Heterosis and Combining Ability of Drought-Tolerant Maize Lines for Grain Yield in Contrasting Moisture and Plant Density Environments

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Abstract

In drought prone areas of Ethiopia, maize is produced by small-scale farmers' where additional inputs are rarely applied. Although genetic tolerance is recommended for moisture stress, there is limited information on drought-tolerant genotypes reaction to variable environments. In this study, eight drought tolerant lines and their diallel crosses were tested separately in randomized complete block design under normal and high plant densities that combined with well watered and drought stress to estimate performance, heterosis and combining ability for grain yield. Both types of genotypes gave highest grain yield under well watered high plant density. However, least performance of inbred lines and highest heterosis was recorded under drought stressed high density, which confirmed more stress tolerance of hybrids than their parents. Although the predominant role of non-additive effects was observed for grain yield in most environments, the highly significant GCA x E and SCA x E interactions shows that combining ability effects change with growing conditions. Moreover, the observed weak association between grain yield of hybrids and inbred lines per se suggested the importance of evaluation of crosses in variable environments. Some of the new crosses gave better yield than local hybrids in less stress and stress environments. Generally, this study confirmed that hybrids developed from drought-tolerant inbred lines combined stress tolerance and high yield potential.

Introduction

Most tropical maize (*Zea mays* L.) is produced under rain-fed conditions, in areas where drought is widely considered to be the most important abiotic constraint for production. Severe drought occurs each year in at least one country within eastern and southern Africa, resulting in frequent crop failures (Waddington *et al*., 1995). For instance, although the affected area coverage and intensity vary, this stress is a common phenomenon in Ethiopia where about 70% of the land is considered as dry land (Mati, 2005). In addition, increased population pressure, high input costs, and extreme poverty also force smallholder farmers in these areas to implement low input farming systems.

Maize is most sensitive to drought during two weeks of bracketing flowering that often results in barrenness and serious yield loss with little chance of replanting or compensation (Bolaños and Edmeades, 1996). The stress can be alleviated either through improvement in agronomic practices or genetic stress tolerance of the crop. However, improvement of maize tolerance to drought at flowering remains the best option especially to small-scale farmers who cannot afford additional inputs (Vasal *et al.*, 1997). Furthermore, the maize genotypes bred for drought tolerance at flowering are reported to be tolerant to low-N stress (Bänziger *et al.*, 1999), and have improved broad adaptation (Chapman and Edmeades, 1999). Thus, considering the unpredictable nature of drought and resource-poor farmers, hybrids that exhibit heterosis are considered as the best alternative due to their performance as compared to open pollinated varieties in both favourable and stress environments (Duvick, 1999; Vasal *et al.*, 1997). The degree of heterosis depends on the relative performance of inbred lines and crosses, as well as on differential effect of the environment (Betran *et al.*, 2003a). Studies have proved that heterosis is greater under stress than favourable conditions due to higher sensitivity of inbred lines to stress than their crosses (Duvick, 1999; Betran *et al.*, 2003b). Furthermore, Duvick (1999) emphasized that yield gains in hybrids always were accompanied by improvement in tolerance to biotic and abiotic stresses.

CIMMYT (International Maize and Wheat Improvement Research Centre) has developed drought tolerant maize inbred lines especially for better performance during drought at flowering, while maintaining good performance under non-stressed conditions (Bolaños and Edmeades, 1996; Vasal *et al.*, 1997). However, there is limited information on their combining abilities and heterosis generated among these inbred lines under contrasting moisture and plant population levels. It is generally considered that inbred lines with superior yields under drought condition will provide superior hybrids under stress (Vasal *et al.*, 1997). Hybrids derived from inbred lines tolerant to high-plant density also showed superior performance under high plant population (Troyer, 1996). However, some studies on combining abilities showed that general combining ability (GCA) and specific combining ability (SCA) for yield interacted with environmental (E) change (Debnath and Sarkar, 1990), while Betran *et al.* (2003a) reported non-significant SCA x E interaction. The objectives of this study were to examine performance, heterosis and combining ability effects for grain yield in drought-tolerant inbred lines and their crosses under contrasting moisture and plant-density environments.

Material and Methods

In 2001, eight drought tolerant maize inbred lines were requested and obtained from CIMMYT's Drought Tolerant Improvement Unit. Detail descriptions of the eight inbred lines are given elsewhere (Gezahegn et al., 2007). A diallel cross excluding reciprocals was made among these lines at the Grain Crops Institute at Potchefstroom, Republic of South Africa in 2002. The study was conducted during the off-season, from September 2002 to February 2003, in Ethiopia at Melkassa Agricultural Research Centre (8°24′N, 39°21′E, 1550 masl) under the following four partially controlled growing conditions: (i) Well-watered normal plant density (WWND), where about 44

400 plants ha^{-1} were established with a spacing of 30 cm between plants within rows, and irrigated at seven days intervals until maturity; (ii) Well-watered high plant density (WWHD), where the plant density in environment 'i' was doubled with a spacing of 15 cm between plants; (iii) drought stressed normal plant density (DSND), where irrigation was suspended from 15 days prior to 50 % anthesis until 25 days after anthesis when one additional irrigation was applied, the plant population was the same as in 'i'; and (iv) drought stressed high plant density (DSHD), drought stressed as in 'iii' but with plant density increased as in 'ii'.

During evaluation of the crosses, two Ethiopian maize hybrids, BH-540 and BH-140, were included as checks to assess the extent of adaptation of the new hybrids to Melkasa. A furrow irrigation system was used to apply about 40 mm of water (estimated by partial flume) every seven days over all growing conditions, until watering was suspended for the drought stressed environments. Rain didn't interfere during the trial as there was drought in most part of the country. Soil texture of the trial site was clay loam. In each environment, lines and hybrids were evaluated separately in adjacent experiments to eliminate the effects of differences in vigor between inbred lines and hybrids. A randomized complete block design with four replications was used for each trial under each growing condition. For hybrids, each block was folded to minimize soil variability within block. Each entry was planted in four 5.1 m long rows using 0.75 m inter-row spacing, and intra-row spacing as determined above. For each trial, an additional plot was added at each end of a block where BH-140 was planted to avoid border effects. The four trials under each maize type were sown in adjacent blocks within the same field, while five free rows between well watered and drought stressed conditions were left to avoid leaching to the stressed environments. Two seeds $hill^{-1}$ were planted, and plots were later thinned to obtain the required plant density. For each trial, the recommended fertilizer rate was applied at a rate of 50 kg P_2O_5 ha^{-1} and 25 kg N ha^{-1} at planting, followed by a side dressing of 25 kg N ha^{-1} 35 days later. All trials were kept free of weeds.

Grain yield per plot was measured in gram from well-bordered plants in the central two rows by excluding a plant nearest the alley of each row. In the text it was reported in ton $hectare^{-1}$ (t ha^{-1}) at 15% moisture content. In each environment, grain yield data from each trial was first tested for normality. Then it was analyzed using environment (plant densities and moisture levels) and genotype (hybrids and inbred lines) as fixed effects, and replicates within environment as random effects. After detection of significant F-values for genotypes, a separate combining ability analysis under each growing condition was performed, using Agrobase 20 Software (Agronomix Software Inc., 1999). The analysis of combining ability across environments was also computed using PROC GLM in SAS (1997). Griffing's Method 4, Model I of the diallel cross analysis was used to estimate general combining ability (GCA) of the inbred lines and specific combining ability (SCA) of the hybrids effects (Griffing, 1956). For individual trials, significance of GCA and SCA values was determined by t-test, using gi and sij variances, respectively. For combined environments, the significance of GCA and SCA sources of variation were determined using the corresponding interaction with environments as error terms (Zhang and Kang, 1997). The significance of GCA × E and SCA × E interactions was determined using the pooled error. Furthermore, the ratio between GCA and SCA mean squares were also estimated to determine the relative magnitude of mean squares due to GCA and SCA (Baker, 1978). Mid-parent heterosis (MPH) for grain yield also was calculated as: $MPH = \frac{(F_1 - MP)}{MP} x100$ where F_1 is the mean of the cross and MP is the mean of the two parents. Pearson correlation coefficients between inbred line *per se* and hybrid performance were estimated by regressing the F_1 grain yield on mid parent value, and also by regressing the GCA values on inbred line *per se* yield.

Results and Discussion

Environment mean grain yields for the inbred lines (Table 1) ranged from 0.81 (DSHD) to 3.52 t ha^{-1} (WWHD), while for hybrids (Table 2), ranged from 2.66 (DSHD) to 6.98 t ha^{-1} (WWHD). Based on the performances of the tested maize genotypes in this study, WWHD and DSHD were considered as high yielding and unfavorable (severe stressed) environments, respectively. Although WWND was expected as high yielding (optimum) environment, highest performance of the inbred lines and crosses were recorded under WWHD. However, the productivity of the inbred lines was reduced more (77%) than hybrids (62%) in severe drought stressed (DSHD) condition. Similar results were reported by Betran et al. (2003a) who pointed out that yield of hybrids under severe and intermediate drought stress were 13 and 50% of the yield under well-watered conditions, while their drought tolerant parental lines provided 5 and 48% respectively.

In addition to verification of the superiority of a hybrid in relation to its parents, the observed results have taken our attention to suggestion by Duvick (1999) who indicated that yield gains in hybrids always supported by improvement in tolerance to biotic and abiotic stresses. However, a greater yield reduction was recorded in Mexico than Melkasa, which may be due to differences in intensity of stress and improvement of the parental lines. Besides, considerable number of the new crosses performed better in both stress and non-stress environments than the local hybrids. Thus, the results in this study confirmed that some of the hybrids from drought tolerant inbred lines combined stress tolerance and high yield potential.

Combining ability

GCA mean squares were significant for grain yield only when well watered, while SCAs were important in different level of stresses and over all environments (Table 3). The GCA/SCA ratios in most environments, except in WWND, were also less than unity. These results indicated the predominant role of non-additive genetic effect in controlling the expression of the trait under stressed growing conditions. It was in agreement with a study made with eight inbred lines in USA (Sughroue and Hallauer, 1997). However, the observed highly significant GCA x E and SCA x E interactions indicated that both additive and non-additive genetic effects were influenced by the environment. Similar result was observed when these materials tested under rainfed condition (Gezahegn et al., 2007). This suggests the need of selecting different parental lines for hybrids to be used in specific environment. Furthermore, the highly significant SCA x E confirmed that the specific hybrid combinations for this trait was not stable across environments. Some of the crosses also showed inconsistent performances across the contrasting growing conditions. Consistent with this study Debnath and Sarkar (1990) reported crosses interaction with environments. However, some of the superior crosses like Mex103 x CML202 and CML440 x Ken had consistent performance across the contrasting environments.

Table1. General combining ability effects (GCA), inbred line *per se* performance in t ha^{-1} (Line) across environments, and association between GCA and Line.

Source and Lines' name	Environments†									
	WWND		WWHD		DSND		DSHD		Over All	
	GCA	Line	GCA	Line	GCA	Line	GCA	Line	GCA	Line
Mex101	-0.469	3.39	-0.208	4.22	0.142	0.82	0.414*	0.83	-0.084	2.32
Mex102	-0.094	3.55	-0.135	4.15	-0.142	1.10	-0.055	1.60	-0.146	2.60
Mex103	-0.091	2.10	-0.095	3.31	-0.090	0.85	0.074	1.05	-0.027	1.83
CML440	-0.494	2.50	0.175	3.20	0.285	1.15	-0.041	0.74	-0.016	1.90
CML442	0.188	2.49	0.272	4.54	0.048	0.99	-0.254	0.32	0.019	2.08
CML202	0.380	3.32	0.305	3.62	-0.077	1.54	0.064	0.63	0.15	2.28
Ken	0.523*	3.28	-0.210	3.62	-0.017	1.76	-0.137	0.66	0.081	2.33
CML445	0.057	3.74	-0.101	4.11	-0.149	1.04	0.034	0.79	0.023	2.42
Environment's mean GY		2.80		3.52		1.10		0.81		2.01
SED(GCA)/ LSD Line	0.237	0.818	-0.208	0.95	0.124	0.609	0.331	0.703	0.089	0.33
r (GCA. Line)	0.2		-0.06		-0.13		0.23		-0.17	

† WWND= Well watered normal-plant density; WWHD= Well watered high-plant density; DSND= Drought stressed normal density; DSHD= Drought stressed high density; SED= Standard error of difference between two GCAs; LSD = The least significant difference for inbred line *per se* means; *Indicates significance of GCA effects estimates at P = 0.05; r(GCA. Line) = Correlation between GCA and line per se in yield.

The GCA effects of the parental lines for the tested trait under contrasting environments were variable in both magnitude and direction (Table 1). However, only Ken under WWND, and Mex101 under DSHD showed significant positive effects for yield. CML202 and CML445 showed consistent positive GCA effects in most environments, with promising *per se* yield. Furthermore, CML442 showed considerable GCA effects and *per se* performance under WWHD, but the least in both terms under drought stressed conditions. In other report, intermediate GCA for CML442, and good GCA for CML445 and CML202 under optimum and drought growing conditions were reported (CIMMYT, 2002).

Table2. Mean grain yield (t ha^{-1}) in each and across environments.

	Environments					
Crosses' name	WWND	WWHD	DSND	DSHD	Across	Rank
Mex101xMex102	6.35	7.13	2.50	2.75	4.68	18
Mex101xMex103	5.09	6.52	3.25	4.00	4.71	16
Mex101xCML440	3.50	5.83	3.50	2.75	3.89	30
Mex101xCML442	6.27	7.42	2.75	3.25	4.92	9
Mex101xCML202	5.94	6.12	3.00	3.50	4.64	20
Mex101xKen	6.01	6.45	3.50	2.75	4.68	19
Mex101xCML445	6.53	8.01	4.50	2.25	5.32	4
Mex102xMex103	4.83	6.06	3.00	2.50	4.10	29
Mex102xCML440	4.90	6.49	3.75	2.50	4.41	24
Mex102xCML442	6.38	7.07	2.75	2.00	4.55	22
Mex102xCML202	7.34	7.89	3.00	1.75	4.99	7
Mex102xKen	6.61	6.65	2.75	3.00	4.75	15
Mex102xCML445	5.53	6.62	3.25	3.75	4.79	12
Mex103xCML440	6.00	7.51	3.75	1.25	4.30	27
Mex103xCML442	6.43	7.64	3.50	2.50	5.02	6
Mex103xCML202	7.17	7.66	3.75	3.00	5.39	2
Mex103xKen	5.76	5.98	3.50	2.25	4.37	26
Mex103xCML445	6.68	6.78	2.75	3.50	4.93	8
CML440xCML442	6.33	7.97	3.25	3.00	5.14	5
CML440xCML202	6.06	8.26	3.00	4.00	5.33	3
CML440xKen	6.87	7.99	3.75	3.00	5.40	1
CML440xCML445	5.88	6.21	3.75	1.75	4.40	25
CML442xCML202	5.62	6.64	3.00	1.50	4.19	28
CML442xKen	7.26	6.90	3.75	1.75	4.91	10
CML442xCML445	5.34	6.70	3.50	3.00	4.63	21
CML202xKen	6.45	7.08	3.00	2.75	4.82	11
CML202xCML445	6.21	6.90	3.25	2.75	4.78	13
KEN1xCML445	6.69	6.89	2.75	2.50	4.71	17
BH-540 (Check-1)	6.55	6.35	3.59	1.55	4.51	23
BH-140 (Check-2)	6.22	6.78	3.30	2.82	4.78	14
Mean	6.07	6.98	3.23	2.66	4.75	
LSD (0.05)	1.33	1.15	1.02	0.94	1.11	

WWND= Well watered normal-plant density; WWHD= Well watered high-plant density; DSND= Drought stressed normal density; DSHD= Drought stressed high density; SED= Standard error of difference between two GCAs; LSD = The least significant difference for inbred line

The relationship between inbred lines and hybrid performance was weak positive and negative as estimated by regressing of GCA values on inbred *per se* performance (Table 1). Consistent with the present result, Samanci (1996) recorded negative correlation, while Betran *et al*. (2003a) reported weak associations under intermediate drought stress at Tlaltizapan in Mexico. The largest SCA effects was contributed by Mex102 x CML202, Mex101 x CML445, Mex103 x CML440, CML440 x CML202 and CML440 x Ken under WWND, WWHD, DSND, DSHD and across all, respectively. These crosses were also superior in yield in the respective environments (Table2). Consistent negative SCA effects with poor performance under each and across environments were observed with Mex101 x CML440 and Mex102 x Mex103. On the contrary, CML440 x CML442, Mex103 x CML442, CML440 x Ken, and Mex103 x CML202 were relatively superior in SCA effects and performance under each and across environments. Consistent with the findings reported by Betran *et al*. (2003a), this study demonstrated that high yielding crosses showed high SCA values. Further it has also confirmed that SCA predicts hybrid yield better than heterosis, since it is not affected by parental performance

Table3. Mean squares of variance for combining ability of drought tolerant maize inbred-lines evaluated in four partially controlled environments at Melkasa, 2002.

	Sources				
Environments	GCA	SCA	GCA x E	SCA x E	GCA / SCA
	(7)	(20)	(21)	(60)	
WWND	0.804*	0.634*			1.268
WWHD	0.481*	0.535**			0.899
DSND	0.154	0.219			0.703
DSHD	0.276	0.542**			0.511
Across all	0.812	2.786**	1.748**	1.646**	0.291

Numbers in parenthesis represent degrees of freedom; WWND= Well watered normal-plant density; WWHD= Well watered high-plant density; DSND= Drought stressed normal density; DSHD= Drought stressed high density; SED= Standard error of difference between two GCAs; LSD = The least significant difference for inbred line GCA= General combining ability; SCA= Specific combining ability; * , ** indicate, significantly different from zero at P = 0.05 and 0.01, respectively.

Heterosis

For all crosses, the recorded mean mid-parent heterosis (MPH) under WWND, WWHD, DSND and DSHD were 102, 83, 187 and 242%, respectively (Table 4). This demonstrated that MPH for grain yield of the hybrids increased with increasing stress or decreasing yield. Accordingly, the crosses expressed lowest mean hetrosis (83%) under high yielding environment (WWHD) and the highest (242%) under low yielding conditions (DSHD). Consistent with the present result, high expression of heterosis for yield under severe drought stress condition was reported by Betran *et al*. (2003a) who indicated poor performance of inbred-lines under stress as compared to their hybrids. In addition this study pointed out that heterosis is dependent not only on the parent combinations but also on the effect of environmental conditions.

Crosses made in combination with Mex102 were relatively low yielder and inferior in expression of heterosis in most growing conditions, reflecting its similarity with most of the inbred lines genetically and high *per se* performance, respectively (Tables 1). On the contrary, crosses with Mex103 or CML440 had high MPH in most environments, mainly due to their low *per se* performance. Most crosses with each of them also gave high grain yield, indicating that most of the inbred lines were unrelated to Mex103 and CML440. Similar observations were reported in other studies (Duvick, 1999; Betran *et al*., 2003a). This confirmed that MPH expression of most hybrids was dependent on genetic diversity between parents, relative parental *per se* performance and environmental conditions. Thus, a high degree of heterosis alone should not be taken as a reliable criterion for selection of inbred lines, but rather its performance in each combination and growing condition. Generally, this study confirmed that

Table4. Mid-parent heterosis (percent; above diagonal) and specific combining ability (SCA; below diagonal) for grain yield (t ha^{-1}) of the tested crosses in four environments.

Lines’ name	Environments															
	WWND								DSND							
	Mex101	Mex102	Mex103	†C440	C442	C202	Ken	C445	Mex101	Mex102	Mex103	C440	C442	C202	Ken	C445
Mex101		83.1	85.4	19.0	113.4	76.9	80.2	83.1		152.7	273.1	241.7	169.2	153.4	175.7	378.5
Mex102	0.84		70.9	61.8	111.4	113.7	93.7	51.6	0.24		201.5	234.3	169.0	133.2	94.3	194.2
Mex103	-0.42	-1.06*		161.0	179.9	164.8	114.2	128.8	-0.37	-0.26		244.2	278.8	190.6	164.3	200.2
CML440	-1.61**	-0.59	0.52		153.7	108.4	137.7	88.4	-0.02	-0.28	0.56*		208.3	115.9	167.5	210.1
CML442	0.48	0.23	0.26	0.56		93.5	151.5	71.6	0.051	-0.44	0.37	0.25		146.0	171.6	255.7
CML202	-0.05	0.98*	0.81	0.12	-1.02*		95.3	75.8	0.09	0.20	0.19	-0.41	-0.02		82.1	143.9
Ken	-0.12	0.11	-0.74	0.77	0.47	-0.53		90.5	-0.35	0.19	-0.19	0.03	-0.15	0.31		91.7
CML445	0.87	-0.51	0.64	0.24	-0.97*	-0.30	0.04		0.35	0.34	-0.30	-0.14	-0.06	-0.36	0.17	
	WWHD								DSHD							
Mex101		70.3	73.3	57.0	69.3	56.1	64.4	92.2		130.9	33	248.7	46	349.9	271.3	167.8
Mex102	0.51		62.4	76.7	62.7	103.1	71.1	60.2	-0.19		91.3	113.6	101.4	63.6	152.3	216.5
Mex103	-0.13	-0.67		130.8	94.6	121.0	72.6	82.6	0.92*	-0.14		45.8	253.8	265.6	162.3	268.2
CML440	-1.10*	-0.51	0.47		106.0	142.1	134.2	70.0	-0.27	-0.04	-1.36**		464.5	462.9	323.1	150.3
CML442	0.39	-0.03	0.50	0.57		62.7	69.1	55.0	0.47	-0.30	0.05	0.74*		214.1	265.2	382.3
CML202	-0.94*	0.76	0.49	0.82*	-0.90*		95.6	78.5	0.15	-0.86*	0.27	1.15**	-0.90*		349.7	272.6
Ken	-0.09	0.04	-0.67	0.57	-0.12	0.03		78.3	-0.16	0.38	-0.34	0.49	-0.39	0.30		214.0
CML445	1.36**	-0.11	0.01	-0.82*	-0.43	-0.27	0.25		-0.93*	1.14**	0.60	-0.72*	0.32	-0.13	0.29	

WWND= Well watered normal-plant density; WWHD= Well watered high-plant density; DSND= Drought stressed normal density; DSHD= Drought stressed high density; SED= Standard error of difference between two GCAs; LSD = The least significant difference for inbred line *,** Indicate significance of SCA effects estimates at P = 0.05 and P = 0.01, respectively.

hybrids developed from drought-tolerant lines combine stress tolerance and high yield potential as best option for resource-poor farmers' fields conditions.

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