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### The Influence of Water Stress on Yield and Related Characteristics in Inbred Quality Protein Maize Lines and Their Hybrid Progeny

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#### 1. Introduction

Water stress is one of the factors most frequently limiting maize production, food security, and economic growth in sub-Saharan Africa. The unprecedented combination of climatic risk, declining soil fertility, the need to expand food production into more marginal areas as population pressure increases, high input costs, extreme poverty, and unavailability of credit systems, have resulted in small holder farmers in southern and eastern Africa producing maize in extremely low-input/low risk systems (Banziger and Diallo, 2004). As a consequence, crop yields are falling to very low levels and food insecurity is widespread amongst agricultural communities (Kamara et al., 2004). The development of maize germplasm able to tolerate water stress is crucial if the productivity of maize based farming systems is to be sustained or increased (Betran et al., 2003).

Maize genotypes perform differently under water stress conditions due to the existence of genetic variability for tolerance to stress (Bolanos and Edmeades, 1993; Lafitte and Edmeades, 1994; Banziger et al., 2000; 2006; Diallo et al., 2004). Betran et al. (2003) observed hybrids performing well under stress and suggested the possibility of combining stress tolerance and yield potential in tropical maize hybrids. Tolerance of maize to water stress is partly related to the development of the root system, which in turn influences water and nutrient uptake by crop plants (Moll et al., 1982; Kamara et al., 2004). In general, however, the amount of grain yields recorded from maize genotypes fall with the severity of water stress (Betran et al., 2003). Breeding strategies to develop stress tolerant maize inbred lines include screening and selection of inbreds under managed stress conditions, multi-location testing of progeny in a representative sample of the target environments, and selection under high plant populations (Beck et al., 1997). Additional information from adaptive secondary traits (ears per plant, anthesis-silking interval and leaf senescence) that show differential expression between optimal and stress conditions is genetically variable and is correlated with grain yield and is commonly used to increase selection efficiency (Bolanos and Edmeades, 1993; 1996; Banziger and Lafitte, 1997). When genetic variance and

heritability for grain yield declines under water stress (Blum, 1988; Bolanos and Edmeades, 1996), variances and heritability of anthesis-silking interval and ears per plant remain stable across water stress levels or may even increase (Bolanos and Edmeades, 1996). Anthesis-silking interval and ears per plant have, therefore, been used in selection indices to increase selection efficiency for water stress tolerance (Bolanos et al., 1993; Bolanos and Edmeades, 1996).

The choice of the most effective breeding scheme and the rate of the genetic improvement are dependent upon the relative magnitude of various gene effects (Dhillon and Pollmer, 1978). The expression and genetic variation of grain yield and secondary traits in maize vary with stress level. Additive genetic effects were found to be more important for grain yield under water stress and well-watered conditions (Betran et al., 2003; Makumbi et al., 2004). Betran et al. (1999) reported that as water stress increases so does the importance of general combining ability (GCA) and additive genetic effects. Derera et al. (2008) reported the preponderance of additive effects for grain yield and ears per plant under water stress and the importance of both additive and non-additive effects in controlling grain yield under well-watered conditions. Both additive and non-additive gene effects are important for days to anthesis, silking and anthesis-silking interval under both water stress and non-water stress environments (Derera et al., 2008).

Determining of the mode of gene action controlling yield and secondary traits in QPM germplasm under water stress, and optimal conditions would help in devising a viable conventional breeding strategy to develop nutritionally enhanced cultivars adapted to stress and optimal environments. The aim of this study was to determine (i) the combining ability and (ii) modes of gene action for grain yield and related traits in QPM inbred lines under water stress, and optimal (well-watered) conditions.

#### 2. Materials and methods

#### 2.1 Environments and stress management

The study was conducted in eastern and southern Africa, in Ethiopia, Kenya, Zambia and Zimbabwe from 2006 to 2008 (Table 1). Nine environments at Harare (HAOM), Rattray Arnold (RAOM), Mpongwe (MPOM), Bako (BKOM), Melkassa (MLOM), Pawe (PWOM), Awassa (AWOM), Jimma (JMOM) and Kiboko (KBOM) research stations comprised optimum management (optimal fertilization and supplemental irrigation as needed to avoid water stress). Fertilizer rates at each location were adjusted to reflect the agronomic recommendations for each location. The trials were conducted during the summer (main cropping) seasons of the respective countries. Two experiments were grown under water stress during the winter (dry) seasons at Chiredzi, Zimbabwe (CHDS) and Kiboko, Kenya (KBDS) research stations.

Both Chiredzi and Kiboko are largely rain free during the winter season, allowing the control of water stress intensity by withdrawing or delaying irrigation for varying lengths of time during flowering and grain filling stages (Edmeades et al., 1999). At Chiredzi, water stress was achieved by applying a total of 220 mm irrigation water in the first 50 days from planting. This regime caused severe water stress at flowering and grain filling time. The trials at Kiboko were irrigated from planting until 15 days before male flowering after which watering was withheld until 15 days after male flowering when additional irrigation was applied to prevent zero yield (Banziger et al., 2000). Care was taken so that irrigation, and

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hence stress, was as uniform as possible and the water stress blocks were not contaminated with irrigation water from neighbouring blocks or leaking pipes and wind drift. Sufficient fertilization and crop management practices were applied, except irrigation management to avoid confined effects from other factors.

Location	Country	Year	Latitude	Longitude	Altitude	Rainfall	Temp	erature C	Type of	Cada	F	ertilizati kg ha-1	on	Plot size	Density
Location	Country	rear	Latitude	Longitude	Altitude	mm	Min	Max	environment	Code	N	P <sub>2</sub> O 5	K‡	(m x m)	plants ha-1
Harare	Zimbabwe	2006/7	17°49′S	31°1′E	1489	890	14.2	26.8	Optimum	HAOM	166	56	24	4.0 x 1.50	53 333
RARS	Zimbabwe	2006/7	17º16'S	31°03'E	1341	865	14.2	27.0	Optimum	RAOM	208	35	21	4.0 x 0.75	53 333
Mpongwe	Zambia	2006/7	13°32'S	28°03'E	1300	1500	n/a†	n/a	Optimum	MPOM	208	35	21	4.0 x 0.75	53 333
Bako	Ethiopia	2007	9∘06′N	37º09'E	1650	1245	14.0	28.1	Optimum	вком	100	100	-	$4.8 \ge 1.50$	44 444
Melkasa	Ethiopia	2007	8º24'N	39º21'E	1550	680	14.6	28.6	Optimum	MLOM	50	25	-	$4.8 \ge 1.50$	$44\ 444$
Pawe	Ethiopia	2007	11º09'N	36º03'E	1100	1577	16.6	33.4	Optimum	PWOM	64	46	-	$4.8 \ge 1.50$	$44\ 444$
Awassa	Ethiopia	2007	7º08'N	38°48'E	1700	1100	12.6	26.8	Optimum	AWOM	110	46	-	4.8 x 1.50	44 444
Jimma	Ethiopia	2007	7° 46' N	36°00'E	1753	1530	12.0	26.2	Optimum	JMOM	75	70	-	$4.8 \ge 1.50$	$44\ 444$
Chiredzi	Zimbabwe	2007	21°02′ S	31°58' E	433	300	14.0	34.2	Stress	CHDS	148	56	24	4.0 x 1.50	53 333
Kiboko	Kenya	2007	2º10'S	37º40'E	975	561	14.0	33.0	Stress	KBDS	156	92	-	4.0 x 1.50	53 333
Kiboko	Kenya	2008	2º10'S	37º40'E	975	561	14.0	33.0	Optimum	KBOM	156	92	-	4.0 x 1.50	53 333

 $^{\dagger}$ n/a= not available;  $^{\ddagger}$ K= potassiu m fertilizer was not used in Ethiopia and Kenya; RARS= Rattray Arnold Research Station

Table 1. Locations and environments used to evaluate F<sub>1</sub> hybrids, with their characteristics and codes

#### 2.2 Germplasm

Fifteen inbred lines were selected based on diverse pedigree backgrounds. These lines showed better combining ability in top-cross evaluations and *per se* performance across a range of tropical and subtropical environments (data not shown). Most of the lines are resistant/tolerant to major foliar diseases of the tropics (CIMMYT, 2004). Diallel crosses were made among the 15 inbred lines in the winter of 2006 at Muzarabani, Zimbabwe. Seeds from reciprocal crosses were bulked to form a set of 105 F<sub>1</sub> hybrids. The F<sub>1</sub> hybrids were evaluated along with two QPM (SC527Q and CML144/CML159//CML176) and one normal maize (SC633) hybrid checks in all experiments conducted in Kenya, Zambia and Zimbabwe, and two normal maize (BH540 and BH541) and one QPM (BHQP542) hybrid checks in all experiments conducted in Ethiopia.

#### 2.3 Experimental design and field measurements

All experiments were laid out as 9 x 12 alpha-lattice designs (Patterson and Williams, 1976) with two replications (Table 1). Measurements were recorded on well-bordered plants by excluding the plant nearest to the alley of each row. Days to anthesis and silking were calculated as the number of days from planting to 50% pollen shed and silk emergence. Anthesis silking interval was calculated as the difference between days to silking and anthesis (ASI = DS – DA). Two weeks after pollen shed, plant height and ear height were measured as the distance from ground level to the first tassel branch or to the node bearing the main ear. Number of ears per plant was obtained by dividing the number of ears by number of plants harvested. An ear was counted if it had at least one

fully developed grain. Grain weight from all the ears of each experimental unit was measured and used to calculate grain yield (expressed in ton ha<sup>-1</sup> and adjusted to 12.5% moisture content).

#### 2.4 Statistical analysis

Before data analysis, anthesis-silking interval (ASI) was normalized using  $\ln \sqrt{(ASI + 10)}$  as

suggested by Bolanos and Edmeades (1996). Analysis of variance per environment was conducted with the PROC MIXED procedure in SAS (SAS, 2003) considering genotypes as fixed effects and replications and blocks within replications as random. Entry means adjusted for block effects generated from individual location analyses according to a lattice design (Cochran and Cox, 1960) were used to perform across environments combined analyses using PROC GLM in SAS (SAS, 2003) and combining ability analysis using a modification of the DIALLEL-SAS program (Zhang and Kang, 1997).

GCA effects of the parents and SCA effects of the crosses were estimated following Griffing's Method IV (crosses only) and Model I (fixed) of diallel analysis (Griffing, 1956). Combined analyses of variance were conducted for each trait that showed significant entry mean squares in individual environment analysis. Combining ability was analyzed, and GCA and SCA effects were estimated accordingly. The mean squares for hybrids and environments were tested against the mean squares for hybrid x environment (E) as error term while hybrid x E interactions mean squares were tested against pooled error.

Since means (over replication) of each of the genotypes were used for combined analysis of variance, estimate of pooled error mean squares were calculated following the procedure of

Dabholkar (1999) as:  $\sum_{i=1}^{n} K_i S_i^2 / \sum_{i=1}^{n} K_i r$ , where  $K_i$  and  $S_i^2$  are error degrees of freedom and

error mean square at *i*<sup>th</sup> environment, respectively, *n* is the number of environments and *r* is the number of replications in each environment. The significance of GCA and SCA sources of variation was determined using the corresponding interactions with the environment as error terms. Error mean squares calculated above were used to test the significance of GCA and SCA interactions with environment; because the combining ability mean squares were calculated based on entry means of each genotype from each environment (Griffing, 1956; Singh, 1973; Dabholkar, 1992). For GCA effects of the inbred lines, the restriction  $\sum gi = 0$  was imposed. Significance of GCA effects was determined by the t-test, using standard errors of GCA effects (Griffing, 1956; Singh and Chaudhary, 1985).

#### 3. Results

Analysis of variance for each environment revealed the existence of significant differences among hybrids for most traits except anthesis-silking interval at Harare, Mpangwe and Pawe optimal (Table 2). Mean squares due to GCA were highly significant for all traits studied at all environments. SCA effects were also significant for most traits. Mean grain yields for the QPM hybrids (excluding the checks) ranged from 0.6 t ha<sup>-1</sup> under severe water stress at Chiredze to 8.4 t ha<sup>-1</sup> under optimum management at Mpongwe (Table 3). At Kiboko, average grain yield of the hybrids tested under water stress was 35.7% of grain yield under optimal conditions (KBOM).

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Environment <sup>†</sup>	Source of variation	DF	GY	DA	DS	ASI	PH	EH	EPP
HAOM	Hybrids	104	4.6**	13.3**	15. 0**	2.0	425.4**	279.1**	0.04**
	GCA	14	6.6**	39.7**	42.4**	-	885.5**	537.9**	0.04**
	SCA	90	1.7**	1.5	2.1	-	108.1**	77.6*	0.02**
RAOM	Hybrids	104	5.5**	12.7**	15.9**	2.1**	341.5**	298.1**	0.05**
	GCA	14	6.9**	35.9**	42.6**	3.2**	467.5**	364.5**	0.07**
	SCA	90	2.1**	1.7**	2.6**	0.7	124.6**	115.5**	0.02**
MPOM	Hybrids	104	10.1**	3.6**	3.3**	0.8	986.7**	459.0**	0.03*
	GCA	14	15.8**	6.4**	5.1**		1278.1**	703.1**	0.02**
	SCA	90	3.4**	1.1	1.1	- 🗌	371.3**	155.8**	0.01
BKOM	Hybrids	104	5.0**	51.2**	51.0**	2.5**	589.4**	280.9**	0.13**
	GCA	14	8.3**	161.9**	157.8**	5.2**	850.5**	627.9**	0.30**
	SCA	90	1.6**	4.4**	4.9**	0.7	208.2**	64.6	0.03**
MLOM	Hybrids	104	3.9**	22.2**	22.2**	1.5**	570.6**	357.9**	0.11**
	GCA	14	6.2**	66.3**	62.5**	2.5**	633.0**	420.7**	0.26**
	SCA	90	1.3**	2.5*	3.1*	0.5*	231.2**	141.4*	0.02**
PWOM	Hybrids	104	3.6**	35.3**	36.6**	1.8	367.7**	212.8**	0.04**
	GCA	14	4.4**	77.5**	85.9**	-	335.9*	150.5**	0.03**
	SCA	90	1.4	8.4**	7.8**	-	160.2**	99.5**	0.02**
AWOM	Hybrids	104	2.6**	20.0**	18.3**	4.4**	571.9**	278.4**	0.12**
	GCA	14	2.9**	63.1**	55.7**	5.4**	757.9**	381.2**	0.16**
	SCA	90	1.0**	1.8**	1.9*	1.7*	212.5**	101.5**	0.04*
JMOM	Hybrids	104	3.2**	39.9**	35.4**	1.7**	598.3**	308.6**	0.07**
	GCA	14	4.8**	124.9**	110.2**	1.1**	924.7**	409.7**	0.13**
	SCA	90	1.1**	3.6**	3.3**	0.8**	201.9**	114.6	0.02**
CHDS	Hybrids	104	0.3**	71.2**	309.2**	108.4**	762.6**	293.3**	0.08**
	GCA	14	0.5**	207.6**	900.5**	271.4**	1598.7**	314.3**	0.19**
	SCA	90	0.1*	8.9**	38.6**	20.4*	191.9**	120.6**	0.02**
KBDS	Hybrids	104	3.8**	34.5**	90.9**	20.6**	-		0.09**
	GCA	14	10.2**	115.0**	254.7**	33.1**	$\rightarrow$		0.22**
	SCA	90	0.6**	-2.0**	12.9**	6.8**	-)		0.02*
KBOM	Hybrids	104	9.4**	17.4**	18.4**	2.2**	427.0**	204.5**	0.03**
	GCA	14	14.7**	56.2**	56.7**	5.5**	807.6**	492.3**	0.05**
	SCA	90	3.2**	1.3**	1.8**	0.4	121.1**	41.5*	0.01**

HAOM=Harare optimal, RAOM=Rattray optimal, MPOM=Mpongwe optimal, BKOM=Bako optimal, MLOM=Melkasa optimal, PWOM=Pawe optimal, AWOM=Awassa optimal, JMOM=Jimma optimal, CHDS=Chiredzi stress, KBDS=Kiboko stress, KBOM=Kiboko optimal\*  $P \le 0.05$ ; \*\*  $P \le 0.01$ ; DF= degrees of freedom; GY= grain yield; AD= days to anthesis; DS= days to silking; ASI= anthesis-silking interval; PH= plant height; EH= ear height; EPP= ears per plant

Table 2. Mean squares for hybrids, general (GCA) and specific (SCA) combining ability for grain yield and agronomic traits in stressed and optimal environments, 2006 – 2008

Combined analysis of variance across water stress environments revealed highly significant mean squares due to environments and hybrids for all traits analyzed (Table 4). Mean grain yield across water stress environments ranged from 0.3 to 3.7 t ha<sup>-1</sup> with a mean of 1.8 t ha<sup>-1</sup>. Higher grain yields were recorded for VL052 x VL05561 (3.7 t ha<sup>-1</sup>), VL05561 x CML159 (3.5 t ha<sup>-1</sup>), VL054178 x VL06375 (3.4 t ha<sup>-1</sup>), VL05482 x VL05561 (3.3 t ha<sup>-1</sup>) and VL054178 x VL05561 (3.0 t ha<sup>-1</sup>). Mean grain yield across water stress environments (Table 4) was 27.4% of the mean grain yield across optimal environments (Table 5). Mean days to anthesis was 92.3 with a range of 82.8 – 103.5. Days to silking ranged from 83.7 to 120.0 d with a mean of 102.0. Anthesis-silking interval ranged from 0.4 to 21.4 with a mean of 9.7. Ears per plant ranged from 0.10 to 0.88 with a mean 0.50. Combining ability analysis revealed non-significant GCA mean squares for grain yield but significant GCA mean squares for days to anthesis-silking interval and ears per plant. SCA mean squares, however, were not significant for all traits. Hybrid x E, GCA x E and SCA x E interaction mean squares were significant for all traits tested.

Across optimal environments, the effects of environments, hybrids, GCA and SCA were highly significant for all the traits evaluated (Table 5). Grain yields ranged from 1.8 to 9.4 t ha<sup>-1</sup> with a mean of 6.5 t ha<sup>-1</sup>. The highest yielding hybrids were VL05483 x CML491 (9.4 t ha<sup>-1</sup>), CML511 x CML491 (8.8 t ha<sup>-1</sup>), VL05561 x CML491 (8.7 t ha<sup>-1</sup>), CML159 x CML491 (8.5 t ha<sup>-1</sup>) and VL054178 x CML491 (8.1 t ha<sup>-1</sup>). Mean days to anthesis was 73.8 with a range of 66.9 – 80.4. Days to silking ranged from 68.9 to 82.8 with a mean of 75.1. Mean plant and ear height was 225.5 and 110.9 cm with ranges of 189.0 – 248.4 cm and 89.9 – 131.7 cm. Mean ears per plant was 1.14 with ranges of 0.79 – 1.48. Anthesis-silking interval ranged from -0.2 to 3.3 d with a mean of 1.6 d. Hybrid x E, GCA x E and SCA x E interactions were highly significant for all traits except SCA x E for ear height and anthesis-silking interval.

	HAOM	RAOM	MPOM	BKOM	MLOM	PWOM	AWOM	JMOM	CHDS	KBDS	KBOM
Grand mean	7.7	6.5	8.4	6.5	6.7	4.9	4.7	4.6	0.6	2.9	8.1
Hybrid mean	7.7	6.4	8.4	6.5	6.7	4.9	4.7	4.6	0.6	2.9	8.2
Best hybrid	12.9	10.6	13.8	9.7	10.6	8.8	7.2	7.9	2.1	5.7	12.1
Best QPM check	9.1	7.8	9.2	6.4	5.9	3.8	4.7	4.9	1.0	2.4	7.5
Best normal check	11.6	10.0	8.6	7.4	6.5	6.1	6.0	2.5	0.3	3.2	5.5
SE (m)	0.6	0.9	0.7	0.3	0.5	0.8	0.5	0.4	0.2	0.5	0.5
% high yielding hybs‡	1.0	1.0	41.9	31.4	61.0	14.3	10.5	41.0	13.3	45.7	73.3

HAOM=Harare optimal, RAOM=Rattray optimal, MPOM=Mpongwe optimal, BKOM=Bako optimal, MLOM=Melkasa optimal, PWOM=Pawe optimal, AWOM=Awassa optimal, JMOM=Jimma optimal, CHDS=Chiredzi stress, KBDS=Kiboko stress, KBOM=Kiboko optimal. ‡ proportion of QPM hybrid with higher grain yield than the best check (normal maize or QPM); SE(M)= standard error of the mean

Table 3. Means of QPM hybrids, and best normal and QPM checks for grain yield in stress and optimal environments, 2006 -2008

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Sources of variation	DF	GY	DA	DS	ASI	EPP
Environment (E)	1	275.0**	65614.0**	116716.3**	7339.6**	14.24**
Hybrid	104	1.3**	46.7**	159.8**	42.4**	0.07**
GCA	14	7.3	308.8**	1030.3**	233.0**	0.39**
SCA	90	0.4	5.9	24.3	12.7	0.02
Hybrid x E	104	0.7**	6.1**	40.3**	22.1**	0.02**
GCA x E	14	3.3**	13.8**	124.9**	71.5**	0.02**
SCA x E	90	0.3**	5.0**	27.1**	14.4*	0.02**
Error	164	0.2	2.5	11.8	8.8	0.01
Mean		1.8	92.3	102.0	9.7	0.50
Minimum		0.3	82.8	83.7	0.4	0.10
Maximum		3.7	103.5	120.0	21.4	0.88
SE (m)		0.3	1.1	2.4	2.1	0.07
CV%		24.1	1.7	3.4	30.7	20.0

\*  $P \le 0.05$ ; \*\*  $P \le 0.01$ ; ASI= Anthesis silking interval; CV= coefficient of variation; DA= days to anthesis; DF= degrees of freedom; DS= days to silking; EPP= ears per plant; GCA= general combining ability; GY= grain yield; SCA= specific combining ability; SE (m)= standard error of the mean

Table 4. Mean squares from combined analysis of variance and means for grain yield and agronomic traits of QPM hybrids across water stress environments at Chiredzi and Kiboko, 2007

Sources of								
variation	DF	GY	DA	DS	PH	EH	EPP	ASI
Environment (E)	8	231.4**	5263.9**	7362.0**	61527.2**	46311.2**	3.09**	509.0**
Hybrids	104	14.4**	69.8**	71.1**	1356.2**	643.5**	0.11**	2.8**
GCA	14	46.8**	477.1**	472.7**	5289.2**	2925.7**	0.58**	13.2**
SCA	90	9.4**	6.5**	8.6**	744.4**	288.5**	0.04**	1.2**
Hybrids x E	832	1.2**	4.7**	4.6**	135.4**	87.0**	0.02**	0.9**
GCA x E	112	2.6**	17.2**	16.2**	183.5**	129.1**	0.05**	1.6**
SCA x E	720	0.8**	2.2**	2.2**	110.5**	69.3	0.02**	0.6
Error	738	0.6	1.5	1.8	73.1	61.7	0.01	0.6
Mean		6.5	73.8	75.1	225.5	110.9	1.14	1.6
Minimum		1.8	66.9	68.9	189.0	89.9	0.79	-0.2
Maximum		9.4	80.4	82.8	248.4	131.7	1.48	3.3
SE (m)		0.3	0.4	0.5	2.9	2.6	0.03	0.3
CV%		11.6	1.7	1.8	3.8	7.1	8.8	47.8

\*  $P \le 0.05$ ; \*\*  $P \le 0.01$ ; ASI= anthesis-silking interval; CV= coefficient of variation; DA= days to anthesis; DF= degrees of freedom; DS= days to silking; EH= ear height; EPP= ears per plant; GCA= general combining ability; GY= grain yield; PH= plant height; SCA= specific combining ability; SE (m)= standard error of the mean

Table 5. Mean squares from combined analysis of variance and means for grain yield and agronomic traits of QPM hybrids across nine optimal environments, 2006 – 2008

Estimates of GCA effects for grain yield showed that inbred lines VL05561, VL05483, CML511, CML159 and VL06375 combined well in most of the environments (Table 6). These inbred lines mostly showed positive and highly significant GCA effects in most environments. On the other hand, VL052, VL052887, VL0523 and CML144 showed negative and highly significant GCA effects in most of the environments. Inbred lines VL05561, VL05483 and CML511 showed high positive GCA effects across optimum and combined environments.

For days to anthesis, VL054178, VL05482, VL05561, VL05483, CML511 and VL06375 had negative and highly significant GCA effects in most environments (Table 7). On the other hand, inbred lines VL05200, VL054178, VL052887, VL0523, VL05561 and CML144 showed positive and highly significant GCA effects in most environments. VL054178, VL05482, VL05561, VL05483, CML511, CML159 and VL06375 had highly significant negative GCA effects for days to silking for both water stress and optimal environments.

Inbred lines VL054178, VL05482, VL05561, VL05483 and VL06375 had negative and highly significant GCA effects for days to silking (Table 8). On the other hand, VL05468, VL052887, VL0523, VL0524, CML144 and CML491 showed positive and highly significant GCA effects. VL054178, VL05482, VL05561, VL05483, CML159 and VL06375 had highly significant negative GCA effects for days to anthesis for both water stress and optimal environments.

The GCA effects for anthesis-silking interval were negative and highly significant for VL05561 but positive and highly significant for VL054178 in almost all environments (Table 9). Across water stress environments, inbred lines VL054178 and VL05482 showed lower GCA effects. VL052887, VL05561 and CML144 had negative and highly significant GCA effects across optimal environments. VL054178, VL05561, VL05483 and VL06375 showed lower GCA effects for anthesis-silking interval over all environments.

Inbred lines VL05200, VL054178, VL05482, CML144 and CML159 showed negative and significant GCA effects for plant and ear height in most environments (Tables 10 and 11). However, VL05483 and VL06375 had positive and significant GCA effects for plant height while VL053, VL0524 and VL5561 had positive and significant GCA effects for ear height in most environments.

For ears per plant, inbred lines VL05482, VL05483 and CML511 showed positive and significant and VL05200, VL05468, VL0523, VL0524 and CML159 showed negative and highly significant GCA effects in water stress and optimal environments (Table 12). At Chirezi under water stress, VL05482, CML511 and CML491 showed negative and significant GCA effects.

#### 4. Discussion

The results observed in various environments (Table 2) showed that water stress significantly affected grain yield, as previously reported (Bolanos and Edmeades, 1993, 1996; Banziger et al., 1997; Banziger and Lafitte, 1997; Banziger et al., 1999a; Derera et al., 2008). High levels of variation observed among hybrids under water stress, and optimal environments indicate the possibility of selecting for improved grain yield and agronomic traits under stress and non-stress conditions. The existence of genetic variability in maize evaluated under stress conditions has been reported by several investigators (Bolanos et al., 1993; Bolanos and Edmeades, 1996; Banziger and Lafitte, 1997; Beck et al., 1997; Banziger et al., 1997; 1999b; Betran et al., 2003; Derera et al., 2008). Significant GCA and SCA mean squares for most traits in each environment indicate the importance of both additive and non-additive effects for the traits studied. This suggests that effective selection or systematic hybridization could be employed in improving these traits.

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Table 6. Estimates of general combining ability effects of 15 QPM inbred lines for grain yield per environment, 2006 -2008

Table 7. Estimates days to anthesis pe												
of general r environ			$\supset$							$\hat{a}$		
me	Environment <sup>†</sup>	P1	P2	P3	P4	P5	P6	P7	P8	Р9	P10	P11
nt B	HAOM	0.42	1.48*	1.63**	-2.75**	1.89**	-3.84**	1.39**	1.05**	-0.84**	-1.19**	0.26
an	RAOM	0.46*	0.69**	1.87**	-2.32**	1.81**	-2.80**	2.19**	1.52**	-1.03**	-1.56**	-0.61*
d a	MPOM	-0.68**	-0.29	0.12	0.12	-0.46	0.68**	0.17	-0.36	0.14	0.14	1.74**
icr a	ВКОМ	0.90**	0.91**	2.66**	-5.11**	4.87**	-6.15**	3.07**	3.34**	-0.26**	-3.71**	-1.44**
bil	MLOM	0.58	0.78*	1.81**	-2.83**	3.11**	-5.02**	2.28**	2.04**	-0.63	-2.22**	-0.73*
ity	PWOM	1.37*	1.42*	1.79**	-3.48**	3.98**	-4.36**	1.33*	2.16**	-2.89**	-1.39*	1.05
Ni (C	AWOM	1.00**	1.51**	1.55**	-2.88**	3.00**	-4.22**	1.51**	1.39**	-0.76**	-2.30**	-0.99**
ro	JMOM	1.01**	-2.74**	-2.05**	1.99**	-1.65**	2.72**	-2.74**	-0.16	2.66**	-4.26**	4.21**
Ann A	CHDS	2.36**	1.72**	1.35*	-5.31**	3.50**	-5.78**	4.88**	2.79**	-0.81	-3.25**	-3.89**
eff	KBDS	1.88**	1.21**	1.83**	-4.03**	4.46**	-5.00**	2.05**	2.06**	-1.23**	-3.25**	-2.37**
ect	KBOM	1.01**	0.58**	1.51**	-2.81**	2.66**	-4.16**	2.14**	1.61**	-1.17**	-1.86**	-1.09**
20 S	ACDRT‡	2.12**	1.46**	1.59**	-4.67**	3.98**	-5.39**	3.46**	2.42**	-1.02**	-3.25**	-3.13**
06	ACOPT#	0.67**	0.77**	1.73**	-2.92**	2.79**	-3.99**	1.93**	1.77**	-0.77**	-1.87**	-0.43**
5 QPM inbred lines for - 2008	HAOM=Hara PWOM=Pawe optimal; * P≤ VL05200; P3= CML511; P12=	re opti e optima 0.05 ; ** VL054 = CML14	mal, R⁄ al, AWC <sup>6</sup> P≤ 0.01 68; P4= 44; P13=	AOM=R M=Awa ; ‡ ACD VL0541 CML15	attray o assa opt PRT= acr 78; P5= 9; P14=	optimal, imal, JM oss wat VL052 CML49	/ MPON /OM=Jin ter stress 887; P6= 1; P15= \	M=Mpor mma op s enviro = VL054 VL06375	ngwe o otimal, ( onments 182; P7= 5; SE(gi)	optimal, CHDS=C ; # ACO = VL052 = standa	BKOM Chiredzi PT= acr 3; P8= ` ırd error	=Bako stress, oss opt VL0524 of GC

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	SE(gi	0.34	0.29	0.24	0.36	0.39	0.57	0.30	0.37	1.14	0.62	0.23	0.65	0.12	
	P15	-2.05**	-2.36**	0.19	-3.31**	-2.20**	-1.60**	-1.72**	0.23	-7.37**	-3.82**	-2.18**	-5.60**	-1.95**	
	P14	0.93**	$0.61^{*}$	0.21	4.11**	$1.60^{**}$	$1.87^{**}$	2.00**	3.27**	7.12**	$3.11^{**}$	1.73**	5.12**	$1.73^{**}$	
	P13	0.35	-0.16	-0.35	-2.52**	0.2	-1.84**	-0.83**	3.20**	-5.59**	-2.54**	-1.35**	-4.06**	-0.89**	
	P12	$1.08^{**}$	$1.44^{**}$	-1.35**	3.11**	*66.0	$1.91^{**}$	$1.24^{**}$	-5.51**	9.08**	$5.16^{**}$	2.45**	7.12**	$1.43^{**}$	
	P11	0.64	-0.55	$1.56^{**}$	-1.41**	-0.56	0.14	-1.22**	3.71**	-6.18**	-3.72**	-0.71**	-4.95**	-0.47**	
	P10	-1.36**	-1.68**	0.22	-4.04**	-2.22**	-1.68**	-2.78**	-4.16**	-8.23**	-4.48**	-1.35**	-6.35**	-1.96**	
	P9	-0.73	-1.78**	0.05	-1.59**	-1.57**	-3.17**	-1.59**	2.44**	-4.04**	-4.01**	-2.51**	-4.02**	-1.41**	
	P8	$1.81^{**}$	$1.28^{**}$	-0.04	3.98**	$1.87^{**}$	2.14**	$1.86^{**}$	0.26	8.14**	3.24**	$1.52^{**}$	5.69**	$1.97^{**}$	
	P7	$1.57^{**}$	$1.89^{**}$	0.27	3.31**	2.09**	$1.50^{*}$	2.25**	-2.28**	$11.49^{**}$	3.28**	$1.66^{**}$	7.39**	$1.97^{**}$	
	P6	-3.84**	-2.36**	0.45	-5.58**	-4.75**	-4.59**	-3.40**	2.53**	-11.57**	-6.50**	-3.28**	-9.04**	-3.65**	
	P5	$1.59^{**}$	$1.55^{**}$	-0.52*	3.50**	2.62**	$4.16^{**}$	2.56**	-1.49**	6.00**	6.65**	2.11**	6.32**	2.36**	
	P4	-3.03**	-2.48**	0.04	-4.69**	-2.40**	-3.66**	-2.25**	$1.99^{**}$	-13.41**	-5.32**	-2.78**	-9.36**	-2.82**	
MAPE	P3	1.93**	3.36**	0.13	3.35**	2.55**	$1.88^{**}$	2.53**	-2.16**	7.35**	4.33**	2.56**	5.84**	2.30**	
	P2	0.52	0.75*	-0.33	0.52	0.97*	$1.47^{*}$	0.75*	-2.73**	2.92*	1.43*	1.20**	2.18**	0.68**	
	Ы	0.57	0.51	-0.53*	$1.27^{**}$	$0.83^{*}$	1.49*	$0.61^{*}$	0.71	$4.28^{**}$	$3.18^{**}$	0.93**	3.73**	0.71**	
	Environment <sup>†</sup>	HAOM	RAOM	MPOM	BKOM	MLOM	PWOM	AWOM	JMOM	CHDS	KBDS	KBOM	ACDRT <sup>‡</sup>	ACOPT#	

Table 8. Estimates of general combining ability effects of 15 QPM inbred lines for days to silking per environment and across environments, 2006 – 2008

Environmontt	P1	P2	P3	- P4	P5	P6	P7	P8	PQ	P10	P11	
RAOM	0.05	0.09	1.47**	-0.14	_0.22	0.47**	-0.30	-0.22	_0 80**	_0.14	0.01	
	0.00	0.07	0.76**	0.14	1 78**	0.4/**	-0.50	0.22	-0.00	0.14	0.01	-
OM	0.34	0.16	0.70	0.41	-0.45**	0.04	-0.30	-0.18	-1.24	0.01	-0.01	-(
IOM	-0.35	-0.78**	0.92**	0.57*	-0.51	0.84**	0.68*	0.10	-0 78**	-0.39	-0.32	-(
) M	-0.31	0.02	-0.03	-0.05	0.06	-0.19	0.52**	0.37*	-0.27	0.12	-0.32	(
75	1.85	1.18	6.01**	-8.08**	2 45*	-5 71**	6.62**	5.39**	-3 24**	-5 00**	-2 27*	3
S	1.00	0.23	2 47**	-1 23*	2.10	-1.53**	1 17*	1 16*	-2 73**	-1 19*	-1.30**	1
)M	-0.10	0.69**	1 07**	-0.02	-0.55**	0.88**	-0.55**	-0.02	-1 29**	0.46**	0.35*	-
DRT‡	1.55**	0.71	4.24**	-4.65**	2.34**	-3.62**	3.89**	3.27**	-2.99**	-3.09**	-1.79**	2
OPT#	-0.02	0.01	0.78**	0.22**	-0.58**	0.59**	-0.10	0.14	-0.91**	-0.05	0.03	-(
HAOM=Ha ?WOM=Pa ptimal; * <i>I</i> VL05200; P CML511; P1	rare c we opt ≥≤ 0.05 3= VL 2= CM	optimal, A imal, A ; ** <i>P</i> ≤ ( 05468; 1 IL144; P	RAOM WOM=A 0.01; ‡ A0 P4= VL0 13= CMI	=Rattray wassa oj CDRT= a 54178; P5 L159; P14	optima ptimal, Jl cross wa 5= VL052 = CML49	l, MPOI MOM=Ji ter stress 2887; P6 287; P15= 7	M=Mpo mma oj enviro: VL054 VL06375	ngwe otimal, nments 482; P7 5; SE(gi	optimal CHDS= ; # ACC ?= VL05 )= stand	, BKON Chiredz PT= acro 23; P8= lard erro	M=Bako i stress, oss opti: VL0524 or of GCA	oj KI mu ; F A e

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silking interval per environment and across environments, 2006 - 2008



Table 10. Estimates of general combining ability effects of 15 QPM inbred lines for plant height per environment and across environments, 2006 – 2008

Environment <sup>†</sup>	P1	P2	 P3	P4	P5	P6	P7	P8	P9	P10	P
HAOM	-5.51**	-6.18**	1.40	-6.45**	6.34**	-12.83**	6.95**	9.42**	4.53*	2.34	2.2
RAOM	-0.38	-8.54**	5.81**	-1.72	2.83	-8.24**	4.39*	6.25**	6.01**	-1.07	5.7
MPOM	2.16	-8.57**	-6.48**	-13.21**	4.66	-6.88**	3.68	6.21*	12.01**	6.96**	7.5
вком	0.11	-9.96**	0.88	-6.39**	4.60*	-5.46**	6.11**	9.01**	14.76**	-3.31	0.
MLOM	-0.2	-12.66**	0.34	1.80	1.57	-3.3	5.07*	5.17*	11.35**	3.30	1.
PWOM	-0.77	-4.67*	-0.82	-1.56	-0.64	-1.46	6.28**	6.68**	-0.70	1.18	-3.
AWOM	-0.72	-10.80**	-4.93*	-7.43**	5.07*	-0.29	4.08*	8.02**	2.36	5.20*	5.7
JMOM	-0.3	-0.43	0.32	-1.51	-4.02	0.54	-1.50	-10.83**	-6.90**	-2.95	8.3
CHDS	0.83	-6.67**	-4.77*	3.86	-5.04*	1.33	5.64*	5.95**	9.31**	0.9	-0.
КВОМ	-1.92	-10.05**	-0.87	-3.90**	1.82	-8.61**	8.35**	9.46**	10.55**	-0.45	1.4
KBOM HAOM=Har PWOM=Paw optimal; * P≤ VL05468; P4	-1.92 are op 2005;* = VL05	<u>-10.05**</u> timal, R nal, AW( * $P \le 0.01$ ; 54178; P5 159: P14-	-0.87 AOM=F DM=Aw ; § ACAL 5= VL05: - CML41	$-3.90^{**}$ Rattray o vassa opti: L= across 2887; P6=	1.82 ptimal, mal, JM s all envi VL054{ U 06375	-8.61** MPOM= OM=Jimi ironment 82; P7= V	8.35** Mpong na opti s; # ACC /L0523;	9.46** gwe opti mal, CH DPT= acr P8= VL	10.55** mal, BK DS=Chiro oss optim 0524; P9=	-0.45 COM=1 edzi st num en = VL0 focts	Bar Tr

ear height per environment and across environments, 2006 - 2008

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HAOM=Harare optimal, RAOM=Rattray optimal, MPOM=Mpongwe optimal, BKOM=Bako op PWOM=Pawe optimal, AWOM=Awassa optimal, JMOM=Jimma optimal, CHDS=Chiredzi stress, KBI optimal; \*  $P \le 0.05$ ; \*\*  $P \le 0.01$ ; \* ACDRT= across water stress environments; \* ACOPT= across optimu VL05200; P3= VL05468; P4= VL054178; P5= VL052887; P6= VL05482; P7= VL0523; P8= VL0524; P9 CML511; P12= CML144; P13= CML159; P14= CML491; P15= VL06375; SE(gi)= standard error of GCA eff

nf gene													
ביי	Environment <sup>†</sup>	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	ŀ
ġ	HAOM	-0.04*	-0.06*	-0.07**	-0.05*	0.01	0.07**	-0.02	0.00	0.04*	0.13**	0.03	0
זין	RAOM	-0.08**	-0.08**	-0.01	-0.03	0.07**	-0.01	-0.05*	0.03	0.02	0.07*	0.19**	-0.
<u>.</u>	MPOM	-0.01	0.00	-0.07**	-0.01	0.01	0.03	0.00	-0.07**	0.03	0.08**	0.05	0
ρq	BKOM	-0.01	-0.19**	-0.11**	-0.27**	0.34**	0.12**	-0.03	-0.01	-0.03	0.12**	0.06*	0.
לנ	MLOM	0.01	-0.04*	-0.05*	-0.18**	0.24**	0.20**	-0.18**	-0.09**	-0.09**	0.14**	0.10**	0.
<u>.</u>	PWOM	-0.01	-0.03	-0.05*	-0.02	-0.05	0.07*	0.00	-0.06*	0.07**	-0.01	0.03	-(
	AWOM	-0.01	-0.04	-0.08	-0.09*	0.17**	0.21**	-0.06	0.09	-0.05	0.05	0.00	0
Ĩ	JMOM	-0.06*	0.00	0.12**	-0.01	-0.04	0.09**	-0.07**	0.00	-0.18**	0.02	0.23**	0.
Ť	CHDS	-0.03	-0.03	-0.13**	0.19**	-0.11**	0.16**	-0.18**	-0.16**	0.05	0.06*	0.08**	-0.
2	KBDS	-0.10**	-0.06*	-0.12**	0.13**	-0.14**	0.15**	-0.18**	-0.15**	0.19**	0.13**	0.07**	-0.
- <b>- - -</b>	KBOM	-0.06**	-0.05**	-0.01	-0.07**	0.13**	0.04*	-0.08**	-0.05**	0.02	0.11**	0.05**	-(
$\hat{\mathbf{D}}$	ACDRT <sup>‡</sup>	-0.07**	-0.04*	-0.13**	0.16**	-0.13**	0.15**	-0.18**	-0.16**	0.12**	0.10**	0.07**	-0.
D V	ACOPT#	-0.03**	-0.06**	-0.07**	-0.08**	0.13**	0.09**	-0.05**	-0.02*	-0.01	0.08**	0.07**	0
$\leq$													

Table 12. Estimates of general combining ability effects of 15 QPM inbred lines for ears per plant per environment and across environments, 2006 - 2008

Combined analysis of variance across water stress (Table 4) and optimal (Table 5) environments indicated the existence of significant variation among hybrids and environments for all traits. Both additive and non-additive genetic effects were not important for grain yield across water stress environments while only additive effect was important for days to anthesis and silking, anthesis-silking interval and ears per plant. This finding is contrary to the reports of other researchers (Betran et al., 1999; 2003; Makumbi et al., 2004; Derera et al., 2008), who reported the importance of additive effects for grain yield of normal maize under water stress. When genetic variance for grain yield is not apparent, secondary traits of adaptive value whose genetic variability increases and whose heritability remains high under water stress can increase selection efficiency (Bolanos and Edmeades, 1996; Edmeades et al., 1997; Banziger and Lafitte, 1997; Banziger et al., 1999b).

Highly significant GCA and SCA mean squares for all traits under optimal environments indicate the importance of both additive and non-additive gene effects for the inheritance of these traits. Similar results have been reported in diallel studies of QPM inbred lines under optimal environments (Pixley and Bjarnason, 1993; Bhatnagar et al., 2004; Hadji, 2004; Fan et al., 2004). Derera et al. (2008) reported the importance of both additive and non-additive effects in conditioning grain yield, days to anthesis and silking, and anthesis-silking interval in Design-II crosses of normal maize inbred lines. Similarly, additive and non-additive effects were important for all traits evaluated across environments except anthesis silking interval which had non-significant SCA effects. Significant mean squares of Hybrid x E, GCA x E and SCA x E interactions for most traits across environments indicate that these effects were not consistent over environments. This implies that different genes are involved in controlling these traits under water stress and optimal conditions. Cooper and Byth (1996) explained that the larger the degree of genotype-by-environment interaction, the more dissimilar the genetic systems controlling the physiological processes conferring adaptation to different environments.

Even though significant cross-over interactions were observed for GCA effects of the inbred lines, some inbred lines were identified with consistent GCA effects across environments. This implies that the genetic systems controlling a given trait under different stress and non-stress conditions are at least partially similar. Hence, it is possible to identify QPM hybrids that perform well across stress levels in Africa. Similar conclusions have been drawn by Betran et al. (2003) who evaluated tropical normal maize inbred lines and their hybrids for grain yield under optimal and water stress conditions.

Inbred lines VL054178, VL05561, VL05483, CML511, CML159 and VL06375 were good general combiners for grain yield in both water stress and optimal environments indicating that these inbred lines contributed to increased grain yield in their crosses under all environmental conditions. Inbred lines VL054178, VL05482, VL05561, VL05483, CML159 and VL06375 contributed to earliness under most environments as inferred from the negative and highly significant GCA effects of days to anthesis and silking. VL05561 was the best general combiner for anthesis-silking interval. Inbred lines VL05200, VL054178, VL05482, CML144 and CML159 were good combiners for plant stature as they contributed to reduced plant and ear height in the crosses. VL05482, VL05483 and CML511 contributed to increased ears per plant in the crosses. Anthesis- silking interval and ears per plant are important secondary traits to be considered in increasing the efficiency of selection for grain yield under stress. The highest grain yielding genotypes under water stress tended to show

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lower anthesis-silking interval, delayed senescence, and a higher number of ears per plant (Bolanos and Edmeades, 1993; Banziger and Lafitte, 1997; Banziger et al., 1999c; Diallo et al., 2004).

Higher SCA variances than GCA variances for grain yield in most optimal environments indicate that additive variability was of greater importance in the inheritance of grain yield under optimal conditions. Under water stress conditions, however, additive variability was more important than non-additive variability. The predominance of additive effects under water stress conditions has been reported by several researchers (Betran et al., 2003; Diallo et al., 2003; Makumbi et al., 2004; Derera et al., 2008).

Additive effects were more important that non-additive effects in the inheritance of days to anthesis and silking in all cases. Similarly, additive effects were more important for anthesis-silking interval, plant and ear height, and ears per plant in most cases.

According to Baker (1978), when SCA mean squares are not significant, the hypothesis that the performance of a single-cross progeny can be adequately predicted on the basis of GCA would be accepted. On the other hand, if the SCA mean squares are significant, the relative importance of GCA and SCA should be assessed by estimating components of variance in determining progeny performance.

#### 5. Conclusions

A large proportion of the maize crop in Africa is grown by small scale farmers under low input systems, without adequate fertilization and irrigation. Significant yield losses due to water stress were realized in this study. The results indicated the availability of considerable variation among QPM hybrids and the possibility of making selections for grain yield and agronomic traits under stress and non-stress conditions. Significant GCA and SCA mean squares, and hence the importance of both additive and non-additive effects was observed for most traits in most environments. Neither additive nor non-additive genetic effects were important for grain yield across water stress environments. In this case, secondary traits such as anthesis-silking interval and ears per plant with high genetic variability and heritability can be used to increase selection efficiency.

Estimates of GCA effects showed that inbred lines VL054178, VL05482, VL05561, VL05483, CML511, CML159, CML491 and VL06375 had good GCA effects for most traits under stress and non-stress conditions. These inbred lines can be used for the development of QPM hybrids and synthetics that perform well across stress and non-stress environments. In general, the inbred lines used in this study were found to be useful sources for genetic variability for the development of new genotypes for stress tolerance and the study confirmed the possibility of achieving good performances across stress and non-stress conditions in QPM germplasm.

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Plants experience water stress either when the water supply to their roots becomes limiting, or when the transpiration rate becomes intense. Water stress is primarily caused by a water deficit, such as a drought or high soil salinity. Each year, water stress on arable plants in different parts of the world disrupts agriculture and food supply with the final consequence: famine. Hence, the ability to withstand such stress is of immense economic importance. Plants try to adapt to the stress conditions with an array of biochemical and physiological interventions. This multi-authored edited compilation puts forth an all-inclusive picture on the mechanism and adaptation aspects of water stress. The prime objective of the book is to deliver a thoughtful mixture of viewpoints which will be useful to workers in all areas of plant sciences. We trust that the material covered in this book will be valuable in building strategies to counter water stress in plants.

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