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Research Article

Estimation of Combining Ability and Heterosis of Highland Maize (*Zea mays* L.) Inbred Lines for Grain Yield and Yield Related Traits

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ABSTRACT

Maize is staple cereal crop in Ethiopia despite its production is constrained by many biotic and abiotic stresses. The objectives of this study was, to estimate heterosis and combining ability of high land maize inbred lines for yield and yield related traits. Twenty-six inbred lines (two heterotic testers and twenty-four lines) were crossed using line × tester mating design and generated 48 F_1 hybrids and the hybrids along with two hybrid checks (AMH853 and AMH 851) were evaluated using alpha lattice design with two replications for grain yield and yield related traits during 2017 cropping season at Ambo and Kulumsa. Analyses of variances showed significant mean squares due to hybrids for all traits in each and across locations. The mean squares for general (GCA) and specific (SCA) combining abilities were significant for most of the traits, implied that importance of both additive and non-additive gene effects in most cases. Inbred lines L2, L9 and L20 were good combiners for grain yield and hence were promising parents for hybrid cultivars development. Based on mid parent, high parent and standard heterosis, SCA effects and per se performance, the cross L20xT1 was identified as a promising hybrid for majority of traits studied.

Key words: Hybrids, Heterosis, GCA and SC

INTRODUCTION

Ethiopia is the fifth largest producer of maize in Africa and smallholder farmers make up 94 % of the crop production (ethioagp.org, 2017). Maize ranks second after *teff* in area coverage and first in total production (CSA, 2017). It is the most widely consumed grain. According to CSA data, 80% of maize production is used for household consumption, 10% is sold on the open market, the remainder is used for seed, wages in kind, and animal feed (USDA, 2015). Maize research in Ethiopia started in 1950's with the evaluation of introduced materials focusing mainly on grain yield, early maturity, decreased plant height, lower ear placement and resistance to major biotic stresses (Benti, 1992). Since then, the research system has developed and released a number of improved varieties with their accompanying agronomic practices and plant protection technologies for all maize growing agro-ecologies of the country (Mosisa *et al*, 2012).

Average national yield of maize is 3.67tha^{-1} (CSA, 2017) which is lower than the world average 5.65t/ha (USDA, 2018). The wide yield gap is attributed to an array of abiotic and biotic stresses, besides other factors. In spite of its wide adaptation and efforts made to develop improved maize technologies for different maize agro-ecological zones, many biotic and abiotic constraints still, limit maize production and productivity in different maize producing area of the country (Abate *et al*., 2017). The major abiotic stresses in the highland zones are frost, hail and water logging (on Vertisols). These are compounded by undulating terrain, low soil fertility and wide variations in climatic and other environmental conditions (Twumasi *et al*., 2002).

The high altitude, sub-humid maize agro ecology (1800-2400 m.a.s.l.) in Ethiopia is estimated to cover 20% of the land devoted to annual maize cultivation. Adoption of maize is increasing in the highland agro-ecology (Demissew *et al*., 2013). To meet the needs of increasing maize production in the highlands of Ethiopia, the Highland Maize Breeding Program in Ethiopian was established in collaboration with the International Maize and Wheat Improvement Center (CIMMYT), in 1998. Since 1999, the breeding program has released seven superior highland maize cultivars for wide production.

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Information is still limited regarding combining ability of maize inbred lines and choosing the best testers to use when developing single and three-way cross hybrids for the highlands. So far, combining ability effects and heterosis in maize inbred lines has been extensively studied under non-stressed conditions in Ethiopia for different sets of new inbred lines developed/introduced and adapted at different times (Amare *et al*., 2016; Ziggy *et al*., 2016, Abakemal *et al*., 2016; Assefa *et al*., 2017). Understanding the relative importance of general (GCA) and specific combing ability effects for different traits for newly developed and/or introduced inbred lines is of paramount importance to design future breeding strategies for the development of hybrid and/or synthetic varieties. In the current study, therefore, an attempt were made to generate information on 24 elite maize inbred lines crossed to two testers of known heterotic groups using line x tester mating design to estimate heterosis and combining abilities of inbred lines.

MATERIALS AND METHODS

Experimental Site

The field experiments were conducted at Kulumsa and Ambo Agricultural Research Centers during the 2017 main cropping season. Geographically, Kulumsa lies at 8^{o}5'N latitude, 39^{o}10'E longitude at an elevation of 2200 m.a.s.l. The average rainfall at the research center is 1078 mm per annum having peaks in July and August. The mean maximum and minimum temperatures are 23.2^{o}C and 10^{o}C, respectively. The soils are luvisol/eutric nitosols with good drainage. The location received a total precipitation of 710.7 mm, and an average maximum and minimum temperature of 22.75 ^{o}C and 11.92 ^{o}C, respectively, during the growing season, May to December 2017 (Kulumsa Agricultural Research Centers Meteorological Station, unpublished data). Ambo is located at 8^{o}57'N latitude, 38^{o}7'E longitude and at an altitude of 2225 m.a.s.l with average annual rainfall of 1110 mm, maximum and minimum temperature of 26˚C and 11˚C, respectively. The soil type of the experimental field is vertisols (http.//www.eiar.gov.et/index.php/ research-centers). The total precipitation during the growing season (May to December 2017) was 864.1 mm, and the mean maximum and minimum temperatures were 24.1^{o}C and 10.51^{o}C, respectively (Ambo Agricultural Research Centers Meteorological Station, unpublished data).

Experimental materials

The experiment was consisted of 48 testcrosses produced by crossing 24 inbred lines to two testers in line x tester mating design, and two standard checks (AMH851 and AMH853). The inbred lines were introduced from CIMMYT-Zimbabwe. The two testers, FS59 (Tester 1) and FS67 (Tester 2), are adapted lines locally developed at Ambo. FS59 is heterotic group B while FS67 is heterotic group A. The lines x tester crosses were made by highland maize breeding program during the main season of 2016. AMH851 and AMH853 are commercial hybrid checks released for and produced in the highland agro- ecologies of Ethiopia. The list and pedigrees of the inbred lines and testers used for the study are presented in Table 1.

Table 1: The Pedigree and source of the lines and testers used in the study

Line code	Pedigree	Source
L1	(LPSC7-F96-1-2-1-1-B-B-B*/OFP9)-3-1-1-1-1-B-B-#	CIMMYT/AHMBP
L2	(LPSC7-F96-1-2-1-1-B-B-B*/OFP39)-6-1-1-1-1-B-B-#	CIMMYT/AHMBP
L3	(LPSC7-F71-1-2-1-2-B-B-B*/OFP1)-B-14-4-1-B-B-B-#	CIMMYT/AHMBP
L4	(LPSC7-F71-1-2-1-2-B-B-B*/OFP2)-B-1-3-1-B-B-B-#	CIMMYT/AHMBP
L5	(LPSC7-F71-1-2-1-2-B-B-B*/OFP3)-B-18-1-1-B-B-B-#	CIMMYT/AHMBP
L6	CML539-B-#	CIMMYT/AHMBP
L7	(CML539*/OFP9)-4-1-1-2-1-B-B-#	CIMMYT/AHMBP
L8	(CML539*/OFP27)-2-1-2-1-1-B-B-#	CIMMYT/AHMBP
L9	(CML539*/OFP14)-2-1-1-2-1-B-B-#	CIMMYT/AHMBP
L10	(CML539*/OFP14)-2-1-3-1-2-B-B-#	CIMMYT/AHMBP
L11	CML539*/OFP1)-B-6-1-1-B-B-B-#	CIMMYT/AHMBP
L12	CML539*/OFP1)-B-11-2-1-B-B-B-#	CIMMYT/AHMBP
L13	(CML539*/OFP4)-B-12-1-1-B-B-B-#	CIMMYT/AHMBP
L14	CML442-#	CIMMYT/AHMBP
L15	(CML442*/OFP1)-B-14-4-2-B-B-B-#	CIMMYT/AHMBP
L16	(CML442*/OFP1)-B-18-2-2-B-B-B-#	CIMMYT/AHMBP
L17	(CML442*/OFP4)-B-4-1-2-B-B-B-#	CIMMYT/AHMBP
L18	(CML442*/OFP4)-B-17-3-2-B-B-B-#	CIMMYT/AHMBP
L19	(CML395*/OFP105)-1-2-3-1-2-B-B-#	CIMMYT/AHMBP
L20	(CML444*/OFP23)-6-3-1-1-2-B-B-#	CIMMYT/AHMBP
L21	([CML312/[TUXPSEQ]C1F2/P49-SR]F2-45-3-2-1-BB//INTA-F2-192-2-1-1-1-BBBB]-1-5-1-1-1-BBB-B-B-B*/OFP106)-1-2-2-2-2-B-B-#	CIMMYT/AHMBP
L23	(CML495*/OFP6)-B-3-3-3-B-B-#	CIMMYT/AHMBP
L24	(CML495*/OFP6)-B-27-1-1-B-#	CIMMYT/AHMBP
	TESTER	
T1	FS59	AMBO
T2	FS67	AMBO
	CHECKS	
1	KOLBA (AMH853)	AMBO
2	JIBAT (AMH 851)	AMBO

AHMBP = Ambo Highland Maize Breeding Program.

Experimental design

The hybrids were planted in alpha-lattice design (Patterson and Williams, 1976) with two replicates while parents evaluated in Randomized complete block design with two replication in adjacent fields. Design and randomization of the trials were generated using CIMMYT's software known as Field book (Banziger and Vivek, 2007). One-row plots of 5.25m length and 75 x 25cm spacing between rows and plants were used to achieve 53,333 plants per hectare. Two seeds were hand planted per hill and later thinned out to one plant per hill after seedlings established well. The recommended dosage of Diammonium phosphate (DAP) fertilizer was applied all at planting at the rate of 100 kg /ha while 200 kg/ha of Urea was applied in split at knee height and just before flowering of the crop. All other crop management practices were carried out as per the recommendations for location.

Data recorded

Data on grain yield and other agronomic traits were collected on plot and individual plant basis. Anthesis date (AD) and silking date (SD) were recorded as 'number of days after planting', when 50% of plants were shedding pollen and silking, respectively. Plant height (PH) was measured as the average height of five randomly selected plants measured in cm from base of the plant to the first tassel branch. Ear height (EH) was measured as the average height of five randomly selected plants measured in cm from base of the plant to the node bearing the upper most ear of the same plants used to measure plant height. At harvest, the number of ears per plant (EPP) was computed as the total number of harvested ears in each plot divided by the stand count at harvest. Number of kernels per row (NKR) this was recorded by counting kernels in each row from five randomly taken ears and the average value was recorded as kernels per row. Number of kernel rows per ear (KRE) this was measured as total number of kernel rows of the ear was counted from five randomly taken ears and the average value was used as kernel rows per ear. Thousand Kernels Weight (TKWT) was recorded as the weight in grams of 1000 random kernels was weighed from each plot using sensitive balance and was adjusted to 12.5 % moisture level. Grain Yield (t ha^{-1}) was measured as the total grain yield in kg per plot and adjusted to 12.5% moisture level was used to calculate grain yield per hectare.

Data analysis

Analysis of variance per environment was conducted with the PROC MIXED procedure in (SAS, 2002) considering genotypes as fixed effects and replications and blocks within replications as random. Combined analysis across environments also computed using PROC GLM in SAS software version 9.0 (SAS, 2002). The combined analysis was done for the significant trait in individual location analysis after testing the homogeneity of error variances through the application of the F- test (Gomez and Gomez, 1984).

Further analysis was done according to the line x tester analysis (Kempthorne, 1957) to partition the mean square due to crosses into lines, tester and line by tester effects (Dabholkar, 1999) using SAS computer program (SAS, 2002) for traits that shows significant differences among crosses. General combining abilities of lines and testers, and specific combining abilities of lines by testers were computed for the characters that show significant differences among crosses in the ANOVA.

RESULTS AND DISCUSSION

Analysis of variance

Hybrids exhibited highly significant (P<0.01) differences in most traits at both locations (Table 2). Combined analyses were performed for the traits that showed significant genotypic mean squares for individual location analysis and homogenous error variance analyzed using F-test (Gomez and Gomez, 1984). Combined analysis of variance across environments revealed that all traits exhibited highly significant (P< 0.01) differences among the hybrids (Table 4). Significant differences observed among hybrids for individual and across environments indicate the existence of a high level of variation for various characteristics that makes selection possible for improved grain yield and agronomic traits. Similar results were reported (Amare *et al*., 2016; Demissew *et al.* 2016; Bullo and Dagne, 2016; Tolera *et al*., 2017; Mafouasson *et al*., 2017).

Table 2: Mean squares due to hybrids and error for grain yield and yield related traits evaluated at Ambo and Kulumsa, 2017

Traits	Df	Mean square				F-ratio
		Ambo optimum N		Kulumsa optimum N		Larger eMS Smaller eMS
		Hybrid	error	hybrid	error	
GYF (tha^{-1})	49	3.91**	1.54	2.24**	0.93	1.66
DA (days)	49	11.57**	2.89	12.03**	1.49	1.94
DS (days)	49	11.79**	3.89	12.46**	1.57	2.48
PH (cm)	49	992.19**	70.42	599.52**	98.77	1.40
EH (cm)	49	438.16**	34.2	447.43**	73.35	2.14
EPP (#)	49	0.01**	0.04	0.09**	0.04	1.00
NRPE (#)	49	1.52*	0.74	1.28*	0.66	1.12
NKPR ((#)	49	16.08*	7.88	18.39*	9.10	1.15
TKW(G)	49	2636.28**	916.91	4350.73**	610.2	1.5

*P<0.05; **P<0.01; # = numbers; Df= degree of freedom of hybrids; GYF= grain yield; DA= days to anthesis; DS= days to silking; PH= plant height (cm); EH= ear height (cm); EPP= ears per plant; NRPE= number of rows per ear; NKPR= number of kernels per row; TKW= thousand kernel weight.

Mean performance of genotypes

The mean grain yield for genotypes tested under this experiment ranged from 6.9 tha^{-1} (L16xT2) to 11.8 tha^{-1} (L20xT1) with a mean value of 9.1 tha^{-1} (Table 3). Among the crosses, six crosses showed significantly higher yield than the hybrid check Kolba (Table 3). The number of days to 50% tasseling ranged from 88.1days to 97.9 days with overall mean of 92.1days (Table 3). The trait days to 50 percent silking showed a similar variation pattern with days to tasseling. The mean value for plant height ranged from 192.5 cm to 298.5 cm and the mean Plant height was 234 cm (Table 3). Seventeen crosses exhibited significantly higher plant height than check Kolba. The mean ear height for all genotypes was 120.8 cm (Table 3). The number of ears per plant ranged from 1.1 to 2.0 (Table 3) with over all mean of 1.5 (Table3). In agreement with the present results, investigators in their studies identified experimental varieties performing better than the best check for these traits (Tessema *et al.*, 2014; Demissew *et al.*, 2016; Talukder *et al*., 2016).

Number of kernels row per ear was a significant difference between crosses. It varies from 10.8 to 14.5 with average 12.3 (Table 3). The minimum number of kernels rows per ear was recorded from L19xT2 cross and the maximum was from L16xT1 cross (Table 3). The number of kernels per row ranged from 26.8 to 38.6 and had mean value of 32.0 for the trait. Thousand kernels weight varies from 245.4 to 470.7g with average 357.5g (Table 3). Amare *et al*., 2016; Teshale *et al.* (2017) in their studies reported that experimental varieties showed better performance than the best check for most of yield and other traits.

Combining ability analyses

The partitioning of significant crosses mean squares into general combining ability (GCA) and specific combining ability (SCA) showed that, in across environments combined analysis, significant GCA and non- significant SCA mean squares were observed for grain yield (Table 4). Similar result was reported by Bayisa (2008) who found non-significant GCA effects for grain yield in line x tester study of transition highland inbred lines at Kulumsa. Significant GCA and non-significant SCA mean squares implied that importance of additive gene actions in governing grain yield. In contrast to these findings, Tessema *et al*. (2014), Girma *et al*. (2015), Bullo and Dagne (2016) and Amare *et al*. (2016) have also reported the importance of both additive and non-additive gene actions in governing grain yield in maize.

General combining ability sums of squares were larger than SCA sums of squares for grain yield across environments 77 and 23% respectively (Table 4). The predominance of GCA sums of squares to SCA sums of squares for grain yield indicated the relative importance of additive gene action to non-additive gene action for this trait (Beck *et al*. 1990). In line with this study, Tessema *et al*. (2014) reported the preponderance of additive gene action in the inheritance of grain yield while in contrast to these findings, Kanagarasu *et al.* 2010 and Melkamu (2013) previously reported dominant role of SCA gene action in the grain yield of maize.

In combined analysis, significant GCA and SCA mean squares were observed for anthesis and silking date (Table 4) implied the importance of both additive and non-additive gene actions in governing these traits.

Table 3: Means for grain yield and other agronomic traits of selected best 20 hybrids and checks across environments

Genotypes	GYF tha^{-1}	AD days	SD days	PH Cm	EH Cm	EPP #	NRPE #	NKPR #	TKW g
L20XT1	11.8	97.2	98.8	279.9	163.7	1.6	13.6	34.9	330.2
L2XT1	10.6	91.5	94.1	255.0	140.0	1.8	13.5	32.0	273.1
L1XT1	10.5	93.0	94.4	254.7	139.1	1.8	13.1	26.8	346.8
L9XT2	10.4	94.2	96.0	227.8	116.5	1.7	11.1	31.7	371.8
L9XT1	10.3	96.3	99.4	245.0	122.1	1.6	12.1	31.1	306.3
L18XT1	10.2	94.7	97.5	251.2	142.6	1.6	13.1	37.5	274.2
check1	10.1	90.2	92.0	246.5	127.3	1.4	12.2	29.2	394.5
L11XT2	9.9	89.4	90.6	250.5	126.8	1.4	12.7	29.3	375.8
L3XT1	9.9	88.8	91.4	235.5	122.7	2.0	12.0	32.4	286.1
L2XT2	9.8	89.4	92.0	215.0	110.9	1.7	13.4	34.0	343.4
L20XT2	9.8	91.0	93.0	245.2	124.0	1.4	12.7	32.7	422.9
L13XT1	9.8	95.4	96.8	243.4	135.0	1.5	12.7	34.1	325.5
L5XT2	9.8	93.3	95.8	218.1	110.9	1.4	11.8	31.9	382.2
L14XT2	9.7	92.6	94.4	204.9	104.6	1.6	11.4	28.8	437.2
L10XT2	9.5	92.4	93.6	215.4	114.8	1.4	11.6	27.1	417.2
L8XT2	9.4	88.1	90.4	206.3	100.9	1.8	12.1	31.5	372.4
check2	9.4	90.0	91.4	240.3	126.3	1.5	12.6	33.2	375.1
L24XT1	9.3	93.7	92.7	224.0	106.6	1.8	11.6	30.8	360.3
L1XT2	9.3	89.3	91.5	213.8	112.1	1.7	12.7	31.6	371.0
L7XT1	9.3	89.2	93.1	246.9	124.8	1.2	12.7	33.9	367.9
Minimum	6.9	88.1	90.2	192.5	93.0	1.1	10.8	26.8	245.4
Maximum	11.8	97.9	99.4	279.9	163.7	2.0	14.5	38.6	470.7
Cross mean	9.1	92.2	94.1	233.6	120.6	1.5	12.3	32.0	356.4
Check mean	9.7	90.1	91.7	243.4	126.8	1.5	12.4	31.2	384.8
Grand mean	9.1	92.1	94.0	234.0	120.8	1.5	12.3	32.0	357.5
CV (%)	12.3	1.6	1.7	3.9	6.3	13.4	7.0	9.3	7.0
LSD $_{0.05}$	1.6	2.1	2.3	12.8	10.8	0.3	1.2	4.2	35.1

GYF=grain yield; DA= days to anthesis; DS= days to silking; PH=plant height; EH= ear height; EPP=ear per plant; NRPE=number of rows per ear; NKPR= number of kernels per row; TKW= thousand kernel weight.

Table 4: Mean squares from line x tester analysis of variance for yield and yield related traits over two locations Ambo and Kulumsa, 2017.

Source of variation	DF	GYF tha^{-1}	DA days	DS days	PH Cm	EH Cm	EPP #	NRPE #	NKPE #	TKW g
Location (Loc)	1	363.2^{**}	986.4^{**}	606.7^{**}	19247.2^{**}	10920.0^{**}	0.0002^{ns}	8.2^{*}	1038.1^{**}	457588.8^{**}
Rep/ (Loc)	2	1.02^{ns}	10.92^{ns}	9.61^{ns}	388.82^{*}	368.97^{**}	0.10^{ns}	0.88^{ns}	57.57^{**}	66.3^{ns}
Genotypes(G)	71	45.84^{**}	121.89^{**}	131.57^{**}	8095.32^{**}	3447.22^{**}	0.22^{**}	2.15^{**}	103.91^{**}	23843.5^{**}
Hybrids (H)	49	3.2^{**}	18.9^{**}	16.5^{**}	1116.7^{**}	638.0^{**}	0.1^{**}	1.9^{**}	16.4^{**}	5876^{**}
Crosses (C)	47	3.37^{**}	26.21^{**}	24.31^{**}	1798.29^{**}	908.38^{**}	0.17^{**}	2.28^{**}	18.56^{**}	7727.7^{**}
Parents(P)	23	1.52^{**}	71.87^{**}	61.74^{**}	1194.54^{**}	414.25^{**}	0.27^{**}	1.93^{ns}	34.03^{**}	9826.7^{**}
G x Loc	71	2.53^{**}	7.32^{**}	7.63^{**}	623.86^{**}	270.81^{**}	0.09^{**}	1.83^{*}	21.58^{**}	1787.3^{**}
H x Loc	49	2.1^{*}	2.2^{ns}	3.4^{ns}	158.7^{**}	87.0^{**}	0.04^{ns}	0.7^{ns}	16.1^{*}	1035.8^{*}
Crosses x Loc	47	2.76^{**}	3.59^{ns}	4.03^{ns}	182.84^{*}	114.61^{**}	0.05^{ns}	0.75^{ns}	19.28^{**}	952.1^{ns}
P x Loc	23	0.64^{**}	14.26^{**}	14.30^{**}	104.49^{ns}	76.01^{ns}	0.19^{**}	1.46^{ns}	7.66^{ns}	2406.1^{**}
P vs (C)	1	3061.5^{**}	5769.7^{**}	6778.8^{**}	462774.1^{**}	192530.8^{**}	1.3^{**}	1.1^{ns}	5722.7^{**}	1103678^{**}
P vs C x Loc	1	35.12^{**}	22.96^{ns}	23.36^{ns}	33297.13^{**}	12092.67^{**}	0.11^{ns}	61.46^{**}	450.09^{**}	26808.6^{**}
GCAL	23	4.78^{**}	40.54^{**}	34.92^{**}	1385.77^{**}	731.08^{**}	0.26^{**}	2.37^{**}	27.54^{**}	8446^{**}
GCAT	1	5.61^{*}	135.01^{**}	208.33^{**}	40420.22^{**}	20933.45^{**}	0.0007^{ns}	25.44^{**}	29.59^{ns}	118960.3^{**}
SCA L x T	23	1.87^{ns}	7.15^{**}	5.69^{*}	531.59^{**}	215.02^{**}	0.08^{ns}	1.19^{ns}	9.10^{ns}	2173.1^{**}
GCAL x Loc	23	2.50^{*}	4.54^{ns}	2.90^{ns}	237.49^{**}	153.40^{**}	0.04^{ns}	1.05^{ns}	16.32^{*}	809.7^{ns}
GCAT x Loc	1	18.41^{**}	5.01^{ns}	24.08^{ns}	706.10^{*}	34.34^{ns}	0.22^{*}	0.04^{ns}	14.84^{ns}	6^{ns}
SCA_{LXT} x Loc	23	2.33^{*}	2.58^{ns}	4.29^{ns}	105.44^{ns}	79.30^{ns}	0.05^{ns}	0.47^{ns}	22.42^{**}	1135.5^{ns}
Error	142	0.93	3.8	4.32	114.77	72.52	0.05	1.22	8.08	712.8
% contr. GCA		73	87	89	86	88	77	74	76	86
% contr. SCA		27	13	11	14	12	23	26	24	14

*, **, = Significant at 0.05 and 0.01; # = number; GYF= grain yield; DA= days to anthesis; DS= days to silking; EH= ear height; PH= plant height (cm); EPP= ears per plant; NKPR= number of kernels per row; NRPE= number of rows per ear; TKW= thousand kernel weight.

Results of this study are in accordance with the findings of Melkamu (2013), Shushay *et al*., 2013, Tessema*et al*. (2014) and Girma *et al*. (2015) who reported significant mean squares due to GCA and SCA for days to anthesis and silking. GCA sums of squares were larger than SCA sums of squares for anthesis and silking dates across locations (Table 4). The predominance of GCA sums of squares to SCA sums of squares for these traits indicates the relative importance of additive gene action to non-additive gene action for the inheritance of these traits. In line with this study, Amare *et al*. (2016) reported the preponderance of additive gene action in the inheritance of days to anthesis and days to silking. While in contrast to these findings, Kanagarasu *et al*., 2010 previously reported dominant role of SCA gene action in the days to anthesis and days to silking.

Mean squares due to crosses for plant and ear height were highly significant (P<0.01). Combining ability analysis revealed that highly significant GCA effects of lines and testers for plant and ear height across environments. SCA mean squares were highly significant for plant height and significant for ear height (Table 4). In line with these findings, Demissew *et al*. (2011) found significant GCA and SCA mean squares for plant and ear height. In contrast to these findings, Gudeta (2007) reported significant GCA and non-significant SCA mean squares for plant height. GCA sums of squares were larger than SCA sums of squares for plant height and ear height under both locations and across locations (Table 4). Similar to the present findings, Amare *et al*. (2016) reported the preponderance of additive gene action in the inheritance of plant height. While in contrast, Kanagarasu *et al*. (2010) previously reported dominant role of SCA gene action in the plant and ear height.

Lines GCA x E effects were significant for grain yield, plant and ear height, number of rows per ear and tester GCA x E effects were significant for grain yield, plant height and number of ear per plant indicated that inbred lines performed differently as reflected in their respective test crosses from one environment to another. SCA x E effects were significant for grain yield and number of kernels per row (Table 4). These results are in agreement with those by Chandel and Mankotia (2014) who reported significant interaction of (L x E), (T x E) for grain yield, ear diameter and (L x T x E) for number of rows per ear and grain yield. Assefa *et al*. (2017) reported GCA × Loc (both for lines and testers) for days to maturity, 1000-seed weight and grain yield while significant SCA × Loc interaction for all traits except number of kernel rows per ear), ear length and ear diameter. Tolera *et al*. (2017) reported highly significant differences among interactions GCAL, GCAT and SCA with the environment for all traits studied except for ear aspect and grain yield in line GCA, ear aspect in testers GCA and for days to anthesis in line x tester (SCA) x environment.

Estimates general combining ability effects

Table 5 shows the estimates of GCA effects for grain yield and agronomic traits of the inbred lines combined across environments. Twelve inbred lines showed positive GCA effects for grain yield. Three inbred lines (L2, L19 and L20) showed positive and significant GCA effects indicating the potential advantage of the inbred lines for the development of high-yielding hybrids. L20 (1.75 t/ha) followed by L9 (1.32t/ha) had higher GCA effects. Two inbred lines (L4 and L16) were poor general combiners for grain yield as they showed negative and significant GCA effects for grain yield. Among the testers (males), none of them showed significant GCA effects for grain yield per hectare. Results of the current study are in accordance with the findings of Shushay *et al*. (2013), Tessema *et al*. (2014), Amare *et al*. (2016), Demissew *et al*. (2016) and Teshale *et*

Table 1: General combining ability effects (GCA) of 24 inbred lines and two testers for grain yield and yield related traits evaluated across environments at Ambo and Kulumsa, 2017

Line	GYF tha^{-1}	AD days	SD days	PH cm	EH Cm	EPP #	NRPE #	NKRE #	TKW g
L1	0.8	-1.4	-1.5	1.5	7.0	0.25^{*}	0.41	-2.4	2.1
L2	1.2^{*}	-1.3	-1.0	2.8	5.1	0.19	0.87^{*}	0.2	-44.4^{**}
L3	-0.2	-4.5^{**}	-4.2^{**}	-13.7^{**}	-9.1^{*}	0.26^{*}	-0.89^{*}	-1.8	-50.6^{**}
L4	-1.2^{*}	0.5	0.2	-10.4	-7.1	0.24^{*}	-0.43	0.7	-73.1^{**}
L5	0.2	2.3^{*}	2.6^{**}	-7.8	-5.0	-0.13	0.19	0.3	16.3
L6	0.1	-0.2	-0.1	11.2^{*}	7.6	-0.07	0.36	-0.5	-16.5
L7	-0.4	-3.2^{**}	-2.5^{**}	8.5	-1.2	-0.21	-0.39	0.8	27.9^{*}
L8	0.1	-3.5^{**}	-3.3^{**}	-17.4^{**}	-14.1^{**}	0.00	0.26	1.3	13.2
L9	1.3^{*}	3.0^{**}	3.4^{**}	3.9	-0.3	0.13	-0.58	-2.5	-11.2
L10	0.3	2.0^{*}	1.8	-1.8	7.6	0.05	-0.04	-2.8	22.7
L11	0.4	-0.3	-0.6	26.9^{**}	11.9^{**}	-0.05	0.01	-2.9	-0.9
L12	-0.7	-2.6^{**}	-2.8^{**}	7.4	1.6	-0.22^{*}	1.11^{*}	-0.6	49.8^{**}
L13	-0.1	0.9	0.4	-6.6	-0.8	0.03	-0.19	1.0	-20.0
L14	0.3	0.9	0.9	-9.3	-8.4^{*}	-0.01	-0.09	1.0	19.7
L15	-1.0	-0.9	0.4	-18.6^{**}	-10.6^{*}	-0.28^{*}	-0.83	3.6^{*}	5.3
L16	-1.2^{*}	-1.9^{*}	-1.2	-27.2^{**}	-18.9^{**}	-0.01	0.46	1.4	1.3
L17	-0.4	2.0^{*}	2.27^{*}	0.2	5.1	-0.19	0.81	-0.1	-3.4
L18	0.7	2.3^{*}	2.27^{*}	2.0	12.5^{**}	0.12	0.22	2.8	-20.7
L19	-0.8	1.7	1.9	15.1^{**}	6.6	-0.38^{**}	-0.68	0.3	85.9^{**}
L20	1.7^{**}	2.8^{**}	2.8^{**}	28.6^{**}	21.1^{**}	-0.08	0.66	2.3	14.1
L21	-0.8	2.3^{*}	0.4	2.3	6.5	-0.11	-0.48	-2.1	9.3
L22	-0.3	1.5	1.2	4.3	0.2	0.20	-0.18	-2.2	-29.1^{*}
L23	-0.4	-3.1^{**}	-2.3^{**}	3.2	-7.8^{*}	0.21	-0.18	2.1	2.0
L24	0.1	0.7	-0.7	-4.8	-9.4^{*}	0.08	-0.36	0.1	0.2
S.E. (gi)	0.6	0.9	0.9	5.3	4.2	0.11	0.43	1.5	13.3
SE(gi-gj)	0.8	1.3	1.3	7.4	5.6	0.15	0.60	2.1	18.8
Testers									
T1	0.2	0.8^{**}	1.0^{**}	14.5^{**}	10.4^{**}	0.00	0.36^{**}	0.4	-24.9^{**}
T2	-0.2	-0.8^{**}	-1.0^{**}	-14.5^{**}	-10.4^{**}	0.00	-0.36^{**}	-0.4	24.9^{**}
S.E. (gi)	0.2	0.3	0.3	1.5	1.1	0.03	0.12	0.4	3.8
SE(gi-gj)	0.2	0.4	0.4	2.1	1.6	0.04	0.17	0.6	5.4

* $P< 0.05$; ** $P< 0.01$; #= numbers; GYF=grain yield; DA= days to anthesis; DS= days to silking; PH=plant height; EH= ear height; EPP= ear per plant; NRPE=number of rows per ear; NKPR= number of kernels per row; TKW= thousand kernel weight.

al. (2017) who reported significant positive and negative GCA effects for grain yield in maize germplasm. Lines with positive GCA effects for grain yield can be extensively used in hybridization program as they contribute favorable alleles in the development of high yielding varieties.

Line GCA effects for days to anthesis ranged between -4.53 days (L2) to 2.97 days (L5). Eleven inbred lines showed negative GCA effects among which six inbred lines had significant GCA effects for days to anthesis, indicating that these lines were good general combiners for early maturity while seven inbred lines exhibited significant and positive GCA effects for days to anthesis, indicating that these lines were undesirable as they show the tendency to increase late maturity. The GCA estimates of parental lines of days to silking ranged from -4.23(L18) to 3.4(L15) for days to silking, the female parents L3, L7, L8, L12, and L23 were the best general combiners for days to silking with negative and significant difference GCA effect. These inbred lines contributed earliness in maturity. Testers showed significant GCA effects for both days to silking and anthesis. Similarly, Girma *et al*. (2015) and Tolera *et al*. (2017) reported significant positive and negative GCA effects for silking date in their combining ability study.

Overall, inbred lines showed similar trends of significant GCA effects for both plant and ear height traits in the combined analysis. For plant height the GCA estimate of parental lines ranged from -27.2(L2) to 28.57(L10) cm. L6, L11, L19 and L20 showed positive and significant GCA effects indicating that these lines significantly contributed to taller plant stature. On the other hand, L3, L8, L15 and L16 showed negative and significant GCA effects, indicating that these lines contributed to reduced plant height. In line with the present study, Girma *et al*. (2015) and Tolera *et al*. (2017) found significant positive and negative GCA effects for ear height.

Inbred lines with positive and significant GCA effects for ears per plant were L1, L3 and L4; hence, it was the best general combiner for prolificacy. On the other hand, inbred lines (L12, L15 and L19) showed significantly negative GCA effects for the same trait. Similar to the present findings, Tessema *et al*. (2014) and Demissew *et al*. (2016) reported significant positive and negative GCA effects for number of ears per plant. Line GCA effects for number of rows per ear ranged between -0.89 (L8) and 1.11 (L9). Even though 11 inbred lines showed positive GCA effects, only two inbred lines (L2, L12) had significant GCA effects hence they were good general combiners for high number of rows per year. Only one inbred lines (L3) exhibited significant and negative GCA effects for number of rows per ear. These results were in agreement with the investigations of Kanagarasu *et al*. (2010) and Abakemal *et al*. (2016).

Table 6: Estimates of specific combining ability (SCA) of line x tester crosses for yield related traits evaluated across environments at Ambo and Kulumsa, 2017.

lines	AD Days		SD days		PH Cm		EH cm		TKW G	
	T1	T2	T1	T2	T1	T2	T1	T2	T1	T2
L1	0.7	-0.7	0.3	-0.3	3.9	-3.9	3.8	-3.8	12.8	-12.8
L2	-0.7	0.7	-0.9	0.9	4.3	-4.3	1.2	-1.2	-2.3	2.3
L3	-0.5	0.5	-0.4	0.4	6.3	-6.3	1.0	-1.0	13.8	-13.8
L4	-0.7	0.7	-0.3	0.3	9.7	-9.7	7.3	-7.3	-9.9	9.9
L5	1.2	-1.2	0.5	-0.5	-5.9	5.9	-1.8	1.8	10.4	-10.4
L6	0.2	-0.2	0.5	-0.5	7.9	-7.9	4.9	-4.9	10.5	-10.5
L7	-0.1	0.1	0.8	-0.8	-9.0	9.0	-2.5	2.5	-1.5	1.5
L8	-0.7	0.7	-0.8	0.8	-1.2	1.2	-1.9	1.9	14.7	-14.7
L9	0.5	-0.5	0.7	-0.7	-8.5	8.5	-7.8	7.8	-1.1	1.1
L10	1.8	-1.8	1.3	-1.3	10.4	-10.4	4.5	-4.5	-15.9	15.9
L11	0.5	-0.5	0.5	-0.5	-4.6	4.6	-1.8	1.8	2.7	-2.7
L12	0.2	-0.2	-0.3	0.3	6.3	-6.3	3.8	-3.8	17.8	-17.8
L13	1.9	-1.9	1.5	-1.5	0.5	-0.5	1.0	-1.0	13.1	-13.1
L14	-0.3	0.3	-0.3	0.3	10.7	-10.7	1.4	-1.4	-38.3*	38.3*
L15	0.2	-0.2	1.0	-1.0	2.1	-2.1	-0.7	0.7	-0.1	0.1
L16	-0.3	0.3	0.1	-0.1	8.9	-8.9	-0.2	0.2	-5.6	5.6
L17	-1.0	1.0	-0.4	0.4	0.3	-0.3	-0.4	0.4	-9.1	9.1
L18	-0.6	0.6	-0.2	0.2	2.8	-2.8	2.0	-2.0	-25.3	25.3
L19	-0.7	0.7	-0.5	0.5	3.5	-3.5	1.6	-1.6	0.7	-0.7
L20	1.7	-1.7	1.3	-1.3	-0.2	0.2	7.5	-7.5	-22.5	22.5
L21	-1.8	1.8	-0.3	0.3	-4.0	4.0	2.7	-2.7	2.8	-2.8
L22	-1.0	1.0	-1.3	1.3	-14.5*	14.5*	-11.8*	11.8*	0.8	-0.8
L23	-0.6	0.6	-1.3	1.3	-9.6	9.6	0.3	-0.3	-10.5	10.5
L24	0.3	-0.3	-1.4	1.4	-20.1**	20.1**	-14.1*	14.1*	41.9*	-41.9*
SE	1.29		1.29		7.41		5.56		18.8	
SE (d)	1.82		1.83		10.49		7.86		26.59	

* P<0.05; ** P<0.01*; DA= days to anthesis; DS= days to silking; PH=plant height; EH=ear height; TKW= thousand kernel weight.

Table 7: Mid, better and standard heterosis of 48 line x tester crosses for yield evaluated at Ambo and Kulumsa, 2017.

Lines	MPH		BPH		SH	
	T1	T2	T1	T2	T1	T2
1	231.0**	195.3**	222.2**	186.6**	3.56	-8.12
2	282.4**	219.9**	227.5**	173.3**	5.15	-2.57
3	280.8**	196.3**	209.4**	140.1**	-1.68	-23.37
4	281.9**	239.1**	159.9**	130.4**	-16.34	-28.22
5	170.2**	180.0**	156.7**	166.8**	-13.17	-3.37
6	250.5**	227.2**	188.8**	168.9**	-8.32	-9.90
7	175.7**	177.3**	160.0**	160.7**	-8.22	-10.20
8	223.2**	244.0**	170.7**	187.4**	-12.77	-7.13
9	384.2**	371.3**	231.8**	222.3**	1.88	3.27
10	250.0**	287.2**	178.9**	207.8**	-9.90	-5.54
11	274.5**	325.7**	169.0**	205.2**	-10.69	-1.58
12	207.4**	208.3**	150.2**	150.4**	-19.01	-14.95
13	276.9**	180.5**	220.8**	138.2**	-2.97	-18.91
14	198.6**	204.5**	186.6**	191.3**	-10.00	-4.26
15	198.8**	169.0**	148.6**	123.2**	-15.74	-24.85
16	257.5**	176.7**	162.7**	102.9**	-12.28	-31.49*
17	234.0**	193.4**	178.4**	144.0**	-14.06	-15.64
18	289.9**	297.3**	206.7**	211.9**	1.39	-9.41
19	168.2**	156.0**	167.1**	155.8**	-14.06	-21.88
20	347.3**	269.2**	278.0**	211.2**	16.34	-2.57
21	250.8**	278.9**	172.5**	193.8**	-23.56	-12.28
22	297.2**	261.4**	212.0**	183.3**	-10.00	-16.04
23	253.7**	266.1**	164.7**	173.5**	-15.25	-14.46
24	267.6**	249.6**	203.3**	187.7**	-7.72	-11.98
$CD_{0.05}$		1.95		2.25		2.26
$CD_{0.01}$		2.58		2.98		3.01

*, **, = Significant at 0.05 and 0.01; MPH= mid parent heterosis, BPH = best parent heterosis, SH= standard heterosis, CD = Critical difference.

One inbred lines showed positive and significant GCA effects for number of kernels per row suggesting that these lines were good combiner for increasing number of kernels per row. None of the inbred lines showed negative and significant GCA effects for number of kernels per row. These results were in disagreement with the findings of Gudeta (2007), Girma *et al.* (2015) and Amare *et al.* (2016) who reported significant and positive GCA effects for some lines, and significant and negative GCA effects for others in number of kernels per ear. General combining ability effects for thousand-kernel weight ranged between -85.97 (L24) to 85.97 (L10). The maximum significant positive GCA effects for TKW were observed in L19 followed by L12 and L8. On the contrary, the minimum and significant negative GCA effects for TKW were shown by L2, L3 and L4. The present results are in agreement with the findings of several researchers who reported significant positive and negative GCA effects for thousand-kernel weight (Tessema *et al*., 2014; Amare *et al*., 2016; Demissew *et al*., 2016).

Estimates of specific combining ability effects

The specific combining ability effects were computed for traits that showed significant SCA mean squares in combining ability analysis. In combined analysis across environments, two crosses (L24 xT1 and L22x10) showed negative and highly significant SCA effects for the plant and ear height (Table 6). In line with the present results at these locations, Demissew *et al*. (2016) reported significantly negative SCA effects for plant height. Cross L24xT1 were the best combinations for thousand-kernel weight (Table 6). In line with the present findings, Shushay *et al*. (2013), Demissew *et al*. (2016) and Assefa *et al*. (2017) reported positive and significant SCA effects for this trait.

Heterosis for yield

Percent mid-parent (MPH), better parent (BPH) and standard heterosis (STH) were computed for yield (Table 7). All crosses showed significant and positive heterotic effects over mid and better parents for grain yield. Five crosses showed positive standard heterosis in desired direction (Table 7). Mid parent, heterosis for grain yield ranged from 156 to 384.2%, for best parent heterosis from 102.9 to 278% and for standard heterosis over the best check, Kolba ranged from -31.49 to 16.34% (Table 7). Habtamu (2015) in his study on heterosis and combining ability for grain yield and yield component traits of maize in Eastern Ethiopia reported similar result. Kumar and Babu (2016), in their study on Combining ability and heterosis in maize for grain yield and yield components reported significant values for mid parent, best parent and standard heterosis in desired direction for grain yield. Positive and negative significant level of standard heterosis for grain yield reported by different investigators Shushay (2014); Ziggiju (2016), Talukder *et al*. (2016). The ranges of heterotic responses observed in this study were on average higher than that reported by Gudeta (2007) and others.

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