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RESEARCH ARTICLE

ANALYSIS OF COMBINING ABILITY AND HETEROTIC GROUPING OF MAIZE INBRED LINES UNDER ACID SOIL CONDITIONS, CONTROL SOIL AND ACROSS ENVIRONMENTS

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ABSTRACT

A line x tester analysis involving 112 test-cross hybrids and their parents was conducted in 12 environments for different agronomic traits from 2012 to 2014 in the Bimodal Humid Forest Zone of Cameroon. The hybrids were crosses between twenty-five inbred lines and three open-pollinated varieties with four testers. The objectives of the study were to estimate general and specific combining ability effects of the inbred lines and to identify heterotic groups of maize inbred lines under stress conditions, control and across environments. A simple lattice design 12 x 12 was used with two replications. Analysis of variance indicated significant mean squares due to line (GCA) for yield, plant aspect, ear aspect, ear height, plant height and anthesis – silking interval under acid soil conditions. The effect of the tester (GCA) was not significant for yield but line x tester (SCA) showed significant effect for all the traits taken under stress environment. The comparison of GCA sum of squares to SCA sum of squares showed that the contribution of SCA was higher for almost all the traits recorded under acid soil, control and across environments except for ear height in acid soil environments. Most of these traits were predominantly controlled by non-additive gene actions in their expression. SCA explained 68%, 73% and 53% of the total sum of squares among crosses under acid soil, control soil and across environments, for yield. Meaning that yield was mainly controlled by the non-additive genes than the additive gene in the study environments. This confers the advantage of exploiting heterosis to improve grain yield of maize hybrids. Four distinct heterotic groups were identified under acid soil and across environments.

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INTRODUCTION

The average yield of maize in Cameroon is very low (1.8 t/ha) and has remained constant over years (Aroga et al., 2001; Ngoko et al., 2002). The yield of maize has reduced and ranged from 0.8 to 1 t/ha (ACDIC, 2010). Maize production in Cameroon has been increasing steadily from an estimated 966,000 metric tonnes in 2004 (USDA, 2013), to 1,380 000

metric tons in 2009 (ACDIC, 2012) and 1,647 036 tons in 2013 (FAOSTAT, 2013). These increases have been mainly due to increases in area harvested rather than yield increase per unit area. Maize suffers from a wide range of production constraints, the most important being infertile soils (Meseka et al., 2008).

Maize hybrids produce superior yields under stress and non-stress conditions. The development of hybrids is a major objective of this research. Predicting the performance of hybrids from visual assessment or measuring the performance of the component inbred lines is difficult because of very low

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correlations between traits in inbred lines and the same traits in the hybrids, especially traits controlled by polygenes (Hallauer and Miranda, 1988). Inbred lines need to be evaluated on the contributions they make to hybrid combinations. Combining ability is the ability of an inbred line to transmit desirable performance to a hybrid (Allard, 1960). It is important for not only selecting desirable parents but also generating information regarding the nature of and magnitude of gene effects controlling quantitative traits (Basbag *et al.*, 2007).

General combining ability (GCA) and specific combining ability (SCA) which identify lines or hybrids with high yield are the most important criteria used to select parental materials in a breeding program (Ceyhan, 2003). Sprague and Tatum (1942) defined general combining ability as the average contribution an inbred line makes to hybrid performance in a series of hybrid combinations in comparison to other inbreds in the same series of hybrid combinations. Specific combining ability is the contribution of an inbred to hybrid performance in a cross with a specific other inbred in relation to its contribution in crosses with an array of other inbreds. GCA is a characteristic of an inbred while SCA is a characteristic of a specific hybrid. Falconer (1981) observed that GCA is directly related to the breeding value of the parent and is associated with additive genetic effects while SCA is associated with non-additive effects such as dominance, over dominance and epistasis.

The line x tester design was used for breeding both self and cross pollinated plants to select favorable parents and crosses, and estimate their GCA and SCA. Combining ability analysis is one of the powerful tools in identifying the better combiners which may be hybridized to exploit heterosis and to select better crosses for direct use or further breeding work (Nigussie and Zelleke, 2001). Combining ability analyses of Cameroonian inbred lines have been conducted in previous studies but few single cross hybrids have been developed and released and none have been released for acid soil tolerance.

The objectives of this study were to:

- Estimate the combining abilities for agronomic traits in acid soil conditions;
- Identify heterotic groups of maize inbred lines in acid soil conditions, in control and across environments.

MATERIALS AND METHODS

Germplasm

Twenty-five inbred lines (11 from Institute of the Agricultural Research for Development (IRAD) and 14 from CIMMYT) and three open-pollinated varieties (C4RR SA4, CMS 8704, ATP SRY) were crossed to four testers (Cam Inb gp1 17, 88069, 9450 and 4001) (Table 1). The resultant 112, testcross hybrids and hybrid parents were used in this study. The lines had different levels of tolerance to acid soil toxicity. The crosses were done at the breeding nursery of IRAD Yaounde / Nkolbisson.

Experimental sites

Trials were conducted at IRAD - Nkoemvone station located in the Southern Region of the country. Nkoemvone is found on altitude 615 m above the sea level and situated on 12° 24 E, 2° 40 N (The *et al.*, 2006). The average temperature is 24° C and the annual rainfall is 1800 mm with bimodal distribution (The *et al.*, 2001). The soil is a highly weathered Kandiodox with high Al toxicity (FAO, 1992; The *et al.*, 2005) and is highly weathered (Yemefack *et al.*, 2005).

Experimental Design

The experimental site was made of 2 treatments of the soil. The first treatment was a native acid soil called (A) and the second treatment was the control or control soil environments. On the control (C), acidity level of the soil was reduced by the use of 4t/ha of dolomite. The genotypes were planted in simple lattice design 12 x 12 (12 incomplete blocks x 12 genotypes) using two replications during three years.

Land preparation, planting and field management

The experimental sites were cleared from grasses manually and plowed. Each experimental site had two treatments of the soil with 2 m alley in between. One treatment was a native acid soil considered as the stress environment and the other was used as a control where the acidity was corrected with the incorporation of 4t/ha of dolomite lime. The dolomite was incorporated into the soil by plowing.

Table 1. Names and codes of maize genotype used in this study

Genotype name	Code	Origin	Type	Genotype name	Code	Origin	Type
ATP S5 31Y-2	1	IRAD	Line	Cml 534	17	CIMMYT	line
ATP S6 20Y-1	2	IRAD	Line	Cml 535	18	CIMMYT	line
ATP S6 21Y-2	3	IRAD	Line	Cml 332	19	CIMMYT	line
ATP S6 31Y-BB	4	IRAD	Line	Cml 479	20	CIMMYT	line
ATP S8 26Y-2	5	IRAD	Line	Cl a 183	21	CIMMYT	line
ATP S8 30Y-3	6	IRAD	Line	Cml 434	22	CIMMYT	line
ATP S9 30Y-1	7	IRAD	Line	Cl a 135	23	CIMMYT	line
ATP S9 36Y-BB	8	IRAD	Line	D300-17	24	CIMMYT	line
ATP-32	9	IRAD	Line	Cam Inb gp1 17 (F)	25	IRAD	line
ATP-50	10	IRAD	Line	Cam Inb gp1 17	26	IRAD	tester
Cml 304	11	CIMMYT	Line	88069	27	IRAD	tester
Cml 357	12	CIMMYT	Line	9450	28	IITA	tester
Cml 435	13	CIMMYT	Line	4001	29	IRAD	tester
Cml 437	14	CIMMYT	Line	C4RR SA4	30	CIMMYT	OPV
Cml 439	15	CIMMYT	Line	CMS 8704	31	IRAD	OPV
Cml 533	16	CIMMYT	Line	ATP SR Y	32	IRAD	OPV

Two different planting dates (three weeks interval) were used to create additional environments as was stated by Singh and Chaudhary (1979). The different environments are presented in Table 2.

Table 2. List of acid soil and control environments

Environment	Component	
Environment 1	Site 1 * treatment 1 (acid) * year 1 (2012)	Acid soil environments (A)
Environment 2	Site 1 * treatment 1 (acid) * year 2 (2013)	
Environment 3	Site 1 * treatment 1 (acid) * year 3 (2014)	
Environment 4	Site 2 * treatment 1 (acid) * year 1 (2012)	Control environments (C)
Environment 5	Site 2 * treatment 1 (acid) * year 2 (2013)	
Environment 6	Site 2 * treatment 1 (acid) * year 3 (2014)	
Environment 7	Site 1 * treatment 2 (control) * year 1 (2012)	
Environment 8	Site 1 * treatment 2 (control) * year 2 (2013)	
Environment 9	Site 1 * treatment 2 (control) * year 3 (2014)	
Environment 10	Site 2 * treatment 2 (control) * year 1 (2012)	
Environment 11	Site 2 * treatment 2 (control) * year 2 (2013)	
Environment 12	Site 2 * treatment 2 (control) * year 3 (2014)	

Data collection

Data were recorded on: plant stand after thinning, number of days to anthesis (DA), number of days to silking (DS), anthesis to silking interval (ASI) calculated using the formula $ASI \text{ (days)} = DS - DA$, plant height (cm), ear height (cm), moisture content, and grain yield (GY) measured on a whole plot basis following standard CIMMYT procedure (CIMMYT, 1985) adjusted to 15% moisture using the formula below

$$GY \text{ (t/ha)} = [\text{Grain Weight (kg/plot)} \times 10 \times (100 - MC) / (100 - 15)] / (\text{Plot Area})$$

Where MC = Grain Moisture Content.

The number of ears at harvest was also recorded and ears per plant (EPP) was calculated using the formula $EPP = EC/PC$, Where EC and PC = number of ears and number of plants per plot, respectively. Also, ear aspect and plant aspect were recorded using the scale 1 to 5 (5 being the worst and 1 the best).

Data analysis

• Analysis of variance

Analyses of variance were computed for each environment (E) and combined acid soil environments, control soil environments and across environments for all the traits recorded. The environment effects were treated as random and cross effects as fixed. The line by tester analyses were performed for each environment using the method described by Kempthorne (1957). The statistical model used to obtain the different effects was as follows:

$$Y_{ijk} = \mu + l_i + t_j + (l \times t)_{ij} + Bk_{ke} + e_{ijk}$$

Where: Y_{ijk} is the kth observation on ijth progeny, μ is the general mean, l_i is the effect of the ith line, t_j is the effect of the jth tester, $(l \times t)_{ij}$ is the interaction effect of the cross between ith line and jth tester, Bk_{ke} is the effect of block nested within

replicate k by environment e and e_{ijk} is the error term associated with each observation.

General combining ability (GCA) and specific combining ability (SCA) were generated for each of the traits according to the procedure described by Kempthorne (1957). The statistical model for the analysis study was as followed:

$$Y_{ijke} = \mu + E_e + l_i + t_j + (l \times t)_{ij} + Bk_{ke} + gE_{eg} + sS_{es} + \epsilon_{ijke}$$

Where Y_{ij} is the observed measurement for the ijth cross grown in kth replication in the eth environment; μ is the grand mean; E_e is the main effect of Environment; g_i and g_j are the line and tester effects; s_{ij} is the line by tester effect; gE_{eg} is the interaction effect between line, tester and Environment; Bk_{ke} is the effect of block nested within replicate k by environment e, sE_{es} is the interaction effect between line by tester and the Environment, and ϵ_{ijke} is the error term associated with the ijth cross evaluated in the kth replication in eth environment.

Estimation of general (GCA) and specific combining ability (SCA) effects

The GCA and SCA effects for the lines, testers and line by tester were generated through SAS version 9.2 software.

Proportional contribution of line, tester and line x tester

The estimation of lines (l), testers (t) and lines x testers (lxt) was done using the formula below (Singh and Chaudhary, 1979):

$$\text{Contribution of line} = SS(l) * 100 / SS(\text{crosses})$$

$$\text{Contribution of tester} = SS(t) * 100 / SS(\text{crosses})$$

$$\text{Contribution of line x tester} = SS(lxt) * 100 / SS(\text{crosses})$$

Where SS is sum of squares

Heterotic grouping of inbred lines

The inbred lines were assigned to heterotic groups by using the traditional method of specific combining ability (Vasal *et al.*, 1992). Lines in genetically different heterotic groups are usually identified by positive SCA effects between them while inbred lines in the same heterotic group have a tendency to exhibit negative SCA effects when crossed (Vasal *et al.*, 1992). The inbred line classified into heterotic groups had to perform well in crosses when compared to the best check (10% of superiority).

RESULTS

Analysis of variance for all the traits

The analysis of variance across acid soil environments showed significant differences among the lines (GCA) for yield, plant aspect, ear aspect, ear height, plant height and anthesis-silking interval while, for the testers (GCA), significant differences were recorded for ear aspect, ears per plant, ear height and plant height. Lines x tester (SCA) effects were significant for all traits (Table 3).

Table 3. Mean squares for various traits recorded on lines, tester and lines by testers in acid soil environments

Source	DF	Yield (t/ha)	Pltasp	Earasp	Epp	Earght (cm)	Pltght (cm)	Asi (day)
Block (rep*env)	120	7.4***	0.7***	1.1**	0.06***	612.3***	1403.3***	19.1***
Line (GCA)	27	7.2*	0.98**	1.2*	0.06 NS	961.9**	1801**	10.09**
Tester (GCA)	3	3.1 NS	0.7 NS	0.8*	0.1*	3786***	6649***	2.6 NS
Line x tester (SCA)	81	5.7***	0.5*	0.8**	0.05*	412.9**	989.6***	6.3**
Env x line	135	4.5**	0.4*	0.7*	0.04 NS	443.9***	447.5***	4.9 NS
Env x tester	15	1.4 NS	0.3 NS	0.2 NS	0.03 NS	359.7 NS	519.2 NS	6.3 NS
Env x line x tester	405	3.3 NS	0.3 NS	0.5*	0.04 NS	281.5 NS	511.2 NS	4NS
Error	652	3	0.3	0.4	0.04	284.2	567.1	4.2
Mean		3.4	3.2	2.7	1	71.8	158.9	10.6

*Significant at 5% level; **Significant at 1% level;*** Significant at 0.1% level; NS = non-significant; pltasp = plant aspect; earasp = ear aspect; epp = ear per plant; earght = ear height; pltght = plant height; asi = anthesis-silking interval; GCA = general combining ability; SCA = specific combining ability, rep = replication, env = environment.

Table 4. Mean squares for various traits recorded on all lines, testers and lines by testers in control soil environments

Source	DF	Yield (t/ha)	pltasp	earasp	epp	Earght (cm)	Pltght (cm)	Asi (day)
Block (rep*env)	120	7.6***	0.5***	0.7***	0.05 NS	616.5***	1290***	8.5***
Line (GCA)	27	4 NS	0.6*	0.7 NS	0.1 NS	672 NS	1113.9 NS	6.3*
Tester (GCA)	3	22.9*	0.07 NS	0.5 NS	0.04 NS	791NS	197 NS	10.5*
Line x tester (SCA)	81	6.5 NS	0.35 NS	0.7***	0.06*	512.6**	637 NS	4.3***
Env x line	135	8.3***	0.4**	0.6**	0.07***	435**	748.8**	4***
Env x tester	15	4.4 NS	0.4 NS	0.3 NS	0.05 NS	305.4 NS	689 NS	2.4 NS
Env x line x tester	405	5.6*	0.3*	0.4***	0.04 NS	323.2 NS	587**	2.6 NS
Error	652	4.6	0.2	0.3	0.05	221	446.7	2.6
Mean		5.3	2.5	2.1	1.1	93.5	194.6	2

*Significant at 5% level; **Significant at 1% level;*** Significant at 0.1% level; NS = non-significant; pltasp = plant aspect; earasp = ear aspect; epp = ear per plant; earght = ear height; pltght = plant height; asi = anthesis-silking interval; GCA = general combining ability; SCA = specific combining ability, rep = replication, env = environment.

Table 5. Mean squares for various traits recorded on lines, testers, and lines x testers across environments

Source	DF	Yield	pltasp	earasp	epp	earght	pltght	asi
Block(rep*env)	231	7.4***	0.6***	0.9***	0.6**	614.3***	1349***	14***
Line (GCA)	27	5.5 NS	0.9**	1.3***	0.09*	1366.6***	2455.2***	14.5***
Tester (GCA)	3	17.4 **	0.45 NS	1.3***	1.13*	3927.7***	7907.6***	10 NS
Line*tester (SCA)	81	7.8***	0.5**	1***	0.07***	611***	945.5***	7.8***
Env*line	297	6.3***	0.4***	0.6***	0.05***	431***	808.8***	4.2***
Env*tester	33	3.4 NS	0.3 NS	0.2 NS	0.04 NS	356.5 NS	615.9 NS	4.3 NS
Env*line*tester	891	4.4*	0.3*	0.5***	0.04 NS	302.7 NS	561.1 NS	3.2 NS
Error	1323	3.8	0.3	0.4	0.04	287.6	506.4	3.4
Mean		4.4	2.8	2.4	1.1	82.6	176.7	2.3

*Significant at 5% level; **Significant at 1% level;*** Significant at 0.1% level; NS = non-significant; pltasp = plant aspect; earasp = ear aspect; epp = ears per plant; earght = ear height; pltght = plant height; asi = anthesis-silking interval; GCA = general combining ability; SCA = specific combining ability, rep = replication, env = environment.

The interaction environment by lines was significant for yield, plant aspect, ear aspect, ear height and plant height. The interaction environment by tester and environment by (line x tester) was not significant for all the traits recorded.

In control environments, significant differences were recorded in lines (GCA) for plant aspect and anthesis-silking interval; in testers (GCA) for yield and anthesis-silking interval; in line x tester (SCA) for ear aspect, ears per plant, ear height and anthesis-silking interval and in environments for all the traits measured across environments (Table 4). The interaction environment by lines was significant for all the traits recorded. Across environments, line effect were significant for all traits except yield, tester effect were significant for all traits except plant aspect and anthesis-silking interval, and line x tester were significant for all the traits (Table 5). The environment x line interaction effects was highly significant for all traits. The environment by tester interaction was not significant for all the traits. The line x tester interaction with environment was significant for yield, plant and ear aspect.

Relative contribution of GCA lines, GCA testers and SCA of traits in acid soils, control and across environments

The relative contribution of GCA and SCA to the total sum of squares of crosses indicated that, for grain yield, GCA accounted for 28% for lines and 1% for testers to the variation among crosses and SCA accounted for 68% of the variation in acid soil conditions; GCA accounted for 17% of lines and 6% of testers whilst SCA accounted for 53% of the total variation across environments; and GCA accounted for 15% of lines and 10% for testers of the variation among crosses and SCA accounted for 73% of the variation in control environments (Table 6). For ears per plant, GCA accounted for 25% for lines and 6% for the testers of the variation among crosses and SCA accounted for 70% of the variation in acid soil environments; GCA accounted for 35% of lines and 1% for testers and SCA accounted for 63% of the variation in control environments, and GCA accounted for 28% for lines, 4% for testers while SCA accounted for 64% of the variation across environments.

Table 6. Relative contribution (%) of GCA and SCA for yield, ears per plant, anthesis-silking interval and ear height in acid soil, control and across environments

Component	Yield (t/ha)			Ears per plant			Anthesis-silking interval (day)			Ear height (cm)		
	Acid soil	Control	Across	Acid soil	Control	Across	Acid soil	Control	Across	Acid soil	Control	Across
Line (GCA)	28	15	17	25	35	28	35	32	38	36	30	38
Tester (GCA)	1	10	6	6	1	4	1	6	3	16	4	12
Line x tester (SCA)	68	73	53	70	63	64	75	66	62	47	68	51

GCA = general combining ability; SCA = specific combining ability.

Table 7. General combining ability of 'lines' for all the traits in acid soil environments

Inbred lines	Yield (t/ha)	Pltasp	Earasp	Epp	Earght (cm)	Pltght (cm)	Asi
ATP S5 31Y-2	0.17	-0.08	-0.06	0.03	2.35	-3.28	0.00
ATP S6 20Y-1	0.33	0.05	-0.09	-0.04	0.69	-5.23	0.24
ATP S6 21Y-2	0.41	0.09	-0.10	-0.01	1.15	-3.03	0.40
ATP S6 31Y-BB	0.28	-0.07	-0.15	0.05	12.5*	8.64*	0.13
ATP S8 26Y-2	0.87*	-0.12	-0.24*	0.02	2.93	-0.13	-0.40
ATP S8 30Y-3	0.98*	-0.05	-0.28*	0.00	7.53*	10.27*	-0.30
ATP S9 30Y-1	0.69*	-0.2*	-0.39*	-0.02	6.88*	12.7*	0.70*
ATP S9 36Y-BB	0.64*	-0.21*	-0.08	0.02	2.03	3.03	0.80*
ATP-32	-0.68*	0.21*	0.40*	-0.04	-7.19*	-6.43	0.80*
ATP-50	-0.62*	0.13	0.33*	0.04	-0.08	5.42	0.00
Cml 304	-0.39	0.06	0.09	-0.04	1.56	-0.16	0.40
Cml 357	-0.21	0.08	0.04	-0.01	-3.44	-0.17	0.97*
Cml 435	0.13	0.09	0.04	0.04	-7.11*	-6.24	0.80*
Cml 437	0.11	0.05	-0.10	-0.06	-0.81	-1.77	0.97*
Cml 439	0.25	-0.01	-0.20*	-0.04	-7.23*	-6.76	-0.40
Cml 533	-0.57*	0.17*	0.20*	-0.01	-7.35*	-11.8*	-0.70*
Cml 534	-0.23	0.10	-0.04	-0.02	-4.83	-3.15	-0.30
Cml 535	-0.38	-0.3*	-0.02	0.04	1.44	-3.38	0.83*
Cml 332	-0.4	0.02	0.09	0.00	-3.38	-4.88	0.00
Cml 479	-0.67*	0.05	0.03	0.04	-4.00	2.85	-1.10*
Cla 183	0.73*	-0.3*	-0.29*	-0.03	10.8*	15.2*	-0.30
Cml 434	0.16	-0.14	-0.09	-0.01	0.03	7.48*	-0.70
Cla 135	-0.23	0.08	0.02	0.02	-2.81	-2.02	-0.50
D300-17	-0.23	0.06	0.04	0.04	2.77	1.94	-0.40
Cam Inb gp1 17 (F)	0.00	-0.02	0.06	0.06	-1.30	-6.17	-0.60
C4RR SA4	-0.09	0.07	0.28*	-0.02	0.89	-0.97	0.00
CMS 8704	-0.57*	0.10	0.20*	-0.03	-4.09	-5.07	-0.80*
ATP SR Y	-0.49	0.10	0.29*	-0.01	0.04	3.06	-0.70

Pltasp = plant aspect, earasp = ear aspect, epp = ear per plant, earght = ear height, pltght = plant height, asi = anthesis-silking interval, * = significant at P<0.05.

Table 8. General combining ability of 'lines' for all the traits in control environments

Inbred lines	yield (t/ha)	pltasp	earasp	epp	earght (cm)	pltght (cm)	asi
ATP S5 31Y-2	-0.42	-0.06	0.12	0.12	1.03	-0.93	-0.37*
ATP S6 20Y-1	0.46	-0.09	-0.27*	-0.04	-1.42	-6.18	-0.11*
ATP S6 21Y-2	0.24	0.10	-0.11	0.02	1.76	-2.46	-0.09*
ATP S6 31Y-BB	-0.09	0.01	-0.07	0.05	8.82*	1.84	-0.17*
ATP S8 26Y-2	0.12	0.10	-0.07	0.10	-1.08	-6.80*	-0.63*
ATP S8 30Y-3	0.36	0.06	-0.09	0.02	-0.59	0.78	-0.30*
ATP S9 30Y-1	-0.01	0.07	0.06	-0.08	2.88	4.60	0.53*
ATP S9 36Y-BB	0.08	0.01	0.03	-0.03	-3.40	-4.64	0.16*
ATP-32	-0.26	0.04	0.17	0.00	-3.22	-9.00*	0.27*
ATP-50	-0.09	0.11	0.23*	0.08	-1.46	3.10	0.53*
Cml 304	0.43	-0.17*	-0.20*	-0.03	6.70*	6.96*	0.46*
Cml 357	0.48	-0.14	-0.15	-0.01	2.08	4.34	0.82*
Cml 435	0.00	0.02	0.05	-0.05	-10.65*	-9.60*	0.59*
Cml 437	0.59	0.07	-0.19*	-0.01	1.24	-0.39	1.12*
Cml 439	0.41	0.02	-0.01	-0.04	-8.80*	-8.60*	-0.20*
Cml 533	-0.36	0.16*	0.18*	0.02	-2.55	-6.58	-0.65*
Cml 534	-0.36	0.08	0.06	0.04	-3.23	-2.78	0.00
Cml 535	-0.34	-0.12	0.09	0.08	0.11	-3.04	1.01*
Cml 332	-0.45	0.06	0.07	0.04	-3.90	-6.16	0.12*
Cml 479	-0.38	-0.02	-0.03	-0.04	2.83	8.53*	-0.38*
Cla 183	-0.22	-0.03	0.06	0.01	4.60	3.91	0.10*
Cml 434	0.49	-0.09	-0.20*	0.01	-4.55	2.36	-0.45*
Cla 135	0.46	-0.06	-0.19*	-0.04	0.95	6.98*	-0.59*
D300-17	-0.33	0.10	0.03	-0.03	4.12	1.86	-0.40*
Cam Inb gp1 17 (F)	-0.55	0.30*	0.00	-0.01	-3.11	-3.17	-0.20*
C4RR SA4	-0.66*	-0.15*	0.27*	-0.06	7.80*	13.99*	-0.13*
CMS 8704	0.49	0.26*	0.04	-0.08	2.41	3.39	-0.40*
ATP SR Y	-0.09	-0.10	0.16	-0.05	0.62	7.66*	0.26*

Pltasp = plant aspect, earasp = ear aspect, epp = ear per plant, earght = ear height, pltght = plant height, asi = anthesis-silking interval, * = significant at P<0.05.

For anthesis-silking interval, GCA accounted for 35% for lines, 1% for testers and SCA accounted for 75% for the total variation among crosses in acid soils; GCA accounted for 32% for lines, 6% for testers and SCA for 66% of the variation in control soil conditions; and GCA accounted for 38% of lines, 3% testers and SCA accounted for 62% of the variation across environments. For ear height, GCA accounted for 36% for lines, 16% for testers of the total variation among crosses in acid soil environments while SCA accounted for 47%.

General combining ability for lines and testers in acid soil, control soil and across environments

Estimates of general combining ability for yield, ear aspect, plant aspect, ear height, plant height, ears per plant and anthesis-silking interval showed significant difference for yield of ten lines (ATP S8 26Y-2, ATP S8 30T-3, ATP S9 30Y-1, ATP S9 36Y-BB, ATP-32, ATP-50, Cml 533, Cml 479, Cla 183 and CMS 8704) in acid soil conditions (Table 7). Among those genotypes, five had positive value of GCA for yield. These were ATP S8 26Y-2 (0.87 t/ha), ATP S8 30Y-3 (0.98 t/ha), ATP S9 30Y-1 (0.69 t/ha), ATP S9 36Y-BB (0.64 t/ha) and Cla 183 (0.73 t/ha). The GCA of plant aspect was significant for six genotypes. Among the significant effects of GCA, two genotypes were positively significant ATP-32 (0.21), and Cml 533 (0.17). GCA of 6 genotypes was positively significant for ear aspect. Twelve genotypes had significant effect of GCA for ears per plant while four genotypes had positive and significant GCA effects for ear height. For plant height, 5 genotypes had positive significant effect of GCA. These genotypes were (Cml 301 (6.96 cm), Cml 479 (8.53 cm), Cla 135 (6.98 cm), C4RR SA4 (13.99 cm) and ATP SR Y (7.66 cm)) had positive significant effect. Anthesis-silking interval had significant effect of GCA throughout except for genotype Cml 534 which had positive and non-significant value. Fourteen of 29 genotypes had positive significant GCA effect for anthesis-silking interval (Table 7).

The estimate of the general combining ability of all the quantitative traits in control environments gave only one negative significant difference for yield observed with C4RR SA4 (-0.66 t/ha) (Table 8). Five lines had significant GCA for plant aspect, among them 3 had positive effects. For ear aspect, three genotypes gave positive significant effect of GCA. There were no significant effects of GCA for ears per plant whilst three lines (ATP S6 31Y-BB (8.82 cm), Cml 304 (6.70 cm) and C4RR SA4 (7.80 cm)) showed positive significant effect of GCA for ear height. Similarly, five genotypes (Cml 304 (6.96 cm), (Cml 479 (8.53 cm), Cla 135 (6.98 cm), C4RR SA4 (13.99 cm), ATP SR Y (7.66 cm)) had positive and significant GCA effects for plant height. For anthesis-silking interval, only Cml 534 gave a positive value of GCA in control environments.

The testers Cam Inb gp1 17 and 9450 showed positive GCA for yield while testers 88069 and 4001 gave negative GCA for yield in acid soil environments (Table 9). A significant and positive GCA was observed in tester 88069 for plant aspect, in tester 9450 and 4001 for ear aspect and with tester 88069 for plant height. In control environments, only the GCA of Cam

Inb gp1 17 had positive and significant effect for yield and anthesis-silking interval (Table 10).

Specific combining ability of the hybrids in acid soil, control soil and across environments

Significant and positive SCA effects for grain yield were obtained for ATP S5 31Y-2 with 4001 and a negative and significant SCA was obtained with the same line when crossed with Cam Inb gp1 17 in acid soil environments (Figure 1). More than ten lines had positive effect of SCA in stress environments when cross with all the testers. In control environments, Cml 535 had significant and positive SCA with Cam Inb gp1 17, and ATP S6 31Y-BB specifically combined with 9450 and 4001, respectively, for yield (Figure 2).

Across environments, 14 inbred lines had positive SCA values with Cam inb gp1 17, 11 gave positive values with 88069, 15 lines with 9450 and 12 lines with 4001 (Table 11). The SCA of 8 lines (ATP S5 31Y-2, ATP S6 31Y-BB, ATP S8 30Y-3, ATP-50, Cml 437, Cml 535 and Cml 434) were significant and four of them were positive with Cam Inb gp1 17; 4 inbred lines were positively significant with 9450 (ATP S5 31Y-2, ATP S6 31Y-BB, Cml 304 and Cla 183). ATP S5 31Y-2 had positive and significant effect of SCA with 9450, ATP S9 36Y-BB had positive and significant SCA with 4001 and D300-17 had positive and significant SCA with Cam Inb gp1 17 (Table 11).

Heterotic groups in acid soil, control soil and across environments

Inbred lines were classified into heterotic groups based on their specific combining ability with each of the four testers (Cam Inb gp1 17, 88069, 9450 and 4001) and also based on their yield compare to the yield of the best hybrid check in a given environment (Table 12). The best check under acid soil conditions was 9405 x Cam Inb gp1 17 which yielded 4.0 t/ha. Any testcross hybrids with a positive specific combining ability and expressing a yield of 10% greater than the best check when crossed with a tester was classified in the anti group of that tester. Ten out of 25 inbred lines were classified into four heterotic groups in acid soil environments. For instance, Heterotic group A had three inbred lines (ATP S8 26Y-2, ATP S8 30Y-3 and Cml 434) which were anti to Cam Inb gp1 17.

In control condition, the best hybrid check was 4001 x 88069 which yielded 6.1 t/ha under. The inbred lines expressing yield 10% higher than the yield of the best check were classified into anti heterotic group of the tester. Heterotic group A had three introduced inbred lines (Cml 437, Cml 439 and Cml 434) and heterotic group C had one inbred line (ATP S6 31Y-BB). Group B and D were empty.

Across environments, 17 inbred lines out of 25 were classified into heterotic groups. Group A had the highest number of lines (10 inbred lines) which yielded at least 10% higher than the best check when crossed with Cam Inb gp1 17. Heterotic group C had 8 inbred lines; group B and D had four lines each. Four checks out of six yielded 4.3 t/ha across environments.

Table 9. General combining ability of the testers in acid soil environments for all the traits

Tester	Yield (t/ha)	pltas	earasp	epp	earhgt (cm)	pltght (cm)	asi
Cam Inb gp1 17	0.03	-0.05	-0.04	0.02	-1.1	1.79	0.04
88069	-0.07	0.07*	0.07	0.02	-4.28*	-6.13*	0.03
9450	0.11	-0.003	0.004	-0.01	2.96*	3.87*	-0.13
4001	-0.06	-0.01	-0.04	0.01	2.4*	0.47	0.07

pltas = plant aspect, earasp = ear aspect, epp = ear per plant, pltght = plant height, asi = anthesis-silking interval, * = significant at P<0.05.

Table 10. General combining ability of the testers in control soil environments for all the traits

Tester	yield (t/ha)	pltas	earasp	epp	earhgt (cm)	pltght (cm)	asi
Cam Inb gp1 17	0.35*	-0.002	-0.02	0.02	-0.72	1.04	0.25*
88069	-0.14	-0.01	0.04	-0.01	-1.77	-3.4*	-0.1
9450	0.03	-0.01	0.03	-0.01	1.50	2.13	-0.08
4001	-0.25*	0.02	-0.04	0.00	0.99	0.27	-0.07

pltas = plant aspect, earasp = ear aspect, epp = ear per plant, pltght = plant height, asi = anthesis-silking interval, * = significant at P<0.05.

Table 11. SCA and GCA of genotypes for grain yield across enviro

Genotypes	SCA for yield						GCA
	Cam Inb gp1 17	88069	9450	4001			
ATP S5 31Y-2	-1.40*	-0.47	0.91*	1.08*			-0.06
ATP S6 20Y-1	-0.47	0.76	0.41	0.28			0.24
ATP S6 21Y-2	-0.09	0.7	0.09	0.27			0.18
ATP S6 31Y-BB	-0.83*	-0.8	1.34*	-0.22			0.32
ATP S8 26Y-2	0.64	0.62	0.19	-0.55			0.37
ATP S8 30Y-3	1.04*	-0.25	0.13	0.59			0.39
ATP S9 30Y-1	-0.02	-0.13	0.3	-0.15			0.43*
ATP S9 36Y-BB	0.34	0.15	-0.76	0.99*			0.27
ATP-32	0.43	-0.13	-0.5	0.12			-0.36
ATP-50	-0.88*	-0.16	0.32	-0.29			0
Cml 304	0.34	-0.54	0.94*	-0.35			0.02
Cml 357	-0.06	-0.31	-0.35	0.56			0.27
Cml 435	0.06	0.13	0.06	0.35			0.01
Cml 437	0.83*	0.16	0.15	-0.14			0.2
Cml 439	0.35	-0.01	-0.13	0.21			0.32
Cml 533	-0.31	-0.25	0.01	0.39			-0.33
Cml 534	-0.55	-0.4	-0.4	0.44			0.03
Cml 535	0.89*	0.24	-0.56	-0.33			-0.33
Cml 332	0.45	0.61	-0.58	-0.28			-0.38
Cml 479	0.11	-0.33	-0.4	0.5			-0.40*
Cla 183	-0.22	0.54	1.06*	-0.64			0.16
Cml 434	1.09*	0.23	-0.13	-0.26			0.19
Cla 135	0.39	0.36	0.34	-0.41			0.04
D300-17	0.73	-0.21	0.22	-1.03*			-0.11
Cam Inb gp1 17 (F)	-0.82	-0.05	-0.01	-0.01			0.04
C4RR SA4	-	-	-	-			-0.02
CMS 8704	-	-	-	-			0.28
ATP SR Y	-	-	-	-			0.01
GCA	-2.59*	-1.8*	-2.4*	-2.2*			

Nments, Pltaspe = plant aspect, earasp = ear aspect, epp = ear per plant, earhgt = ear height, pltght = plant height, asi = anthesis-silking interval, NS = non-significant, * = significant at P<0.05, Prob = probability

Table 12. Heterotic grouping of inbred lines in acid soil control soil and across environments

Group A/Anti Cam Inb gp1 17	Group B/Anti 88069	Group C/Anti 9450	Group D/Anti 4001
Under acid soil environments			
ATP S8 26Y-2	ATP S6 21Y-2	ATP S6 31Y-BB	ATP S5 31Y-2
ATP S8 30Y-3	ATP S9 36Y-BB	Cla 183	ATP S8 30Y-3
Cml 434	Cla 183	Cam Inb gp1 17 (F)	ATP S9 30Y-1
Best hybrid check			
9450 x Cam Inb gp1 17	4.0 t/ha		
Under control conditions			
Cml 437	/	ATP S6 31Y-BB	/
Cml 439	/		/
Cml 434	/		/
Best hybrid check			
4001 x 88069	6.1 t/ha		
Across environments			
ATP S8 26Y-2	ATP S6 20Y-1	ATP S5 31Y-2	ATP S5 31Y-2
ATP S8 30Y-3	ATP S6 21Y-2	ATP S6 20Y-1	ATP S8 30Y-3
ATP S9 36Y-BB	ATP S8 26Y-2	ATP S6 31Y-BB	ATP S9 36Y-BB
Cml 304	Cla 183	ATP S8 26Y-2	Cml 357
Cml 437		ATP S8 30Y-3	
Cml 439		ATP S9 30Y-1	
Cml 535		Cml 304	
Cml 434		Cla 183	
Cla 135			
D300-17			
Best hybrid checks			
4001 x 9450	4.3 t/ha		
88069 x Cam Inb gp1 17			
9450 x 88069			
9450 x Cam Inb gp1 17			

Anti A = opposite tester Cam Inb gp1 17, Anti B = opposite tester 88069, anti C = anti 9450 and anti D = anti 4001.

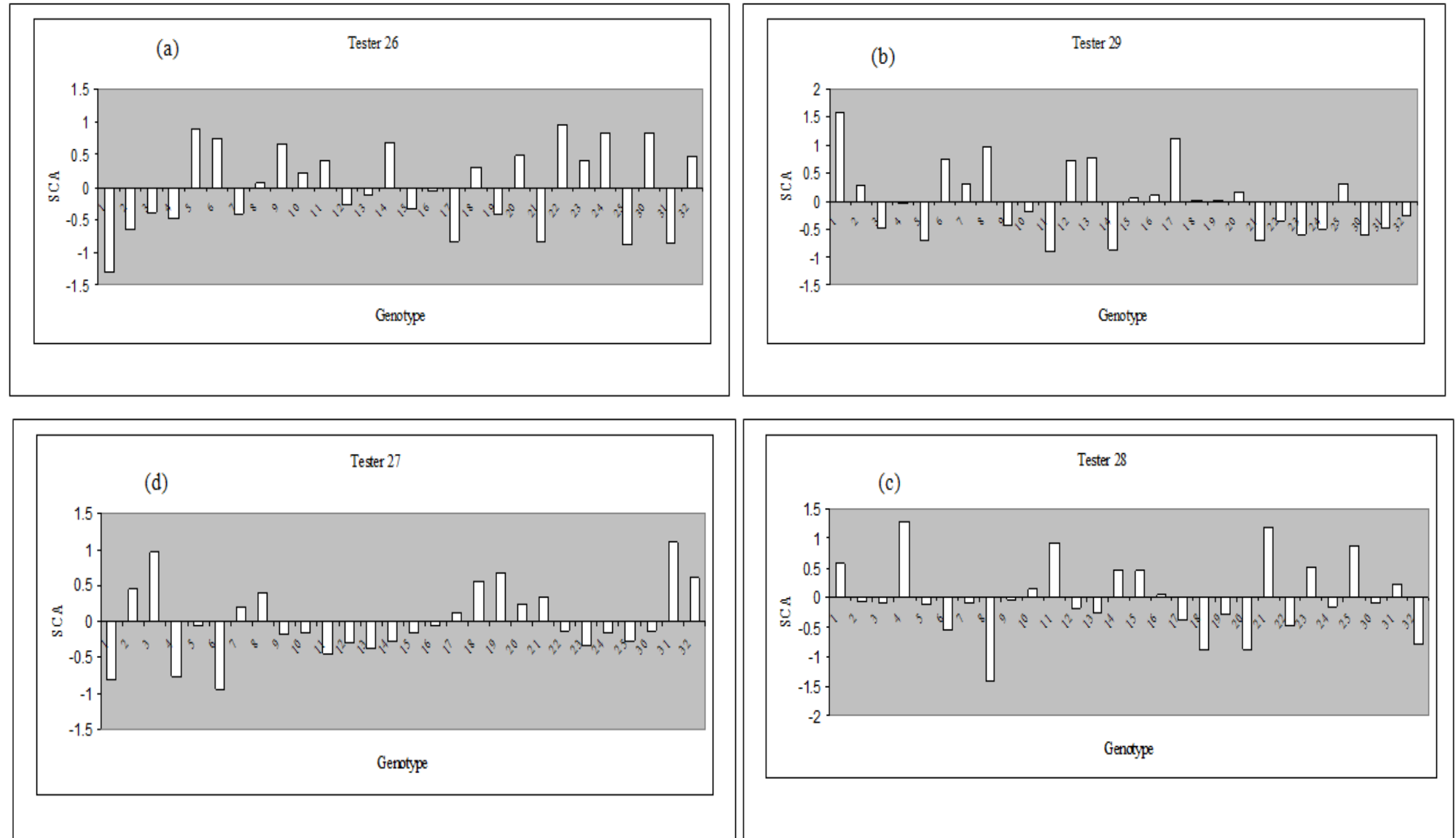


Figure 1. Specific combining ability of testers 26 (a), 27 (d), 28 (c) and 29 (b) with the 28 'lines' for yield trait under acid soil environments

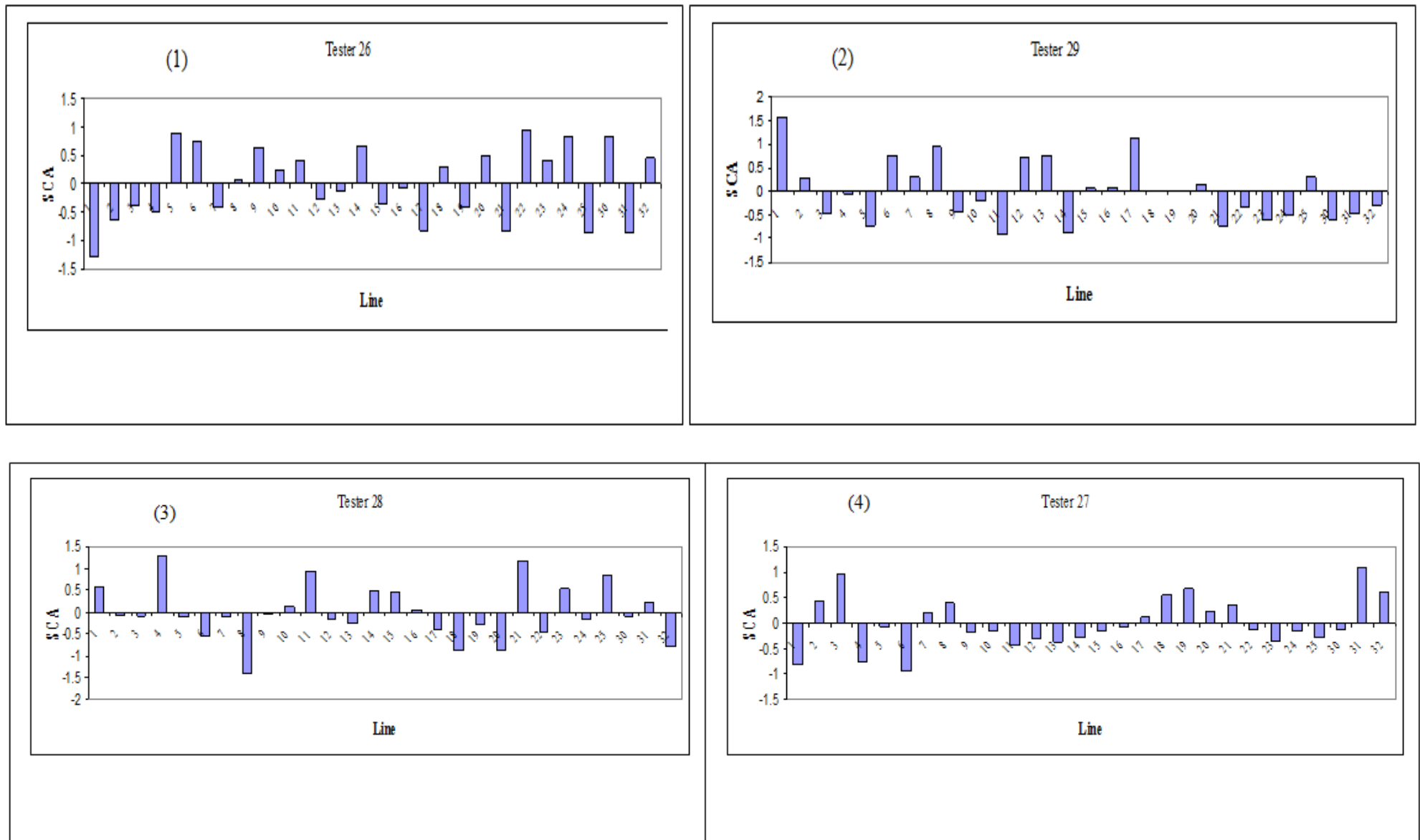


Figure 2. Specific combining ability of testers 26 (1), 27 (4), 28 (3) and 29 (2) with the 28 'lines' for yield trait under control environments

DISCUSSION

The significant differences recorded among environment and line x tester interaction across environments indicated that genotypes were different from each other and responded differently in different acid soil environments, control environments and across environments. Similar results were reported by The *et al.* (2006), Badu-Apraku *et al.* (2013) and Ifie (2013). The presence of significant GCA and SCA mean squares for all the traits recorded under acid soil and across environments for anthesis-silking interval under control environments revealed that these traits were controlled by both additive and non-additive gene actions. Similar results were reported The *et al.* (2005), Badu-Apraku *et al.* (2013) and Ifie (2013).

The comparison of GCA sum of squares to SCA sum of squares showed that the contribution of SCA was higher for almost all the traits (yield, anthesis-silking interval, ears per plant) recorded in acid soil, control and across environments except for ear height in acid soil environments. This result revealed that all these traits were predominantly controlled by non-additive gene actions in their expression. On average, SCA explained 68%, 73% and 53% of the total sum of squares among crosses in acid soil, control soil and across environments, respectively, for yield. Therefore yield was mainly controlled by the non-additive genes than the additive gene in the study environments. This confers the advantage of exploiting heterosis to improve grain yield of maize hybrids in acid soil control soil and across environments. This implied that appreciable breeding progress could be made using hybridization, backcrossing, and recurrent selection methods for the development of hybrids and synthetic varieties as well as in population improvement after classifying inbred lines into heterotic groups. Similar findings were reported by Fan *et al.* (2008), Meseka *et al.* (2008), Worku *et al.* (2008), Badu-Apraku *et al.* (2011) and Ifie (2013). The result obtained in the present study was different to that of The *et al.* (2005) who reported that tolerance to soil acidity was predominantly controlled by additive gene actions. The difference observed in the two studies could be due to the difference in plant materials utilized as well as the environments used for the evaluation. The larger proportion of GCA effects of inbred lines for ear height than the SCA effects in acid soil environments suggested that additive gene action played a dominant role in the inheritance of the measured traits. This result implied that additive gene action was more important than the non-additive for this trait and that GCA was the main component accounting for the differences among the hybrids for the study environment. Similar results were reported by Akinwale *et al.* (2014) and Badu-Apraku *et al.* (2013) under different stress environments studied.

The results of the current study were also different from the findings of Tekeu *et al.* (2014) who found that tolerance to acid soils with aluminum toxicity was controlled by additive gene effects while on acid soil manganese toxicity, the contribution of non-additive gene effects was dominant. The difference observed in these two studies might be due to the difference of genotypes and the environments used.

In the present study, five inbred lines had positive and significant GCA effects under acid soils. They were ATP S8 26Y-2, ATP S8 30Y-3, ATP S9 30Y-1, ATP S9 36Y-BB and Cla 183. ATP S8 26Y-2 gave positive SCA with Cam Inb gp1 17; ATP S8 30Y-3 gave positive SCA with Cam Inb gp1 17 and 4001; ATP S9 30Y-1 gave positive SCA with 88069 and 4001; ATP S9 36Y-BB gave positive SCA with Cam Inb gp1 17, with 88069 and with 4001; and finally Cla 183 gave SCA with 88069 and with 9450. The five inbred lines stated above also gave positive SCA with Cam Inb gp1 17, 88069 or 9450 in control environments. These lines also gave good GCA and SCA values across environments. Moreover, genotypes ATP S5 31Y-2, ATP S6 31Y-BB, ATP S9 30Y-1, Cml 304, Cml 437 and Cml 434 had positive and significant SCA across environments when crossed with all the testers. They also gave positive GCA across environments except ATP S5 31Y-2 which had a negative GCA value with Cam Ing gp1 17 and 88069. These results suggested that the lines contributed to higher grain yield of their hybrids. These inbred lines could be of potential use in breeding new lines. Similar findings were reported by Makumbi *et al.* (2011), Badu-Apraku *et al.* (2013) and Ifie (2013).

The specific combining abilities for lines with testers associated with high yield performance compare to the best check were used to develop heterotic groups. Four heterotic groups (A, B, C and D) of lines were identified in acid soil and across environments. In control environments, two heterotic groups (A and C) were formed with Cam Ing gp1 17 and 9450. The hybrids made of inbred lines in group A combined well with Cam Inb gp1 17 and yielded 10% higher than the yield of the best check. The inbred lines in group B combined well with the tester 88069 and yielded 10% more than the best hybrid check. The lines of group C combined well with 9450 and yielded 10% more than the best checks and the lines of group D combined well with 4001 and yielded 10% more than the best hybrid check in each environmental condition. The inbred lines ATP S5 31Y-2, ATP S6 31Y-BB, ATP S8 30Y-2, Cml 434, ATP S9 36Y-BB, ATP S6 21Y-2, ATP S8 26Y-2 and Cla 183 were in different heterotic groups under acid soil, in control soil and across environments. These inbred lines could be potential testers for further studies and also they could be used in new source population for development of new high-yielding hybrids. Among these inbred lines, Cml 434 and Cla 183 were introduced from CIMMYT. This means that the introduction of inbred lines was efficient in creating variability and developing high-yielding hybrids. Similar results were reported by Fan *et al.* (2008).

Tandzi *et al.* (2015b) reported ten best hybrids identified under acid soil conditions (Cla 183 x 9450, ATP S9 36Y-BB x 4001, Cla 183 x 88069, Cml 434 x Cam Inb gp1 17, ATP S5 31Y-2 x 4001, Cml 437 x Cam Inb gp1 17, ATP S8 26Y-3 x Cam Inb gp1 17, Cml 534 x 4001, Cla 183 x Cam Inb gp1 17, Cml 439 x 4001). Among those hybrids, only six were classified into four heterotic groups using the same testers.

In the present study, even though the variability among inbred lines was not very high (Tandzi *et al.*, 2015a), 10 inbred lines out of 25 were classified into heterotic groups in acid soil environments, four out of 25 inbred lines were classified in

control conditions and 17 out of 25 were classified across environments. All the lines could not be classified into to heterotic groups based on the criteria of classification used. Similar results have been reported in previous studies (Vasal *et al.*, 1992; Menkir *et al.*, 2003; Akinwale *et al.*, 2014 and Rajendran *et al.*, 2014). Additionally, under control environments, only Cam Inb gp1 17 and 9450 were able to assign four inbred lines into two heterotic groups. According to Tekeu *et al.* (2014), Cam Ing gp1 17 was a good progenitor in acid soil conditions. The testers 88069 and 4001 were not good testers in control environments. In the present study, the testers used were parents of high-yielding hybrids but they have not yet been released for commercial purpose.

Conclusion

AI tolerance is in both additive and non-additive genetic control with the predominance of the non-additive gene action. Faster progress could be made by selecting for traits that are largely controlled by additive gene effect than those controlled by non-additive gene effects but such selection will not identify heterosis that would significantly increase yields. Therefore, the classification of lines into heterotic groups is required. Four distinct heterotic groups (group A, group B, group C and group D) were identified in acid soil and across environments based on the positive specific combining ability and yield compared to the best hybrid check. The lines of group A gave high-yielding hybrids when cross with Cam Inb gp1 17 and out-yielded the best check by 10%, the lines of group B gave high-yielding hybrids when cross with 88069 and out-yielded the best hybrid check by 10%, the lines of group C out-yielded the best check by 10% when crossed with 9450 and the lines of group D out-yielded the best check by 10% when crossed with 4001. In control environments, only Cam Inb gp1 17 and 9450 were able to assign four inbred lines into two heterotic groups. These testers were the best under control and across environments while under acid soil conditions, 4001 was the best. The testers 88069 and 4001 were not good testers under control environments. The inbred lines ATP S5 31Y-2, ATP S6 31Y-BB, ATP S8 30Y-2, Cml 434, ATP S9 36Y-BB, ATP S6 21Y-2, ATP S8 26Y-2 and Cla 183 expressed good and positive SCA and GCA in acid soil and across environments. These lines could be used as testers for further studies. Among these lines, Cml 434 and Cla 183 were introduced from CIMMYT. This showed that the introduction of lines was efficient for the development of high-yielding hybrids since they raised the variability and increased the probability of identifying some high-yielding hybrids tolerant to AI toxicity.

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