

# Gene action controlling grain yield and secondary traits in southern African maize hybrids under drought and non-drought environments

John Derera · Pangirayi Tongoona · Bindiganavile Sampath Vivek · Mark D. Laing

Received: 18 July 2007 / Accepted: 27 September 2007  
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**Abstract** Breeding maize hybrids for drought tolerance would significantly reduce yield loss due to drought in southern Africa. Mode of gene action controlling yield and secondary traits was investigated by mating 27 inbred lines, in sets according to a North Carolina design II scheme. The resultant 72 experimental and eight commercial hybrids were evaluated in  $8 \times 10$   $\alpha$ -lattice design with two replications, in four drought and two non-drought environments. Under drought conditions, only general combining ability (GCA) variance was significant for yield, indicating predominance of additive effects. In non-drought environments, both GCA and specific combining ability variances were significant for yield, indicating importance of additive and non-additive effects, respectively. Contributions of male ( $GCA_m$ ) and female GCA ( $GCA_f$ ) effects to hybrids varied depending on the trait and conditions. Superior  $GCA_f$  to  $GCA_m$  effects for yield under drought conditions, and for ASI, prolificacy and ear aspect under both drought and

non-drought conditions, suggested that maternal effects might have modified these traits. Larger  $GCA_m$  than  $GCA_f$  for ASI and silking dates under normal conditions indicated that paternal genotypes played a greater role in determining these traits. Similar  $GCA_m$  and  $GCA_f$  for yield under normal conditions, silking and anthesis dates under drought indicated that both parents made similar contribution to hybrids. Possibly, complications due to modification of traits by cytoplasmic effects and cross-over  $G \times E$  for yield might partly explain why only a few drought tolerant hybrids have been developed. Practical implications of these findings in breeding drought tolerance in maize are discussed.

**Keywords** Drought tolerance · GCA · Gene action · Grain yield · Maize · SCA

## Introduction

In southern Africa, maize production is substantially reduced by drought. Drought has been reported to be devastating when it occurs at flowering and pollination (Cakir 2004; Zaidi et al. 2004). Campos et al. (2006) reported 45–60% yield losses when drought occurred at silk emergence. A 60% production decline was reported during severe drought of 1991/1992 in southern Africa (Rosen and Scott 1992). Predominantly, small-scale farmers grow drought susceptible hybrids with limited access to irrigation

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J. Derera (✉) · P. Tongoona · M. D. Laing  
African Centre for Crop Improvement, University of  
KwaZulu-Natal, P. Bag X01, Scottsville 3209,  
Pietermaritburg, South Africa  
e-mail: Dereraj@ukzn.ac.za

B. S. Vivek  
CIMMYT-Zimbabwe, P.O. Box MP163, MT. Pleasant,  
Harare, Zimbabwe

facilities. Dry land production accounts for almost 95% (Banziger and Diallo 2001). Low production of the staple maize has negative impact on regional economies and is reflected by a low annual gross domestic product during drought years in Zimbabwe (Richardson 2005). Drought occurrence is highly unpredictable over time and space (Campos et al. 2004) and it is difficult to control without irrigation. This prompts calls for breeding drought tolerant hybrids in all agro-ecosystems.

Breeding drought tolerant hybrids is discouraged by a perception that drought tolerant hybrids are low yielding in non-drought environments, implying that a yield penalty occurs when rainfall is adequate. Drought tolerant germplasm might be specifically adapted to low yield environments. Moreno et al. (2005) reported that traits that confer drought tolerance lack positive relationship with high yield potential. Hybrids with high yield potential in both drought and non-drought conditions are desired. Possibly, such hybrids could be developed by combining drought tolerant lines with lines that were selected for high GCA for yield potential under normal conditions.

Literature review reveals that little research has been directly focused on studying the mode of gene action controlling yield, especially in southern African germplasm under drought. One study by Betran et al. (2003b) reported that additive effects were more important than non-additive gene action in controlling yield in some tropical varieties under drought. Response to selection for yield in three tropical populations under drought has also been reported (Chapman and Edmeades 1999; Edmeades et al. 1999), suggesting that additive gene action might be important in controlling yield. In addition, many drought tolerance QTLs (quantitative trait loci) have been reported especially in temperate maize (Tuberosa et al. 2005). These might have limited direct application to subtropical environments. Agrama and Moussa (1996) reported QTLs with both additive and dominance effects for yield and associated flowering traits. However, impact of QTLs in generating drought tolerant hybrids has been scarcely reported (Tuberosa et al. 2005). Genetic engineering has also not resulted in usable products because drought tolerance is a complex trait (Moreno et al. 2005); but a few products have been developed using conventional breeding methods (Vasal et al. 1999).

Quantitative analysis of the mode of gene action controlling yield and secondary traits in regional germplasm under drought would be helpful in devising a viable conventional breeding strategy. Regional germplasm has been improved for tolerance to other yield-limiting factors such as maize streak virus—peculiar to Africa. Significance of anthesis-silking interval, silk emergence, anthesis date, number of ears plant<sup>-1</sup> and ear aspect scores in breeding drought tolerance in maize has been reported (Bolanos and Edmeades 1996; Betran et al. 2003a; Campos et al. 2006). Therefore, the mode of gene action controlling yield and these secondary traits was investigated in southern African germplasm under drought and non-drought environments.

## Materials and methods

### Germplasm

Twenty-seven maize inbred lines, comprising six drought-tolerant (D), nine drought susceptible (S) and 12 conventional (C) lines, were drawn from nine major heterotic patterns used in Southern African region (Table 1). These heterotic groups were presented in detail by Gevers and Whyte (1987) and Mickelson et al. (2001). Drought tolerant lines were selected under managed drought environments at CIMMYT, in Zimbabwe. The drought susceptible set comprised lines that were primarily selected for resistance to grey leaf spot disease (caused by *Cercospora zea-maydis*) under humid conditions. “Conventional lines” consist of lines that were principally selected for high GCA for yield potential in multi-environment trials at Seed Co, in Zimbabwe. The base populations from which these lines were derived are shown in Table 1.

Inbred lines were divided into sub-groups of three each; according to their genetic background such that hybrids were formed between lines from different heterotic groups to maximize heterosis. Three lines in one sub-group were used as female and crossed with three lines from another sub-group used as male parents, according to a North Carolina design II (NCD II) mating scheme to generate 72 hybrids in eight sets. Each line was used once as female and once as male, but in different sets (Table 1). The ninth set did not yield adequate seed for

**Table 1** Characteristics of 27 maize inbred lines used in a North Carolina design II mating scheme

Line	Heterotic group <sup>a</sup>	Source population	Drought tolerance <sup>b</sup>	Male (Set)	Female (Set)
L10	K	(L48 × L49)	C	9	8
L11	K	(L46 × L42)	C	9	8
L12	K	(L47 × L41)	C	9	8
L19	K	(L43 × L28)	C	7	2
L20	K	(L44 × L29)	C	7	2
L21	K	(L45 × L30)	C	7	2
L25	AB	(CML202 × LPSC3H297)	C	4	9
L26	I	(L91 × L95)	C	4	9
L27	A	[P501c2 × EV7992# × EV8449SR]	C	4	9
L7	M	(L50 × L55)	C	3	5
L8	M	(L51 × L56)	C	3	5
L9	NAW	(L71 × L72)	C	3	5
L1	M	[M37W × ZM607]	D	1	3
L2	A	(S89500F2)	D	1	3
L3	AB	[[TUXPSEQ]C1F2 × P49–SR]	D	1	3
L4	B	[90323(B)]	D	2	4
L5	B	[P43C9]	D	2	4
L6	B	[DTPWC8]	D	2	4
L13	A	[EV7992 × CML202]	S	5	7
L14	A	[Z97SYNGLS(A)]	S	5	7
L15	N	[CML197 × N3 × CML206]	S	5	7
L16	I	[MSR123 × I137TNxLZ956441]	S	6	1
L17	B	[LZ956441 × LZ966205]	S	6	1
L18	B	[Z97SYNGLS(B)]	S	6	1
L22	S	(L31 × L32)	S	8	6
L23	S	(L32 × L34)	S	8	6
L24	S	(L33 × L35)	S	8	6

<sup>a</sup> Heterotic group A is composed of lines related to B73 and populations Tuxpeno and Kitale; Group B consists of lines that are related to the populations Eto, Ecuador and Mo17; AB group is composed of the lines that show heterosis with testers from both group A and B at CIMMYT. N-group consists of lines relating to the population Salisbury white; NAW group comprises lines relating to the population Potchefstroom pearl; S group comprises lines that are related to the population Southern Cross; K is composed of derivatives from Pride of Saline; M group lines are derivatives from (21A<sup>2</sup>.Jellicorse); and lines in group I are derivatives from Teko Yellow

<sup>b</sup> Principal selection criteria of the lines was drought tolerance (D); or high GCA for yield potential in multilocation environments i.e., conventional (C); disease resistance under wet and humid conditions i.e., not typical of drought environment hence “drought susceptible” (S)

evaluation. Eight widely grown commercial hybrids were included as checks.

#### Experimental design and management

Experiments were conducted at Save Valley Experiment Station (SVES) (20°22' S; 32°17' E; 556 m altitude) and Kadoma Research Centre (KRC)

(18°19' S; 29°17' E; 1,149 altitude) in Zimbabwe, during the dry winter season (May–August) in 2004 and the summer of 2005. Six environments were established and artificially managed to simulate drought in four environments; and non-drought conditions (control) in two environments. All experiments were laid out as 8 × 10  $\alpha$ -lattice block designs with two replications. During 2005 summer, populations of 44,000 plants ha<sup>-1</sup> were established in both

drought and control environments, at KRC. During 2004 dry season, established plant populations were 53,000 plants ha<sup>-1</sup> in both drought and control environments at SVES. During 2005 summer, two drought environments were established with population densities 26,000 and 53,000 plants ha<sup>-1</sup>, at SVES. At KRC, fertilizer was applied at 138 kg N: 64 kg P: 20 kg K ha<sup>-1</sup>. At SVES, 104 kg N: 18 kg P: 11 kg K ha<sup>-1</sup> were applied. All experiments were maintained clean of weeds by hand weeding.

Drought conditions were simulated for 6 weeks in four environments; three at SVES and one at KRC, by withdrawing irrigation water for 21 days before flowering and throughout 21 days of pollination. Average pollination dates, to estimate periods to initiate drought stress, were predicted based on previous data of standard hybrids. Banziger et al. (2000) provide a detailed description of the carefully managed drought screening protocol used at CIMMYT. Incidentally, there was a dry spell, which coincided with flowering and pollination period, at both locations during the summer of 2005 season; hence the drought conditions were both artificial during the winter and natural during the summer seasons. A non-drought environment was created at each site by applying full irrigation ( $\pm 100\%$  field capacity) using a sprinkler system throughout the crop growing cycle. This was established 120 m away from drought environments to avoid problems of water seepage. In summary the six environments were established as follows:

1. At SVES, during 2004, with 53,000 plants ha<sup>-1</sup> under drought conditions;
2. At SVES, during 2004, with 53,000 plants ha<sup>-1</sup> under normal conditions;
3. At KRC, during 2005, with 44,000 plants ha<sup>-1</sup> under drought conditions;
4. At KRC, during 2005, with 44,000 plants ha<sup>-1</sup> under normal conditions;
5. At SVES, during 2005, with 53,000 plants ha<sup>-1</sup> under drought conditions;
6. At SVES, during 2005, with 26,000 plants ha<sup>-1</sup> under drought conditions.

Anthesis (DMP) and silk emergence (DMS) dates were estimated as number of days from planting to when 50% of plants were shedding pollen and had silks emerged, respectively. Anthesis-silking interval (ASI) was then derived as: DMS – DMP. Ear aspect

was rated using a scale of 1–5, with 1 = uniform, large and filled ears, and 5 = variable, small, and partially filled ears. Prolificacy or number of ears plant<sup>-1</sup> (EPP) was determined as number of ears averaged over number of plants plot<sup>-1</sup>. Yield (t ha<sup>-1</sup>) was determined from shelled grain weight (adjusted to 12.5% H<sub>2</sub>O). Average yield ranking of hybrids was calculated as arithmetic mean of hybrid rank across environments. Drought tolerance index (%) was calculated as yield difference of a hybrid in the control environments 2 and 4, and drought environments 1 and 3.

General analyses of variance were performed for all yield and secondary data of hybrids including checks. Analyses of variance of NCD II pooled over sets and across environments (Hallauer and Miranda 1988) were conducted for yield and secondary data of experimental hybrids in GenStat. Main effects due to female and male effects within sets are independent estimates of GCA; while male  $\times$  female interaction effects represent SCA variance within sets. Pearson's phenotypic correlations were conducted among four drought environments for yield ranking of the 80 hybrids.

## Results and discussion

### Gene action and drought tolerance

The hybrid data from the drought environments 1 and 3 which were planted together with the non-drought environments 2 and 4 (Table 2) were used to compare gene action controlling yield and secondary traits under drought and normal conditions. There was a significant ( $P \leq 0.01$ ) variation among experimental hybrids for grain yield under drought (Table 2), which is a measure of drought tolerance (Rosielle and Hamblin 1981). Under drought, yield ranged between 0.95 and 4.05 t ha<sup>-1</sup> (Table 3); whereas under non-stress yield ranged between 4.53 and 7.17 t ha<sup>-1</sup>. The trial mean yield of 2.75 t ha<sup>-1</sup> under drought was less than 50% of the trial mean (5.92 t ha<sup>-1</sup>) under non-stress conditions (Table 3). This level of yield reduction was associated with moderate drought stress (Banziger et al. 2000), and falls within previously reported yield reduction range of drought stress levels used to screen maize genotypes (Campos et al. 2006). Hybrid yield depression due to drought

**Table 2** Analyses of variance for grain yield of 72 experimental hybrids under two drought and two non-drought stress environments (Env.), during 2004–2005

Source of variation	D.F.	Drought Env. (Env. 1 and 3) <sup>a</sup>		Non-drought Env. (Env. 2 and 4) <sup>a</sup>	
				MS	
Environment	1	0.87	ns	11.62	**
Sets	7	3.70	**	5.44	**
Hybrids/sets	64	1.88	**	1.77	**
GCA <sub>M</sub> /sets	16	2.44	**	2.06	**
GCA <sub>F</sub> /sets	16	3.41	**	2.03	**
SCA/sets	32	0.96	ns	1.47	*
Env. × sets	7	3.31	**	1.81	*
Env. × hybrids/sets	64	1.46	ns	1.62	**
Env. × GCA <sub>M</sub> /sets	16	1.14	ns	1.59	ns
Env. × GCA <sub>F</sub> /sets	16	1.54	ns	1.86	*
Env. × SCA/sets	32	1.511	ns	1.52	*

<sup>a</sup> Key to the environments: 1. At SVES, during 2004, with 53,000 plants ha<sup>-1</sup> under drought conditions; 2. At SVES, during 2004, with 53,000 plants ha<sup>-1</sup> under normal conditions (control); 3. At KRC, during 2005, with 44,000 plants ha<sup>-1</sup> under drought conditions; 4. At KRC, during 2005, with 44,000 plants ha<sup>-1</sup> under normal conditions (control)

\*,\*\* Data significant at  $P \leq 0.05$  and  $P \leq 0.01$ , respectively; ns = Data not significant ( $P > 0.05$ )

(drought tolerance index) ranged between 28 and 83% (Table 4). Hybrid resistance to barrenness under drought could explain the drought tolerance observed in this set of germplasm, because drought tolerant hybrids had a higher number of ears plant<sup>-1</sup> and superior ear aspect compared to susceptible hybrids (Tables 3 and 4). Both traits displayed strong and significant correlation with yield under drought (Table 3). Clearly hybrids displayed higher prolificacy under normal than drought conditions. A similar trend was observed for ear aspect which accounts for cob size and extent of grain filling. Hybrids were of similar flowering dates; hence the weak correlations of yield with silking and anthesis dates (Table 4) suggested that only a few hybrids could have escaped the drought at flowering. However, hybrids flowered earlier by  $\pm 10$  days under drought than normal conditions indicating a shorter growing cycle and reduced leaf area duration which might partly explain the yield decline under drought.

Under drought conditions, both GCA<sub>m</sub> and GCA<sub>F</sub> effects within sets were highly significant ( $P \leq 0.01$ ) for yield, indicating importance of additive gene effects. The SCA effects within sets were not significant ( $P > 0.05$ ) for yield, indicating that non-additive effects were not important in controlling yield under drought. Predominance of additive effects in controlling yield under drought confirms previous

findings in tropical maize (Betran et al. 2003b). Further evidence for the preponderance of additive effects is provided by analysis of the hybrid sets that were also highly significant ( $P \leq 0.01$ ) for yield under drought (Table 2). Consistent with expectations of additive gene action, inbred combinations of drought tolerant (D) with conventional (C) lines (i.e., D × C or C × D) were more drought tolerant than C × S or S × C; while S × S hybrids were susceptible (Table 4) reflective of drought tolerance dosage effects. This implies that both parents should be drought tolerant in a single cross hybrid and that selection for drought tolerance should be emphasized in more than one heterotic group, because hybrids are formed between complementary inbred lines. In contrast, both GCA and SCA effects within sets were significant ( $P \leq 0.05$ ) for yield under non-drought conditions, indicating that both additive and non-additive effects, respectively, were important for controlling grain yield. This implies that both parents should not necessarily have high GCA for yield in breeding hybrids for normal conditions, because dominance gene effects could also be exploited to enhance yield in hybrids.

The GCA<sub>m</sub> within sets was not significant ( $P > 0.05$ ) for ear aspect, but GCA<sub>F</sub> was significant under drought (Table 5). Both GCA<sub>m</sub> and GCA<sub>F</sub> within sets effects were highly significant ( $P \leq 0.01$ )

**Table 3** Mean of grain yield, drought tolerance and secondary traits of selected 20 of the 72 experimental hybrids over two drought and two non-drought environments<sup>a</sup>

Hybrid	Set	Line combination	Grain yield (t ha <sup>-1</sup> )		DTI <sup>b</sup> (%)	Secondary traits under drought <sup>c</sup>				
			Drought Env.	Non-stress Env.		EPP (no.)	EASP (1–5)	DMP (d)	DMS (d)	ASI (d)
<i>Top 10</i>										
L6 × L26	4	D × C	4.05	6.15	34.17	1.00	2.63	80.5	80.5	0.0
L2 × L9	3	D × C	4.05	6.10	33.63	0.93	2.38	81.5	81.5	0.0
L14 × L19	7	S × C	3.80	5.30	28.23	0.95	2.25	80.0	81.5	1.5
L17 × L2	1	S × D	3.78	5.93	36.29	0.83	2.50	80.8	81.3	0.5
L7 × L14	5	C × S	3.75	6.09	38.45	0.98	2.00	82.0	82.5	0.5
L3 × 8	3	D × C	3.73	6.55	43.11	0.85	2.00	82.0	80.8	-1.3
L5 × L27	4	D × C	3.70	6.78	45.39	0.73	2.38	85.3	83.1	-1.9
L19 × L22	8	C × S	3.68	5.03	26.94	0.93	2.38	80.0	80.3	0.3
L1 × L9	3	D × C	3.65	6.04	39.62	0.90	2.63	80.3	81.5	1.3
L17 × L3	1	S × D	3.55	5.97	40.56	0.90	2.88	79.0	79.5	0.5
<i>Bottom 10</i>										
L7 × L13	5	C × S	1.98	6.26	68.45	0.70	3.38	82.5	84.5	2.0
L5 × L25	4	D × C	1.98	6.15	67.90	0.85	3.25	85.3	84.5	-0.8
L11 × L23	8	C × S	1.85	5.50	66.35	0.70	3.63	82.3	85.0	2.8
L9 × L13	5	C × S	1.78	4.53	60.84	0.68	3.25	80.5	81.5	1.0
L15 × L20	7	S × C	1.68	4.92	65.94	0.63	3.63	82.3	84.3	2.0
L18 × L2	1	S × D	1.50	5.27	71.54	0.60	3.50	82.8	85.0	2.3
L10 × L23	8	C × S	1.48	4.86	69.62	0.60	4.13	81.8	81.5	-0.3
L24 × L16	6	S × S	1.33	6.74	80.33	0.53	3.75	81.5	82.5	1.0
L13 × L19	7	S × C	1.23	5.43	77.43	0.58	3.63	81.8	81.8	0.0
L24 × L17	6	S × S	0.95	5.88	83.83	0.35	4.13	81.8	83.3	1.5
<i>Statistics</i>										
Min			0.95	4.53	26.94	0.35	1.88	78.50	78.75	-1.92
Mean			2.75	5.92	53.29	0.80	2.98	81.81	82.71	0.90
Max			4.05	7.17	83.83	1.02	4.13	85.25	88.00	4.75
<i>P</i> value			**	**		**	*	**	**	**
Corr. with yield under drought				0.28*	-0.91**	0.76**	-0.85**	-0.19	-0.35**	-0.32**
Corr. with yield under non-stress					0.13	0.42**	-0.25*	-0.11	0.18	0.10

<sup>a</sup> Key to environments: 1. At SVES, during 2004, with 53,000 plants ha<sup>-1</sup> under drought conditions; 2. At SVES, during 2004, with 53,000 plants ha<sup>-1</sup> under normal conditions; 3. At KRC, during 2005, with 44,000 plants ha<sup>-1</sup> under drought conditions; 4. At KRC, during 2005, with 44,000 plants ha<sup>-1</sup> under normal conditions

<sup>b</sup> DTI = Drought Tolerance Index (%)

<sup>c</sup> EPP = number of ears plant<sup>-1</sup>; DMP = days to 50% anthesis; DMS = days to 50% silk emergence; ASI = anthesis to silking interval

\*,\*\* Data significant at  $P \leq 0.05$  and  $P \leq 0.01$ , respectively

for prolificacy, ear aspect, silking and anthesis dates under non-drought conditions, but only GCA<sub>m</sub> was significant for ASI (Table 6). The SCA effects were significant for anthesis and silking dates under drought and non-drought conditions, indicating

importance of non-additive effects. The SCA effects were not significant ( $P > 0.05$ ) for prolificacy and ear aspect scores, under both drought and non-drought conditions, suggesting that non-additive effects were not important for these traits. Whereas SCA effects

**Table 4** Mean of grain yield and secondary traits of eight sets of hybrids over drought environments 1 and 3<sup>a</sup> and non-drought stress environments 2 and 4<sup>a</sup>

Set <sup>b</sup> (No.)	Inbred line combinations <sup>c</sup>	Yield (t ha <sup>-1</sup> )	Number of ears plant <sup>-1</sup>	Ear aspect score (1–5) <sup>d</sup>	Anthesis-silking interval (d)	Silking dates (d)	Anthesis dates (d)
<i>Drought environments 1 and 3<sup>a</sup></i>							
3	D × C	3.19	0.82	2.59	0.5	83.1	82.7
4	D × C	2.96	0.85	2.91	0.2	83.5	83.0
1	S × D	2.94	0.81	2.97	1.1	82.3	81.2
2	C × D	2.85	0.85	2.86	0.5	82.9	82.4
5	C × S	2.76	0.78	2.93	0.9	83.2	82.3
8	C × S	2.56	0.79	3.24	1.1	82.3	81.2
7	S × C	2.54	0.78	3.06	1.5	81.7	80.3
6	S × S	2.22	0.71	3.25	1.5	82.9	81.5
Significance (P)		**	**	*	**	**	**
<i>Non-drought environments 2 and 4<sup>a</sup></i>							
3	D × C	6.54	1.14	2.38	-0.58	92.0	92.6
4	D × C	6.04	1.10	2.21	-0.03	92.9	93.2
2	C × D	6.04	1.05	2.47	0.78	92.6	91.9
6	S × S	6.00	1.06	2.15	0.33	92.2	91.8
1	S × D	5.98	1.02	1.92	0.25	91.2	90.9
5	C × S	5.75	1.09	2.26	0.61	92.4	91.8
8	C × S	5.63	1.04	2.72	-1.22	90.4	91.4
7	S × C	5.35	1.03	2.50	1.08	90.3	89.2
Significance (P)		**	**	*	**	**	**

<sup>a</sup> Key to environments: 1. At SVES, during 2004, with 53,000 plants ha<sup>-1</sup> under drought conditions; 2. At SVES, during 2004, with 53,000 plants ha<sup>-1</sup> under normal conditions; 3. At KRC, during 2005, with 44,000 plants ha<sup>-1</sup> under drought conditions; 4. At KRC, during 2005, with 44,000 plants ha<sup>-1</sup> under normal conditions

<sup>b</sup> Lines combined to form hybrids in each set are presented in Table 1

<sup>c</sup> Principal selection criteria of the lines was drought tolerance (D); or high GCA for yield i.e., conventional (C) and “drought susceptible” (S)

<sup>d</sup> Ear aspect score: 1 = uniform, large and well-filled ears, and 5 = variable, small, and partially filled ears

\*,\*\*Data significant at  $P \leq 0.05$  and  $P \leq 0.001$ , respectively

were significant for ASI under drought, they were not significant ( $P > 0.05$ ) under non-drought conditions, suggesting that non-additive effects were not important for ASI under normal conditions.

#### Relative importance of male GCA and female GCA effects

There is a gap in the literature regarding effects of male and female parents in contributing to yield and secondary traits in hybrids, especially under drought. In addition to studying GCA and SCA effects, the NCD II is also useful for estimating maternal effects and has advantage over the diallel when many

parents are involved (Hallauer and Miranda 1988). In comparing relative importance of GCA to SCA effects in a fixed model, Kang (1994) suggested using ratio of their sum of squares. There was similar magnitude of  $GCA_m$  and  $GCA_f$  sum of squares (29 vs. 31%) for yield under non-drought environments (Table 7), indicating that both parents had similar contribution for yield in hybrids. However, under drought the  $GCA_f$  (44%) was larger than  $GCA_m$  (32%) sum of squares for yield suggesting importance of maternal effects for drought tolerance. The  $GCA_f$  was also larger than  $GCA_m$  sum of squares for prolificacy and ear aspect (Table 7), which were closely associated with yield especially under drought conditions ( $r = 0.76^{**}$  and  $-0.85^{**}$ ,

**Table 5** Analysis of variance for secondary traits across two drought environments 1 and 3<sup>b</sup>

Source of variation	D.F.	Anthesis-silking interval		Number of ears plant <sup>-1</sup>		Ear aspect score <sup>a</sup>		Anthesis date	Silking date		
						Mean square					
Environments	1	38.28	ns	0.36	**	22.9	**	58285.81	**	55015.98	**
Sets	7	8.98	**	0.09	**	1.71	*	23.57	**	7.82	**
Hybrids/sets	64	5.38	**	0.07	**	0.83	*	9.56	**	17.35	**
GCA <sub>M</sub> /sets	16	6.43	**	0.09	**	0.727	ns	16.30	**	27.23	**
GCA <sub>F</sub> /sets	16	8.47	**	0.14	**	1.35	*	14.65	**	25.83	**
SCA/sets	32	3.46	**	0.03	**	0.62	ns	2.14	ns	6.86	**
Env. × sets	7	3.23	ns	0.09	**	2.38	**	3.96	*	8.22	**
Env. × hybrids/sets	64	2.61	*	0.05	**	0.99	*	3.44	**	7.59	**
Env. × GCA <sub>M</sub> /sets	16	2.53	ns	0.05	ns	1.18	*	3.96	**	6.98	**
Env. × GCA <sub>F</sub> /sets	16	3.46	*	0.059	*	1.10	ns	6.94	**	17.33	**
Env. × SCA/sets	32	2.12	ns	0.05	*	0.79	ns	1.53	ns	3.15	ns

<sup>a</sup> Ear aspect score: 1 = uniform, large and well-filled ears, and 5 = variable, small, and partially filled ears

<sup>b</sup> Key to environments: 1. At SVES, during 2004, with 53,000 plants ha<sup>-1</sup> under drought conditions; 3. At KRC, during 2005, with 44,000 plants ha<sup>-1</sup> under drought conditions

\*,\*\*Data significant at  $P \leq 0.05$  and  $P \leq 0.001$ , respectively

ns = Data not significant ( $P > 0.05$ )

**Table 6** Analysis of variance for secondary traits over two non-drought environments 2 and 4<sup>b</sup>

Source of variation	D.F.	Anthesis-silking interval		Number of ears plant <sup>-1</sup>		Ear aspect score <sup>a</sup>		Anthesis date	Silking date		
						Mean square					
Environment (Env.)	1	21.16	**	82.54	**	1.81	ns	53.89	**	86.09	**
Sets	7	8.80	**	3.80	**	5.02	**	19.45	**	12.63	**
Hybrids/sets	64	1.47	**	2.37	**	2.68	**	7.06	**	6.41	**
GCA <sub>M</sub> /sets	16	2.73	**	1.90	**	3.66	**	12.18	**	12.06	**
GCA <sub>F</sub> /sets	16	1.08	ns	5.40	**	5.00	**	12.00	**	9.31	**
SCA/sets	32	0.99	ns	1.07	ns	0.94	ns	1.71	**	1.82	**
Env. × sets	7	2.33	ns	3.68	**	1.80	ns	0.90	ns	0.88	ns
Env. × hybrids/sets	64	1.02	ns	1.93	**	1.52	**	0.95	ns	1.19	ns
Env. × GCA <sub>M</sub> /sets	16	0.76	ns	2.35	**	2.06	**	1.11	ns	1.17	ns
Env. × GCA <sub>F</sub> /sets	16	1.36	ns	2.94	**	1.36	ns	1.22	ns	1.52	ns
Env. × SCA/sets	32	1.00	ns	1.19	ns	1.29	ns	0.72	ns	1.04	ns

<sup>a</sup> Ear aspect score: 1 = uniform, large and well-filled ears, and 5 = variable, small, and partially filled ears

<sup>b</sup> Key to environments: 2. At SVES, during 2004, with 53,000 plants ha<sup>-1</sup> under normal conditions (control); 4. At KRC, during 2005, with 44,000 plants ha<sup>-1</sup> under normal conditions (control)

\*,\*\* Data significant at  $P \leq 0.05$  and  $P \leq 0.001$ , respectively

ns = Data not significant ( $P > 0.05$ )

respectively), adding credence to possible role of maternal effects for yield under drought and for its components under both drought and normal conditions. In fact GCA<sub>m</sub> mean squares were not significant ( $P > 0.05$ ) for ear aspect, while GCA<sub>F</sub>

was significant under drought conditions (Table 5), indicating predominance of female genotypes for prolificacy and ear aspect scores. Kearsey and Pooni (1996) suggested using ratio of GCA<sub>m</sub> and GCA<sub>F</sub> mean squares to estimate maternal effects.

**Table 7** Percentage of cross sum of squares attributable to GCA and SCA effects for yield and secondary traits over two drought and two non-drought environments

Traits	Environment <sup>a</sup>	Female GCA	% Cross sum of squares	
			Male GCA	SCA
Grain yield (t ha <sup>-1</sup> )	Drought	44	32	24
	Non-drought	29	31	40
Number of ears per plant	Drought	49	30	21
	Non-drought	57	21	22
Ear aspect (score of 1–5) <sup>b</sup>	Drought	41	22	37
	Non-drought	47	36	17
Anthesis-silking interval (d)	Drought	39	30	31
	Non-drought	18	49	32
Days to 50% anthesis	Drought	42	46	12
	Non-drought	42	46	12
Days to 50% silk emergence	Drought	39	41	20
	Non-drought	36	50	14

<sup>a</sup> Key to environments: 1. At SVES, during 2004, with 53,000 plants ha<sup>-1</sup> under drought conditions; 2. At SVES, during 2004, with 53,000 plants ha<sup>-1</sup> under normal conditions; 3. At KRC, during 2005, with 44,000 plants ha<sup>-1</sup> under drought conditions; 4. At KRC, during 2005, with 44,000 plants ha<sup>-1</sup> under normal conditions

<sup>b</sup> Ear aspect score: 1 = uniform, large and well-filled ears, and 5 = variable, small, and partially filled ears

The  $GCA_f$  was slightly larger than  $GCA_m$  sum of squares for ASI under drought, but there was a reverse trend under normal conditions. Clearly,  $GCA_f$  mean square within sets was not significant ( $P > 0.05$ ) for ASI in non-drought environments (Table 6). The  $GCA_m$  was also larger than  $GCA_f$  sum of squares for silking dates under non-stress conditions, but the  $GCA_m$  and  $GCA_f$  were similar under drought. Perhaps paternal genotypes played a greater role in determining ASI and silk emergence date under normal conditions; while maternal genotypes were predominant in determining ASI under drought. Notably, there was a small difference (2–4%) between  $GCA_m$  and  $GCA_f$  sum of squares for anthesis dates under both drought and non-stress conditions, indicating that there was similar contribution by both parents in hybrids for the number of days to 50% anthesis. There was a similar trend for number of days to 50% silk emergence but only under drought, which was difficult to explain. It was equally difficult to explain why maternal effects were observed for yield only under drought, yet its closely associated traits (prolificacy and ear aspect scores) showed maternal effects under both conditions.

A review of the literature seems to indicate that cytoplasmic gene effects for grain yield and most of

these secondary traits, especially under drought, have not been reported. However, Khehra and Bhalla (1976) examined reciprocal differences under non-drought conditions and reported that cytoplasmic effects were not significant for grain yield, which is consistent with observations in the current study. Contrary to findings in the current study and that of Khehra and Bhalla (1976), Bhat and Dhawan (1971) reported significant cytoplasmic effects for grain yield and non-significant cytoplasmic effects for prolificacy in  $F_1$  and backcross populations of varietal crosses under non-drought conditions. Khehra and Bhalla (1976) reported significant reciprocal differences for silking dates, which again agrees with the findings in the current study under non-stress conditions. However, the report by Khehra and Bhalla (1976) of reduced silking dates when early parents were used as female in hybrids contrasts with observations in the current study. Whereas only  $F_1$  generation hybrids were evaluated in the current study, Khehra and Bhalla (1976) reported that cytoplasmic effects were also significant in  $F_2$  and backcross generations for silking dates. The contrasts between findings from different studies could be explained by the different germplasm used and as reported by Khehra and Bhalla (1976) the cytoplasm might also interact with the genotypes.

The implications of cytoplasmic effects beyond  $F_1$  generation could be serious, because most breeders initiate selection in  $F_2$  or backcross generations to generate new inbred lines (Hallauer 1990; Lamkey 1993). Generally, maternal effects if unchecked would inflate GCA variance for yield and secondary traits; consequently heritability is overestimated which might mislead breeders in adopting a wrong selection strategy. This might partly explain why only a few drought tolerant hybrids have been released in southern Africa. Although a fixed model was used, the lines evaluated in this study represented the germplasm which form the basis of hybrid programmes in the region; hence findings from this study might have implications on improvement of drought tolerance in the populations from which the lines were derived (Table 1 shows the populations from which lines were derived).

#### Genotype $\times$ environment interaction effects

Combined analysis of yield and secondary trait data over all the four drought environments (Env.) 1, 3, 5 and 6 (Table 8) were used to probe genotype  $\times$  environment interaction ( $G \times E$ ) effects. Generally, it

appears that  $G \times E$  effects would present challenges in breeding for drought tolerance in this germplasm. Env.  $\times$  hybrid interaction effects were highly significant ( $P \leq 0.01$ ) for yield (Table 8), indicating that hybrid selection would not be consistent. Env.  $\times$   $GCA_m$ , Env.  $\times$   $GCA_f$  and Env.  $\times$  SCA within sets interaction effects were significant ( $P \leq 0.05$ ) for yield under drought. Probably, this could be explained by population density effects, fertilizer rates, seasonal differences and other complications (e.g., heat stress) that are associated with drought. Although phenotypic correlations among the four drought environments were positive and significant ( $P \leq 0.05$ ) for yield ranking of the 72 hybrids, the correlation coefficients ( $r = 0.11$ – $0.36$ ) were generally weak (data not shown). This suggests observation of crossover  $G \times E$  effects, which cause problems during selection, because different sets of hybrids would be selected in each environment. Under drought conditions,  $G \times E$  interaction effects, mainly due to Env.  $\times$   $GCA_m$  and Env.  $\times$   $GCA_f$  effects within sets were highly significant ( $P \leq 0.01$ ) for all the secondary traits (Table 8). Env.  $\times$  SCA within sets effects were only significant for prolificacy and ASI under drought. This contrasts with previous studies by Betran et al. (2003b) who reported non-

**Table 8** Combined analysis of variance for grain yield and secondary traits over four drought environments (Env.)<sup>a</sup>

Source of variation	D.F.	Yield		Anthesis-silking interval		Number of ears plant <sup>-1</sup>		Ear aspect score <sup>‡</sup>		Anthesis date		Silking date	
		MS											
Env.	3	0.08	ns	24.61	**	5.66	**	9.80	**	3439.44	**	8817.11	**
Sets	7	4.12	**	7.52	**	2.61	**	2.36	*	24.69	**	7.51	**
Hybrids/sets	64	2.37	**	3.69	**	2.03	**	1.27	*	11.40	**	8.16	**
$GCA_m$ /sets	16	3.23	**	5.70	**	2.27	**	1.08	ns	22.91	**	13.40	**
$GCA_f$ /sets	16	3.54	**	4.78	**	3.24	**	2.07	**	17.45	**	12.10	**
SCA/sets	32	1.29	ns	2.03	**	1.28	ns	0.96	ns	1.95	**	3.25	**
Env. $\times$ sets	192	1.37	**	1.57	*	2.38	**	3.67	**	1.99	**	1.83	**
Env. $\times$ hybrids/sets	21	2.19	**	1.90	**	1.78	**	1.52	**	1.48	**	2.12	**
$E \times GCA_m$ /sets	48	1.45	*	2.32	**	1.89	**	1.91	**	1.63	**	2.48	**
Env. $\times$ $GCA_f$ /sets	48	1.49	*	2.59	**	2.52	**	1.69	*	2.38	**	3.70	**
Env. $\times$ SCA/sets	96	1.26	*	1.32	*	1.34	*	1.22	ns	0.93	ns	1.10	ns

<sup>a</sup> Key to the environments: 1. At SVES, during 2004, with 53,000 plants ha<sup>-1</sup> under drought conditions; 3. At KRC, during 2005, with 44,000 plants ha<sup>-1</sup> under drought conditions; 5. At SVES, during 2005, with 53,000 plants ha<sup>-1</sup> under drought conditions; 6. At SVES, during 2005, with 26,000 plants ha<sup>-1</sup> under drought conditions

<sup>b</sup> Ear aspect score: 1 = uniform, large and well-filled ears, and 5 = variable, small, and partially filled ears

\*,\*\*Data significant at  $P \leq 0.05$  and  $P \leq 0.001$ , respectively

ns = Data not significant ( $P > 0.05$ )

significant Env.  $\times$  SCA interaction effects for all the secondary traits associated with drought tolerance. Generally, results suggest that breeding for drought tolerance should be conducted in the target environment.

Although fewer non-drought than drought environments (i.e., 2 vs. 4) were used, the trend showed that G  $\times$  E interaction effects were also highly significant ( $P \leq 0.01$ ) for yield under non-drought conditions (Table 2), underscoring the importance of conducting multi-location trials in representative environments to identify yield stable hybrids under both conditions. The Env.  $\times$  GCA<sub>m</sub> and Env.  $\times$  GCA<sub>f</sub> within sets effects were significant for prolificacy; while Env.  $\times$  GCA<sub>f</sub> within sets effects were not significant ( $P > 0.05$ ), suggesting that female genotypes displayed reduced G  $\times$  E effects for ear aspect under normal conditions. Unlike under drought, the Env.  $\times$  SCA effects within sets were not significant ( $P > 0.05$ ) for all secondary traits under normal conditions (Table 6), suggesting that G  $\times$  E would cause greater challenge under drought than normal conditions.

## Conclusion

Only GCA effects were significant for yield, prolificacy and ear aspect under drought conditions, confirming preponderance of additive effects; whereas both GCA and SCA effects were significant for yield under normal conditions indicating that both additive and non-additive effects were controlling yield. Both GCA and SCA effects were significant for ASI, anthesis and silking dates under both drought and normal conditions, indicating that additive and non-additive effects were important for these traits. Superior GCA<sub>f</sub> to GCA<sub>m</sub> for yield under drought conditions and for ASI, prolificacy and ear aspect under both drought and non-drought conditions suggested that maternal effects were modifying these traits. The possible role of maternal effects or cytoplasmic effects in determining drought tolerance in maize has not been reported. Probably, a critical choice could be made regarding which parent should be used as female in breeding drought tolerant and prolific hybrids. The germplasm evaluated in this study is widely used in southern Africa. Possibly, complications due to modification of yield and its

associated secondary traits by maternal or cytoplasmic effects and the observed cross-over G  $\times$  E interaction effects for hybrid yield might partly explain why only a few drought tolerant hybrids have been developed thus far.

**Acknowledgements** We thank The Rockefeller Foundation for financial support. We also thank CIMMYT and Seed Co Ltd (Zimbabwe) for providing the germplasm. The authors are also grateful for use of research facilities and thank all the supporting staff at Save Valley Experiment Station (Govt of Zimbabwe), Kadoma Research Centre (Seed Co Ltd) and CIMMYT, in Zimbabwe.

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