1	-0.1
[99SADVLA-#/[SYNI137TN-SR]F1]	57.4	16.4	32.8	31.1	-4.7	8.1
[99SADVLA-#/SYNK64R-SR-F2]	-3.0	11.2	5.5	-17.5	-6.0	-10.1
[99SADVLA-#/SYNTemperateB-SR-F2]	14.2	15.9	15.2	-10.9	0.9	-3.3
[99SADVLA-#/SYNSC-SR-F2]	16.0	17.0	16.6	-6.5	4.7	0.7
[99SADVLA-#/P502-SRc0-F3]	22.8	6.1	12.7	4.5	-2.8	-0.2

APPENDIX H

SPECIFIC COMBINING ABILITY EFFECTS FOR GRAIN YIELD (MG HA^{-1}) OF SINGLE AND THREE-WAY CROSS HYBRIDS

	Tx114	CML78	Tx110	CML78 xTx110	Tx114x CML78	Tx114x Tx110
CML343	-0.01	0.19	0.30	0.51	-0.20	-0.75**
CML311	0.44	0.06	0.33	-0.98**	0.62*	-0.42
CML269	0.15	0.14	-0.45	-0.44	0.16	0.48
CML270	0.21	-0.30	-0.24	-0.09	0.13	0.35
CML176	-0.33	0.30	-0.72*	0.24	0.33	0.22
CML322	-0.70*	0.82**	-0.38	-0.01	0.43	-0.12
CML405	0.34	-0.10	-0.12	0.47	-0.60*	0.05
NC340	0.49	-0.15	0.54	-0.52	-0.28	-0.03
T35	0.46	-0.02	0.61*	-0.47	-0.24	-0.30
T39	-0.92**	-0.43	0.62*	0.64*	0.29	-0.15
Tx130	-0.14	0.29	-0.47	0.60*	-0.31	0.09
Y21	-0.20	-0.50	0.24	0.36	-0.10	0.23
Tx601W	0.08		-0.41		-0.38	0.21

VITA

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