

Original Research Article

Estimation of general and specific combining ability effects for quality protein maize inbred lines

Abstract

Back ground: Maize (*Zea mays L.*) plays a critical role in meeting high food demand. It is globally one of the most widely adapted and cultivated crops. Hybrid development from fixed inbred lines is one of the strategies for the improvement of maize production. The national average maize yield in Ethiopia is low and thus, selection of promising germplasm and knowledge of combining ability are prerequisites to developing high yielding maize varieties. Forty-two Quality Protein Maize (QPM) crosses (21 inbred lines each crossed with two testers) along with three popular standard hybrids were evaluated in two replications using alpha lattice during the 2017 cropping season at Ambo, Arsi-Negele, and Kulumsa. The objectives of this study were to identify lines with high GCA and estimate the SCA of crosses for grain yield, and other agronomic and morphological characters.

Result: Significant difference among crosses was observed for 19 traits at Ambo, 14 traits at Arsi-Negele, and 19 traits at Kulumsa in the hybrid trial. Regarding the GCA effect, L8 had a significant difference to the positive side with the highest magnitude of GCA effect at three locations (3.40, 2.03, and 1.88 GCA effect values at Arsi-Negele, Ambo, and Kulumsa, respectively) which is followed by L7 for GY. All crosses did not show a significant SCA effect for GY in both directions at Ambo and Arsi-Negele but at Kulumsa, five crosses: L2xT1(1.89), L13xT2(1.88), L7xT1(1.86), L4xT2(1.49) and L19xT1(1.41) showed significant difference. In the combined analysis for six traits, Additive gene action was more important which was manifested by a higher sum square contribution of DS (79.6) EPP (79.3%), EL (80.0%), KPR (80.1%), ED (78.5%) and TSW (79.1%).

Conclusion: Based on mean grain yield, and combining ability, L8xT2, L7xT1, L8xT1, L19xT1, L6xT2, and L18xT1 are promising crosses that could be forwarded for further use in maize breeding programs for further works.

Keywords: Combiningability, GCA, SCA

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1. Introduction

Maize is a very productive, adaptable, versatile, and most important food security crop in ~~Sub~~ ~~sub~~ Saharan Africa (SSA); Eastern and Southern Africa use 85% of maize produced as food while Africa as a whole use 95% as food (Bekele et al., 2011). In 2021, worldwide production of maize was around 1,205.35 MT with a world average of 5.95t/ha. The world maize production area also covered around 202.72 million hectares (USDA, 2022). Of the world countries, the USA took the leading for production area coverage, the national average, and total production of maize. In Africa, in terms of maize production area coverage, Nigeria (6 million hectares) took the leading and followed by Tanzania (4.10 mh) and South Africa (3mh). Ethiopia (2.40 mh) is the fourth maize producer in Africa in terms of area coverage. The national average production per hectare, Egypt took the leading 8 t/ha and followed by South Africa (5.67t/ ha and Ethiopia (3.75 t/ha). Whereas concerning the total production, the highest to lowest, producers are South Africa, Nigeria, and Ethiopia with the value of 17.0, 11.6, and 9.0 MT, respectively (USDA, 2022).

Food security is a major challenge facing the countries in ~~sub Saharan Africa (SSA)~~ (Badu-Apraku et al., 2013). ~~Despite its the importance of,~~ maize, ~~its~~ yield in Africa is lower than 4.30 t/ha in major maize-producing ~~African~~ countries compared to the world average of 5.95 t/ha (USDA, 2022). In Ethiopia, too, the national average maize yield is low compared to the world average grain yield. This is due to several biotic and abiotic stresses that limit maize productivity across countries in ~~sub-Saharan Africa SSA~~ (Badu-Apraku et al., 2011). Among abiotic stresses, drought and low soil fertility are the most important stresses that affect maize production (Mosisa et al., 2007; Lobell et al., 2011; Weber et al., 2012).

Maize is one of the five strategic crops for food security in Ethiopia. In 2018, maize was grown on 21% of the total cereals area and it ranked 2nd following teff (30%) in terms of total production contributing 31% of the total cereals grain produced in the country (CSA, 2018). Of all the smallholder cereals framers in the country, 70% grow maize in variable scales (CSA, 2018).

The maize crop is an important source of protein, although its protein is low in essential amino acids such as Lysine (Lys) and Tryptophan (Trp) (Mbuya et al., 2011 Gudeta et al., 2015). It is also a source of minerals, vitamin B, iron, and carbohydrate (Rouf Shah et al., 2016). Maize grain protein has long been known to have low nutritional value and research on improving the nutritional value of maize grain protein was started ~~before one century~~ (Osborne and Mendel, 1914). While millions of people worldwide are overly dependent on maize as a staple food, ~~this the~~ nutritional deficiency caused ~~for know~~ askwashiorkor is a concern in the area where maize is a staple food, particularly for people with high protein requirements (Bain et al., 2013; Morley, 2016).

In Sub-Saharan Africa, where maize is the major source of calories ~~and the existence of malnutrition~~, emphasis has been given to the introduction and development of QPM varieties as a means to solve malnutrition ~~caused due to heavy dependence on maize as a source of protein~~. In Africa or elsewhere the most followed QPM breeding strategy relies on the conversion of existing adapted genotypes to QPM (Krivanek et al., 2007). Adapted

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CM genotypes that resist major biotic and abiotic stresses are converted to QPM mostly following backcrossing or modified backcross breeding methods (Adefris et al., 2015).

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Sprague and Tatum (1942) introduced the concepts of GCA and SCA to distinguish between the average performances of parents in cross combinations and the deviation of individual crosses from the average performance of the parents involved, respectively (Hallauer and Miranda, 1988). The LxT line by tester (L x T) mating design is used as one of the methods used to analyze crosses and, or parents and crosses for GCA and SCA (Kempthorne, 1957). These estimates provides an assessment of their relative merits to guide which will be useful in selection and testing schemes.

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Information on the combining ability (CA) of maize germplasm has great value to maize breeders. GCA and SCA effects are important indicators of the potential value of inbred lines in hybrid combinations (Sprague and Tatum, 1942). GCA of inbred lines is the ultimate factor determining the future use of the lines for hybrid development (Hallauer and Miranda, 1988). Using the concept of CA, genetic variance is partitioned into two components: variance due to GCA and variance due to SCA (Sughroue and Hallauer, 1997). GCA is recognized primarily as a measure of additive gene action and SCA as an estimate of non-additive gene action such as dominance and epistasis (Kambal and Webster, 1965).

According to Hallauer and Miranda (1988), characterization of genetic variance and type of gene action operative in crosses of inbreds are interpreted relative to GCA and SCA of inbred lines. The proportion of additive and non-additive components of genetic variance depends on the genetic structure of the crosses analyzed and the environmental conditions in which they were grown (Khotyleva and Trutina, 1973). Kebede (1989) reported that additive gene effects were more important in determining traits in the population crosses while non-additive gene actions were important in inbred line crosses. Younes and Andrew (1978) reported that additive gene action is more important than non-additive components for most traits in previously unselected material. GCA is predominant for parents that have been developed through selection for GCA and for parents that have not been separated into heterotically complementary groups during their development (Pixley and Bjarnason, 1993). Birhanu (2009) in the LxT and Beyene (2016) in the diallel analysis reported that both additive and non-additive effects played role in controlling grain yield and other secondary traits including the phenological traits.

On the other hand, Kambal and Webster (1965) reported the importance of non-additive gene action for some traits including grain yield in materials that were previously selected for GCA. Dagne (2008) reported a higher contribution of an additive effect than a non-additive. Betranet *al.* (2003) found negative SCA for hybrids involving inbred lines with the same germplasm origin or related by pedigree and greater SCA for hybrids involving inbred lines of different source germplasm origin. Birhanu (2009) and Abiy (2017) reported that although both additive and non-additive genetic effects influence grain yield in inbred line crosses, the higher genetic variance is attributed to the additive genetic component. The average of nearly 100 estimates indicates that, assuming no epistasis and no linkage, additive genetic effects on average account for 61.2%, and dominance count for 38.8% of total genetic effects (Hallauer and Miranda, 1988). Theoretically, the choice of the most effective breeding scheme and the

rate of genetic improvement is dependent upon the relative magnitude of various gene effects (Dhillon and Pollmer, 1978).

Vasalet *al.* (1993b) observed significant GCA variance for grain yield, time to silk, ear height, plant height, and endosperm hardness for most traits and implied additive gene actions to be more important in controlling grain yield and MOD. Cordova *et al.* (2003) and Fan *et al.* (2004) reported the importance of GCA effects on grain yield in QPM inbred lines from two heterotic groups.

Several investigators reported the greater importance of additive genetic variance relative to dominance genetic variance for percent protein in grain, percent Trp or Lys in grain, and percent Trp or Lys in protein for different *o2* germplasm (Pixley and Bjarnason, 1993; De-quan and Shi-huang, 1995). The absence of SCA effects on protein quality traits is undesirable because heterosis cannot be exploited to ensure gains in these traits (Pixley and Bjarnason, 1993). However, Dagne (2008) and Ngaboyisonga *et al.* (2008) reported the significance of both additive and non-additive gene action in controlling protein content.

The inheritance of *o2* modifier genes for endosperm texture is complex (Wessel-Beaver and Lambert, 1982). Several researchers reported that additive genetic effects are more important than non-additive effects for endosperm hardness in the *o2* background of QPM (De-quan and Shi-huang, 1995). Non-additive genetic components also contribute to the expression of kernel virtuousness (Wessel Beaver and Lambert, 1982). According to Dagne (2008), both additive and non-additive gene actions are important for kernel modification (MOD). The genetic variance associated with protein and Lys concentrations in modified *o2* material was mostly additive (Bjarnason *et al.*, 1977). Wessel-Beaver *et al.* (1985) suggested effective selection in increasing the frequency of the favorable alleles for endosperm modification. Environmental conditions affect the gene action governing protein and Trp concentration (Ngaboyisonga *et al.* 2008). The objective of this study was to identify lines with high GCA effects for phenology, yield, yield related, and morphological traits and assess their suitability for further cultivar OPVs development, and estimate the SCA effect of the lines.

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2. Materials and methods

2.1. Description of Experimental Sites

The study was conducted at three locations in the highland agroecology of Ethiopia including; Ambo, Arsi-Negele (transition highland), and Kulumsa Agriculture Research Centers during the 2017 main cropping season.

Table 1. Latitude, longitude, altitude (masl), long-term annual rainfall (mm), maximum temperature (MaxT) (°C), minimum temperature (MinT) (°C), soil type, and soil pH of the study sites.

Site	Latitude	Longitude	Altitude	A.rainfall	MaxT	MinT	Soil type	pH
Site1	8° 57' N	38° 7' E	2225	1115	25.5	11.7	Heavy clay	7.8
Site2	7° 19' N	38° 39' E	1960	886	26.0	9.1	clay loam	6.5 -7.5
Site3	8° 02' N	39° 10' E	2200	830	23.2	10.0	luvisol	6.0

Where Site1= Ambo, Site2= Arsi-Negele, Site3= Kulumsa

2.2. Experimental Materials

Twenty-one highland QPM inbred lines, named here after as lines (L1 to L21) and two elite QPM inbred lines (CML159 and CML144), named here after as testers (T1 and T2, respectively), and constituted the basic genetic materials of this experiment (Table 1). From the 21 inbred lines and the two testers, 42 F₁ hybrids were generated in Ambo Highland Maize Breeding Program (AHMBP). The experiment was conducted during the main cropping season (May to December) of 2017 GC. The 42 F₁ hybrids along with three standard checks: one QPM (AMH852Q) and two CM (Jibat and AMH853), designated as hybrid checks, were ~~tested~~ used in this study.

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Table 2. List of parental inbred lines used to generate the single-cross hybrids using line x tester mating design.

Code	Pedigree	Remark
L1	[CML144/[CML144/CML395] F2-8sx]-1-2-3-2-B*5-1-B-B-B-#	QPM
L2	[CML144/[CML144/CML395] F2-8sx]-1-2-3-2-B*5-2-6-B-B-#	QPM
L3	(CLQRCWQ50/CML312SR)-2-2-1-BB-1-B-B-B-#	QPM
L4	[CML144/[CML144/CML395] F2-8sx]-1-2-3-2-B*5-1-B-B-B-#	QPM
L5	([NAW5867/P49SR(S2#)/NAW5867] F#-48-2-2-B*/CML511) F2)-B-B-39-1-B-#	QPM
L6	(CML197/(CML197/[(CLQRCWQ50/CML312SR)-2-2-1-BB/CML197]-BB) F2)-B-B-9-1-B-#	QPM
L7	(CML197/(CML197/[(CLQRCWQ50/CML312SR)-2-2-1-BB/CML197]-BB) F2)-B-B-35-2-B-#	QPM
L8	(CML197/(CML197/[(CLQRCWQ50/CML312SR)-2-2-1-BB/CML197]-BB) F2)-B-B-44-2-B-#	QPM
L9	(CML197/(CML197/(CLQRCWQ50/CML312SR)-2-2-1-BBB) F2)-B-B-18-2-B-#	QPM
L10	(CML197/(CML197/(CLQRCWQ50/CML312SR)-2-2-1-BBB) F2)-B-B-30-1-B-#	QPM
L11	(CML197/(CML197/(CLQRCWQ50/CML312SR)-2-2-1-BBB) F2)-B-B-35-2-B-#	QPM
L12	(CML395/(CML395/[NAW5867/P49SR(S2#)/NAW5867] F#-48-2-2-B*4) F2)-B-B-30-1-B-#	QPM
L13	[CML144/[CML144/CML395] F2-8sx]-1-2-3-2-B*5-2-6-B-B-#	QPM
L14	(CML395/(CML395/[CML144/[CML144/CML395] F2-8sx]-1-2-3-2-B*5) F2)-B-B-46-1-B-#	QPM
L15	(CML395/(CML395/[CML144/[CML144/CML395] F2-8sx]-1-2-3-2-B*5) F2)-B-B-50-1-B-#	QPM
L16	(CML395/(CML395/S99TLWQ-B-8-1-B*4-1-B) F2)-B-B-10-3-B-#	QPM
L17	(CML395/(CML395/S99TLWQ-B-8-1-B*4-1-B) F2)-B-B-14-1-B-#	QPM
L18	(CML395/(CML395/S99TLWQ-B-8-1-B*4-1-B) F2)-B-B-29-1-B-#	QPM
L19	(CML395/(CML395/CML511) F2)-B-B-7-2-B-#	QPM
L20	(CML395/(CML395/CML511) F2)-B-B-11-2-B-#	QPM
L21	(CML395/(CML395/CML511) F2)-B-B-37-1-B-#	QPM
T1	CML144	QPM
T2	CML159	QPM

2.3 Experimental Design and Crop management

The hybrid trial was laid out using an alpha lattice design consisting of one-row plots replicated twice. For the hybrid trial, each plot consisted of a 5.25 m long row with 0.75 and 0.25 cm inter- and intra-row spacing. The plot was hand-planted with two seeds per hill and later was thinned to one plant per hill to attain the final plant density of 53,333 plants per hectare. Diammonium phosphate (DAP) fertilizer was applied all at planting at the rate of

150 kg ha⁻¹ while 200 kg ha⁻¹ of urea was applied in partition 1/3 at planting, 1/3 at knee height, and 1/3 at flowering at Ambo and Kulumsa. At Arsi-Negele, 100 kg ha⁻¹ DAP and 150 kg ha⁻¹ urea fertilizer were applied based on the site recommendation following the same time of application mentioned above.

2.4 Data collected

Data were recorded for ~~days~~ Days to tasseling (DT), ~~Days-days~~ Days to silking (DS) ~~Anthesis-anthesis~~ silking interval (ASI) ~~Days-days~~ to maturity (MD), ~~Plant-plant~~ aspect (PAS) ~~Disease-disease~~ score: gray leaf spot (GLS), turicum leaf blight (TLB) and common leaf rust (CLR), ~~Ear-ear~~ aspect (EAS), ~~Number-number~~ of ears per plant (EPP), ~~Kernel-kernel~~ Modification (MOD), ~~Grain yield (GY)~~, ~~Number-number~~ of leaves per plant (LFPP), ~~Number-number~~ of leaves above upper most ear per plant (LFAE), ~~Number-number~~ of leaves bellow upper most ear per plant (LFBE), ~~Leaf-leaf~~ angle (LANG), ~~Leaf-leaf~~ length (LL), ~~Leaf-leaf~~ width (LW), ~~Leaf-leaf~~ area (LFAR), ~~Plant-plant~~ height (PH), ear height (EH), ear length (EL), ~~Ear-ear~~ diameter (ED), ~~Number-number~~ of kernel rows (NKR), ~~Number-number~~ of kernels per row (KPR), ~~Thousand-thousand~~ seed weight (TSW), ~~Biomass-biomass~~ (BIOM) and ~~Harvest~~ harvest index (HI). Grain yield (GY) was calculated and expressed in (t ha⁻¹):

$$\text{Grain yield (t ha}^{-1}\text{)} = \frac{\text{fresh cob weight} \times (100 - \text{MC}) \times 0.8 \times 10}{87.5 \times 3.94} \dots\dots\dots \text{(Equation 1)}$$

Where, fresh ear weight = fresh weight of the cob from the plot in kg, 0.8 = shelling percentage, 87.5 = standard value of grain at the moisture content of 12.5% from the total grain mass, MC = grain moisture content (%) at harvest, 3.94 = plot area harvested in meter square (m²).

2.5 Analysis of variance

The data obtained from field measurements were organized and analyzed using the SAS statistical package (SAS, 2002). CA analysis was carried out for individual locations and across locations.

Before data analysis, the anthesis-silking interval (ASI) was normalized using ln (ASI +10) as suggested by Bolaños and Edmeades (1996). Individual and across locations data were

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subjected to analysis of variance using PROC GLM procedure in SAS software version 9.0 (SAS, 2002). In the analysis, treatments were used as fixed factors while replications and locations were considered as random factors. This was specified using the RANDOM statement in the PROC GLM model. Combined analysis was done for traits that showed significant differences at each location analysis after testing homogeneity of error variances. Whenever traits were found to be significant at three locations combined based on the ratio of error (Gomez and Gomez, 1984). In the combined analysis, the variation among genotypes crosses, and checks effects were tested against their respective interaction effect with the location. The interaction effect of each source of variation by location was tested as per the expected mean square (MS) of the error estimate.

2.6 Combining ability analysis

LxT analysis was done for traits that showed statistically significant differences for L, T, and LxT in each environment and across environments using the adjusted means based on the method described by Kempthorne (1957). GCA and SCA effects for grain yield and other traits were calculated using the LxT model.

The F-test of MS due to lines and testers were tested against LxT interaction but crosses were compared against MS due to error for individual location (Singh and Chaudhry, 1985). In the case of across locations analysis, the F-test for the main effects such as crosses, lines, testers, and LxT interaction MS was tested against their respective interaction with the location. The MS attributable to all the interactions with the locations was tested against pooled error MS. The effect of location was tested by replication within the environment as an error term. Significances of GCA and SCA effects of the lines and crosses were determined by t-test using standard errors of GCA and SCA effects. The main effects due to LxT were considered as GCA effects while LxT interaction effects were represented as the SCA. The GCA and SCA effect was considered for traits that had significant differences among crosses as prior criteria before proceeding to the cross-components MS (line GCA, tester GCA, and LxT SCA). The estimate of the GCA effect considered for traits showed significant MS by both lines GCA and tester GCA or only by line GCA. Similarly, the SCA effect presented traits that had significant SCA MS. In a combined analysis for GCA and

SCA effect, only traits that had significant MS and non-significant MS while they tested against their respective interaction with the location were included otherwise for traits that had significant MS for their interaction with location considered for each location.

2.6.1 Estimation of combining ability effects

Genotypic means of crosses of individual locations were used for the determination of GCA and SCA. The standard checks were excluded while analyzing combining abilities. The significance of the LxT interaction (SCA) was determined using the error MS as an error term. The linear model proposed by Kempthorne (1957) was applied for single location observation recorded on $i \times j^{th}$ in k^{th} replication.

$$Y_{ijk} = \mu + g_i + g_j + s_{ij} + r_k + e_{ijk} \dots \dots \dots \text{(Equation 2)}$$

Where, Y_{ijk} = performance of a cross between i^{th} line and j^{th} tester at k^{th} replication, μ = over all mean, g_i = gca effect of i^{th} line, g_j = gca effect of j^{th} tester, s_{ij} = sca effect of i^{th} line x j^{th} tester, r_k = replication effect and e_{ijk} = random error term for ijk^{th} observation/environmental effect.

The GCA effect of lines and tester, the SCA effect of LxT, and their interactions with the environment were determined following the LxT analysis of Kempthorne (1957) for combined analysis.

$$Y_{ijkl} = \mu + r_i + L_j + T_k + E_l + (LxT)_{jk} + (LxE)_{jl} + (TxE)_{kl} + (LxTxE)_{jkl} + e_{ijkl} \dots \dots \dots \text{(Equation 3)}$$

Where, y_{ijkl} = observed hybrid response, μ = overall trial mean, r_i = i^{th} replication, L_j = effect of the j^{th} line, T_k = effect of the k^{th} tester, E_l = effect of l^{th} environment, $(LxT)_{jk}$ = effect of the interaction of j^{th} line and k^{th} tester, $(LxE)_{jl}$ = effect of the interaction of i^{th} line and l^{th} environment, $(TxE)_{kl}$ = effect of the interaction of k^{th} tester and l^{th} environments, $(LxTxE)_{jkl}$ = effect of the interaction of j^{th} line, k^{th} testers and l^{th} environments, e_{ijkl} = random experimental error.

2.6.2 Estimation of general combining ability effects

The GCA due to lines and testers was calculated as a deviation of line mean from all hybrids mean. GCA effects of lines (g_i) and tester (g_j) for the individual environment:

Lines GCA effect (g_i) = $\frac{X_{i..}}{tr} - \frac{X_{...}}{ltr}$ (Equation 4)

Testers GCA effect (g_j) = $\frac{X_{.j.}}{lr} - \frac{X_{...}}{ltr}$ (Equation 5)

Where, g_i = GCA effect for i^{th} line, g_j = GCA effect for j^{th} tester, $X_{.j.}$ = sum of the j^{th} tester, $X_{i..}$ = Sum of the i^{th} line, $X_{...}$ = grand sum of crosses, l = number of lines, t = number of testers, r = number of replications

$\sum g_i = \sum g_j = 0$ (Equation 6)

2.6.3 Estimation of specific combining ability effects

SCA effects were calculated as a deviation of each cross mean from all hybrids mean adjusted for corresponding GCA effects of parents. The specific combining ability effects of LxT cross combinations were calculated as:

$S_{ij} = \frac{X_{ij.}}{r} - \frac{X_{i..}}{tr} - \frac{X_{.j.}}{lr} + \frac{X_{...}}{ltr}$ (Equation 7)

Where, S_{ij} = SCA effect of the ij^{th} crosses, $X_{ij.}$ = $i \times j$ cross sum, $x_{i..}$ = i^{th} line sum, $x_{.j.}$ = j^{th} tester sum, $x_{...}$ = grand sum of crosses, l = number of lines, t = number of testers r = number of replications.

2.4.4 Standard errors for combining ability effects

To test the significance of GCA and SCA effects or that of the difference between any two GCA and SCA effects, the SE and SEd were calculated as follows.

1. Standard error for general combining ability effects

a) Line: SE (GCA for line) = $\sqrt{MSe/tr}$ (Equation 8)

b) Tester: SE (GCA for tester) = $\sqrt{MSe/lr}$ (Equation 9)

2. Standard error for specific combining ability effect

SE (SCA effects) = $\sqrt{MSe/r}$ (Equation 10)

3. Standard error of the differences (SEd) between general combining ability effects

$$SEd (g_i-g_j) \text{ line} = \sqrt{2MSe/rt} \dots \dots \dots \text{(Equation 11)}$$

$$SEd (g_i-g_j) \text{ tester} = \sqrt{2MSe/rl} \dots \dots \dots \text{(Equation 12)}$$

4. Standard error of the differences (SEd) between specific combining ability effects

$$SEd (S_{ji}-S_{kl}) = \sqrt{2MSe/r} \dots \dots \dots \text{(Equation 13)}$$

Calculated t-value of GCA of line, GCA of the tester, and SCA of the cross was obtained by using formulae:

$$T\text{-calculated} = \frac{|g_i-0|}{SE(g_i)}, \frac{|g_i-0|}{SE(g_i)}, \frac{|S_{ij}-0|}{SE(S_{ij})} \text{ for L, T, and LxT, respectively} \dots \dots \dots \text{(Equation 14)}$$

The significance of GCA and SCA effects were tested by dividing the GCA effects of a particular line or tester and SCA effects of the particular cross by its respective standard error. Then, the absolute value of this ratio was used as calculated t and compared with the tabular t-value in a two-tailed t-table at the error degree of freedom.

3. Result and discussion

3.1. Combining Ability Analysis

3.2 Analysis of variance

Forty-two crosses along with three hybrid checks were evaluated for grain yield, yield related traits, diseases, and morphological parameters to estimate heterosis and combining ability using LxT mating designs (Sprague and Tatum, 1942). The details of the results presented are as follows.

3.2.1 Combining ability analysis for the individual location

The MS of crosses, GCA, and SCA at individual locations are presented in Tables 3, 4, and 5. MS of crosses was significant for most of the traits at Ambo (Table 3). At Arsi-Negele, GY, DT, DS, MD, PH, EH, TLB, EPP, EL, KPR, ED, TSW, BIOM, and HI were significant, whereas the remaining traits showed significant differences (Table 4). At Kulumsa, the traits which showed significant differences among crosses were: GY, DT, DS, PH, EH, CLR, EAS, EPP, EL, KPR, ED, TSW, BIOM, LANG, LL, LW, LFAR, LFPP, LFAE and LFBE

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(Table 5). In line with this finding, Birhanu (2009) and Abiy (2017) reported significant MS for grain yield and most of the agronomic traits. Abiy (2017) also reported non-significant MS for DT and DS. At Ambo, GCA MS due to lines was significant for EH, EPP and EL ($P < 0.001$); ASI, PH and MOD ($P < 0.01$); GY, DT, DS and LFBE ($P < 0.05$). MS of testers was significant for DT, ASI, EPP, and TSW ($P < 0.001$); DS, MD, EL, and ED ($P < 0.01$); EAS, PAS, and CLR ($P < 0.05$). DT, DS, ASI, EH, EPP, and EL were the traits that showed significant MS for both line and tester GCA ($P < 0.05$; $P < 0.01$ or $P < 0.001$) but GY, PH, MOD, KPR, and LFBE were the traits which showed significant MS for lines GCA but not for testers for tester GCA. Traits that showed significant MS only for testers were: MD, EAS, PAS, ED, and TSW. The rest of the traits: NKR, BIOM, LFPP, and LFAE showed non-significant line and tester GCA. The SCA MS (LxT) was significant for GY, DT, DS, PH, EH, EAS, PAS, ED, TSW, LFPP, and LFAE but non-significant for ASI, MD, EPP, EL, NKR, KPR, BIOM, and LFBE at Ambo (Table 3). Beyene (2016) and (Demissew 2014) reported significant GCA and SCA for most grain yield-related, other agronomic, and phenology traits. In line with this study, Dagne (2008) reported significant GCA for MOD but against the finding of this result, he reported significant SCA MS.

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Table 3. Mean square for combining ability of variance analysis for grain yield (t/ha) and other agronomic traits in LxT maize hybrids evaluated at Ambo Agricultural Research Center, 2017.

Source of Variation	MS										
	DF	GY	DT	DS	ASI	MD	PH	EH	MOD	EAS	PAS
Rep	1	7.72**	0.43	0.19	0.0003	3.86	786.29**	340.01**	1.86**	1.31**	0.76**
Cross	41	4.90***	22.97***	15.98***	0.01***	3.60*	1276.53***	606.06***	0.48*	0.40***	0.34***
L gca	20	6.59*	24.40*	20.96*	0.01**	2.641	2091.98**	994.79***	0.63**	0.25	0.32
T gca	1	9.473	260.76***	84.00**	0.083***	27.42**	11.44	1288.58*	0.36	2.16*	1.71*
LxTsca	20	2.98***	9.64***	7.60*	0.002	3.38	524.34***	183.21***	0.35	0.46***	0.31***
Error Cross	41	0.71	2.92	3.17	0.002	1.83	72.4	40.84	0.24	0.11	0.07
(%) Line (GCA) SS		65.61	51.84	63.98	58.08	35.73	79.94	80.07	63.22	30.74	44.09
(%) Tester (GCA) SS		4.71	27.69	12.82	26.22	18.56	0.02	5.19	1.81	13.14	11.98
(%) LxT (SCA) SS		29.68	20.47	23.2	15.7	45.72	20.04	14.75	34.96	56.12	43.93

Table 3 (Continued)

Source of Variation	MS										
	DF	EPP	EL	KPR	ED	TSW	BIOM	LL	LFPP	LFAE	LFBE
Rep	1	0.31*	9.56	26.86	0.03	8893.28**	73.90*	10.71	31.77***	0.11	38.67***
Cross	41	0.16***	9.59***	35.77**	0.24***	6373.16***	21.75**	71.28**	2.92***	0.47*	1.84***
L gca	20	0.19***	14.63***	55.67**	0.26	4733.84	28	51.57	3.59	0.45	2.77*
T gca	1	2.04***	32.60**	8.79	1.82**	89725.16***	23.17	97.86	0.11	0.38	0.01
LxTsca	20	0.04	3.39	17.22	0.16***	3844.87***	15.43	89.66*	2.39**	0.50*	1.01
Error Cross	41	0.07	3.2	13.33	0.04	1168.31	14.17	41.54	1.01	0.37	0.59
(%) Line (GCA) SS		57.24	74.44	75.92	50.43	36.23	62.8	35.29	59.96	46.21	73.37
(%) Tester (GCA) SS		29.86	8.29	0.6	17.79	34.34	2.6	3.35	0.09	1.96	0.02
(%) LxT (SCA) SS		12.9	17.27	23.49	31.78	29.43	34.6	61.36	39.95	51.83	26.62

GY = Grain yield (t/ha), DT = Days to tasseling (days), DS = Days to silking (days), ASI = Anthesis Silking Interval (days), MD = Days to Maturity (days), PH = Plant Height (cm), EH = Ear Height (cm), MOD = Kernel Modification (1-5 scoring), EAS = Ear Aspect (1-5 scoring), PAS = Plant Aspect (1-5 scoring), EPP = Ear Per Plant (number), EL = Ear Length (cm), NKR = Number of Kernel Rows (number), KPR = Kernel Per Row (number), ED = Ear Diameter (cm), TSW = Thousand Seed Weight (gram), BIOM = Biomass yield (t/ha), LL = Leaf Length (cm), LFPP = Leaf Per Plant (number), LFAE = Leaf above upper most ear (number), LFBE = Leaf below upper most ear (number).

Table 4. Mean square for combining ability of variance analysis for grain yield (t/ha) and other agronomic traits in LxT maize hybrids evaluated at Arsi-Negele Agricultural Research Center, 2017.

Source of Variation	MS							
	DF	GY	DT	DS	MD	PH	EH	TLB
Rep	1	9.51**	36.01*	33.44	20.01***	2690.53***	762.01***	2.67***
Cross	41	3.53***	27.13***	17.12*	3.49***	542.65***	308.64***	0.32*
L gca	20	5.09*	18.88	13.18	3.42	852.64**	451.84**	0.46*
T gca	1	0.06	500.29***	243.4***	1.44	796.12	1136.68**	0.76*
LxTsca	20	2.14*	11.72	9.74	3.66**	219.98**	124.03**	0.16
Error Cross	41	0.95	7.52	9.49	1.26	71.92	41.99	0.17
(%) Line (GCA) SS		70.36	33.95	37.56	47.8	76.65	71.41	69.89
(%) Tester (GCA) SS		0.04	44.97	34.68	1.01	3.58	8.98	5.73
(%) LxT (SCA) SS		29.59	21.07	27.75	51.19	19.77	19.6	24.37

Table 4 (Continued)

Source of Variation	MS							
	DF	EPP	EL	KPR	ED	TSW	BIOM	HI
Rep	1	0.07*	14.58**	14.86	1.66***	133.21	9.51*	70.59
Cross	41	0.04***	5.42***	29.31***	0.20***	5928.86***	3.84*	208.77*
L gca	20	0.03	8.86**	39.87	0.30**	6060.86*	4.46	199.3
T gca	1	0.69***	1.44	10.71	0.68**	74099.12***	4.92	300.08
LxTsca	20	0.03*	2.19	19.69	0.07	2388.34	3.18*	213.69*
Error Cross	41	0.02	1.7	11.67	0.06	1912.74	1.7	105.09
(%) Line (GCA) SS		33.42	79.69	66.35	74.09	49.87	56.55	46.57
(%) Tester (GCA) SS		34.74	0.65	0.89	8.31	30.48	3.11	3.51
(%) LxT (SCA) SS		31.84	19.66	32.76	17.6	19.65	40.33	49.93

*= significant at 0.05 probability level, **= significant at 0.01 probability level and *** = significant at 0.001 probability level, DF = Degree of freedom, GY = Grain yield (t/ha), DT = Days to tasseling (days), DS = Days to silking (days), MD = Days to Maturity (days), PH = Plant Height (cm), EH = Ear Height (cm), TLB = Turicum Leaf Blight (1-5 scoring), EPP = Ear Per Plant (number), EL= Ear Length (cm), KPR = Kernel Per Row (number), ED = Ear Diameter (cm), TSW = Thousand Seed Weight (gram), BIOM = Biomass yield (t/ha), HI = Harvest Index (%),

Table 5. Mean square for combining ability of variance analysis for grain yield (t/ha) and other agronomic traits in LxT maize hybrids evaluated at Kulumsa Agricultural Research Center, 2017.

Source of Variation	MS										
	DF	GY	DT	DS	PH	EH	CLR	EAS	EPP	EL	KPR
Rep	1	7.92**	8.05	15.42*	520.01	5.25	2.33**	0.01	0.01	13.22*	7.54
Cross	41	4.86***	28.41***	29.35***	469.42**	339.43***	0.82***	0.38**	0.18*	8.06***	24.18*
L gca	20	5.81	27.35*	26.65	765.53**	405.28*	0.71	0.38	0.06	7.34	31.76
T gca	1	2	360.42***	368.76***	186.01	2150.30**	7.44**	0.43	3.91***	43.81*	14.72
LxTsca	20	4.06***	12.87***	15.08***	187.49	183.05*	0.62*	0.39**	0.13	6.99***	17.08
Error cross	41	0.95	2.34	2.72	195.33	82.98	0.3	0.16	0.1	2.13	13.04
(%) Line (GCA) SS		58.24	46.96	44.29	79.55	58.24	41.52	47.62	15.03	44.42	64.06
(%) Tester (GCA) SS		1	30.93	30.64	0.97	15.45	21.89	2.68	51.43	13.25	1.48
(%) LxT (SCA) SS		40.76	22.11	25.07	19.48	26.31	36.58	49.7	33.54	42.32	34.45

Table 5 (Continued)

Source of Variation	MS										
	DF	ED	TSW	BIOM	LANG	LL	LW	LFAR	LFPP	LFAE	LFBE
Rep	1	0.02	1505.53	35.52*	4.76	0.53	0.10	130.42	12.44***	0.03	11.19***
Cross	41	0.21***	4301.81***	21.41***	31.24***	54.18***	0.88**	8835.74**	0.91**	0.25*	0.54**
L gca	20	0.21*	3635.37*	22.26	42.12	45.78	0.84	5265.19	0.96	0.31	0.58
T gca	1	2.63***	71122.79***	81.02*	29.76	5.08	5.00*	14278.45	1.81	0.16	0.89
LxTsca	20	0.10	1627.21	17.58**	20.45***	65.04***	0.72*	12134.16***	0.83*	0.20	0.49*
Error cross	41	0.07	971.44	7.22	6.32	19.61	0.34	3629.30	0.40	0.14	0.24
(%) Line (GCA) SS		48.18	41.22	50.71	65.74	41.22	46.26	29.07	51.03	59.91	51.66
(%) Tester (GCA) SS		29.45	40.32	9.23	2.32	0.23	13.84	3.94	4.81	1.55	4.01
(%) LxT (SCA) SS		22.37	18.45	40.07	31.93	58.55	39.90	66.99	44.15	38.54	44.33

DF = Degree of freedom, GY = Grain yield (t/ha), DT = Days to tasseling (days), DS = Days to silking (days), PH = Plant Height (cm), EH = Ear Height (cm), CLR = Common Leaf Rust (1-5 scoring), EAS = Ear Aspect (1-5 scoring), EPP = Ear Per Plant (number), EL = Ear Length (cm), KPR = Kernel Per Row (number), ED = Ear Diameter (cm), TSW = Thousand Seed Weight (gram), BIOM = Biomass yield (t/ha), LANG = Leaf Angle (degree), LL = Leaf Length (cm), LW = Leaf Width (cm), LFAR = Leaf Area (cm²), LFPP = Leaf Per Plant (number), LFAE = leaf above upper most ear (number), LFBE = Leaf below upper most ear (number).

At Arsi-Negele, the MS of line GCA was significant for GY, PH, EH, TLB, EL, ED, and TSW. Testers' GCA MS was significant for DT, DS, ASI, EH, TLB, EPP, ED, and TSW ($P < 0.001$, $P < 0.01$, or $P < 0.05$) but MD, KPR, BIOM, and HI showed non-significant line and tester GCA MS. The MS of SCA was significant ($P < 0.01$ or $P < 0.05$) for GY, MD, PH, EH, EPP, BIOM, and HI but the other traits of MS of SCA were non-significant (Table 4). Significant line GCA for EPP, NKR, and KPR report by Shushay (2014) disagrees with the present finding. But his study attested/proved significant MS for GCA of line, and tester, and SCA for GY.

At Kulumsa, MS of line GCA was significant ($P < 0.01$ or $P < 0.05$) for DT, PH, EH, ED, and TSW. Testers' GCA MS was also significant ($P < 0.001$, $P < 0.01$ or $P < 0.05$) for DT, DS, EH, CLR, EPP, EL, ED, TSW and BIOM. The MS of SCA was also significant ($P < 0.001$, $P < 0.01$ or $P < 0.05$) for GY, DT, DS, EH, CLR, EAS, EL, BIOM, LANG, LFAR, LFPP and LFBE. A greater number of traits exhibited non-significant SCA MS at Arsi-Negele than at Ambo and Kulumsa (Tables 3, 4, and 5). Differences in the state of significant (significant or not significant) GCA and SCA MS of a trait in different environments are an indication of the effect of environment on the preponderance of additive or non-additive genetic components (Birhanu, 2009). This indicates that the gene which is responsible for the inheritance of a character is highly influenced by the environmental factor. Based on the percent sum square contribution of SCA to the total sum square of the cross for each trait, LxT (SCA) interaction sum square contribution was higher than 50% for EAS, NKR, and LFAE at Ambo, At Arsi-Negele: MD whereas at Kulumsa, by LFAR indicated that these traits were controlled mainly by non-additive gene effect (Tables 3, 4 and 5).

At Ambo, Arsi-Negele, and Kulumsa the proportional sum square contribution of line and tester GCA (sum of line GCA and tester GCA) to the cross sum of the square for GY was 70.32 %, 70.4%, and 59.24%, respectively. Indicating the preponderance of additive gene action over non-additive gene action. The highly significant SCA effects might have resulted from testers used as parents for the formation of crosses. Similar findings indicated the importance of additive and non-additive gene action in the inheritance of grain yield for

QPM hybrids and the importance of both GCA and SCA (Birhanu, 2009; Demissew, 2014; Shah *et al.*, 2015; Beyene, 2016).

The existence of significant MS for line GCA, testers GCA, and SCA for DT is in agreement with the finding of Beyene (2016) and Gudeta *et al.* (2015) for tester GCA. In contrast, Gudeta *et al.* (2015) reported non-significant MS for line GCA and SCA. GCA sum square contribution for DT was 79.53%, 78.93%, and 77.89% at Ambo, Arsi-Negele, and Kulumsa (Tables 3, 4, and 5) which indicates the additive gene action mainly controlled the genetic inheritance. Similarly, Abiy (2017) and Birhanu (2009) reported higher proportions of GCA sum square for DT (60.52 %) and 86.91%, respectively. Other authors also reported the importance of both additive and non-additive gene effects for the control of this trait (Demissew, 2014; Amare *et al.*, 2016; Abiy, 2017).

The highly significant MS of line GCA and SCA for PH (Table 3) at Ambo and Arsi-Negele was to the findings of Birhanu (2009), Demissew (2014), and Gudeta *et al.* (2015). Non-significant MS of tester GCA observed in this study is in line with the report of Gudeta *et al.* (2015). The significant SCA MS for PH in the present study disagrees with the report of Amare *et al.* (2016) from his LxT experiment. The percent sum square contribution of GCA for PH was 79.96%, 80.23%, and 80.52% at Ambo, Arsi-Negele, and Kulumsa, respectively (Tables 3, 4, and 5). The high GCA sum square contribution for PH indicates that the inheritance of this trait was controlled by additive gene action. The MS of line GCA, tester GCA, and SCA were significant at the three locations. The percent sum square contribution of GCA was 85.25%, 80.40%, and 73.69% for EH (Tables 3, 4, and 5). The higher proportional contribution of GCA than SCA sum squares for the total sum square of the cross indicated additive gene effects were more important than the non-additive effect. Similarly, Birhanu (2009), Gudeta *et al.* (2015), and Amare *et al.* (2016) observed a higher proportion of GCA sum of the square than SCA sum square for secondary traits (EH and PH).

At Ambo and Kulumsa for EAS, the percent contribution of the SCA sum square to the total sum square of the cross was 56.12% and 56.21%, respectively for EAS. The MS of SCA was significant at both locations but the MS of GCA was significant only at Ambo (Tables 3 and

5). In line with this Beyene (2016) also reported significant MS for this trait. This indicated that EAS was dominantly controlled by the non-additive gene action. Generally, this study indicates that secondary traits are mainly controlled by additive gene effects except, EAS. For such traits, there is a possibility of accumulating favorable genes in the direction of interest by selection. Breeding programs engaged in inbred line development for their hybrid programs should practice a selection of inbred lines for most of the secondary traits with the reasonable intensity of selection/proper selection. However, the role of non-additive gene effects should not be underestimated as inbred lines recover their vigor upon hybridization and showed heterosis in a negative direction for flowering and maturity (Birhanu, 2009). For MD, the higher percent sum square contribution was obtained from GCA (54.29%) at Ambo (Table 3) but at Arsi-Negele, the higher value was obtained from SCA which indicated that the inheritance was affected by the environment. This shows the effect of the environment on gene expression across locations. Meaning that at Ambo, the variability was controlled by additive gene action whereas, at Arsi-Negele, it was controlled by the non-additive gene action. In contrast to the current finding, Birhanu (2009) reported a significant line GCA which agrees with the non-significant line GCA observed at Ambo and Arsi-Negele in the current finding.

At Ambo for ASI, GCA percent sum square contribution to the total sum square of the cross was 84.3% and was higher than the sum square contribution of SCA. Line and tester GCA MS showed significant but SCA MS was non-significant (Table 3). Amare *et al.* (2016) also reported similar findings for SCA and contrasted results for line and tester GCA.

At Arsi-Negele, tester and line GCA were significant for TLB (Table 4). At Kulumsa, the MS of CLR was significant for testers GCA ($P < 0.01$) and SCA ($p < 0.05$) (Table 5). This result is in line with the finding of Birhanu (2009) for tester GCA but contradicted line GCA and SCA. He reported significant differences between lines and non-significant for SCA. Indicating the presence of high variability within each group of germplasm for TLB and CLR evaluated where diseases occurred. The finding of this result on TLB disagrees with the report of Legesse *et al.* (2009) and Beyene (2016). They reported significant differences between GCA and SCA. The percent sum square contribution of GCA to the total sum square of the cross was 63.41% for CLR at Kulumsa. The sum square contribution of GCA

for TLB was 75.62% at Arsi-Negele. Similarly, Birhanu (2009) also reported a higher sum square proportion of the GCA effect as compared to SCA for TLB. Based on this result, CLR and TLB resistant crosses can be formed from inbred lines having desirable GCA for these traits in areas where the disease is prevalent. The additive gene effect was important in the inheritance of TLB and CLR as it was evident from the higher proportion of GCA sum of squares for TLB (Tables 4 and 5).

At Arsi-Negele and Kulumsa, SCA MS showed significant differences from BIOM. The MS of tester GCA showed significant variation among testers at Kulumsa while at Ambo, the MS of line GCA, tester GCA, and SCA was non-significant. The percent sum square contribution of GCA was 65.4%, 59.67%, and 59.93% at Ambo, Arsi-Negele, and Kulumsa, respectively (Table 3, 4, and 5). The higher sum square contribution of GCA than that of the SCA at the three locations indicates that the genetic variability of this trait was controlled by the additive gene action. Abiy (2017) from his study conducted at Kulumsa found a higher contribution of GCA sum square than SCA whereas the higher SCA sum square contribution than GCA at Ambo disagrees with his study. This indicates that the environment has an impact on genetic expression.

At Arsi-Negele, line and tester GCA MS for HI was non-significant ($P > 0.05$) which disagrees with previous (Birhanu, 2009; Bitew, 2016; Abiy, 2017). Abiy (2017) also reported significant MS for tester GCA at Ambo and Kulumsa. The significant SCA shown at Arsi-Negele is in line with the report of Abiy (2017) from highland materials. Birhanu (2009) also reported similar findings for maize genotypes developed for mid-altitude. Line GCA sum square (50.08%) was almost equal to SCA sum square (49.93%) at Arsi-Negele (Table 4). Based on sum square contribution information, both the additive and non-additive gene effect was equally important in the control of HI by crosses of maize evaluated. This finding was somewhat similar to the result reported by Abiy (2017) but it disagrees with the finding of Birhanu (2009) who reported a higher contribution of GCA than SCA with a value of 59.92%.

At Ambo, PAS showed significant MS ($P < 0.05$ or $P < 0.001$) for tester GCA and SCA whereas line GCA showed non-significant MS. This result agrees with the result reported by

Amare *et al.* (2016) concerning significant tester GCA and SCA whereas his report of significant line GCA disagrees with the current study. The result of this study contradicted Beyene's (2016) non-significant MS for SCA and significant line GCA for PAS. The sum square contribution of SCA was 43.93% (Table 3). At Ambo, GCA sum square contribution was higher than SCA to the total sum square of crosses indicating that PAS was controlled mainly by additive gene action. Regarding MOD, significant MS ($P < 0.01$) was observed by line GCA and non-significant MS for tester GCA and LxT SCA at Ambo. In contrast, Gudeta *et al.* (2015) reported significant MS for tester GCA and SCA. In terms of sum square contribution, the higher sum square (64.91%) contributed to the total sum square of the cross by GCA at Ambo. This higher sum square by GCA was also in contrast with the report of Gudeta *et al.* (2015). He reported a higher sum square contribution of SCA (59.01%) to the total sum square of the cross. The sum square percent contribution and line GCA significant MS at Ambo can imply MOD was dominantly controlled by additive action (Table 3).

At Ambo, MS of line and tester GCA was non-significant for LFPP and LFAE. Line GCA had significant MS but not by tester GCA for LFBE. The MS of SCA was significant for LFBE but it was non-significant for LFPP and LBAE. The percent sum square contribution of GCA was 38.64%, 60.05%, 48.17%, and 73.38% in magnitude for LFPP, LFAE, and LFBE, respectively (Table 3). Based on the values, LFPP and LFBE were mainly controlled by additive gene action but the variability of LFAE was controlled dominantly by non-additive gene action.

At Kulumsa, the MS of line GCA and tester GCA were non-significant for LANG, LFAR, LFPP, LFAE, and LFBE. SCA was highly significant ($P < 0.001$) for LANG and LFAR. It was also significant ($P < 0.05$) for LFPP and LFBE SCA MS except, LFAE which showed non-significant SCA MS. The SCA sum square contribution of LFAR (66.99%) indicates that the non-additive gene action mainly controlled the traits. For LANG, LFPP, LFAE, and LFBE, the contribution of GCA sum square (sum of the tester and line sum square) was higher as compared with the sum square contribution of SCA contributed to the total sum square of cross. The sum square of GCA for LANG, LFPP, LFAE, and LFBE was 68.07%, 60.10%, 61.46%, and 55.67%, respectively (Table 5). These values indicated that these traits

were mainly controlled by the additive gene effect. The non-significant LFAR for line and tester GCA disagrees with the report of Birhanu (2009) and Zakiullah *et al.* (2018) while the significant SCA obtained in this study is in line with the report made by these two authors.

32.2 Combining ability variance across the location

ANOVA for combined analysis across locations, for those traits which had non-significant GxLis presented in Table 6. The traits which had significant MS among crosses were DS, EPP, EL, KPR, ED, and TSW with the absence of significant GxL. Similarly, Birhanu (2009) Badu-Apraku *et al.* (2013), and Beyene (2016) reported significant differences among the crosses for grain yield and yield-related, phenological, and other agronomic traits. Line GCA, tester GCA, and SCA were also significant ($P < 0.001$ $P < 0.01$ or $P < 0.05$) for traits studied except, the GCA of the line for EPP and TSW. In contrast, Birhanu (2009) reported significant MS for EPP and TSW for line GCA. Tester GCA showed non-significant MS for KPR, which disagrees with the report of Birhanu (2009) and Abiy (2017). The non-significant MS of SCA for KPR is in line with previous reports (Abiy, 2017) but it disagrees with the report of Birhanu (2009) and Shah *et al.* (2015). The higher percent sum square contribution of GCA than SCA by all traits which are included in the combined analysis indicates the genetic variability was controlled by additive gene action than non-additive action (Table 6).

Tester GCA x location showed significant MS for DS, EPP, and EL (Table 6), GY, ASI, MD, CLR, TLB, PAS, BIOM, and HI. This indicates that testers' performance was not consistent across locations on these traits. But KPR, ED, and TSW (Table 6), DT, PH, EH, MOD, GLS, EAS, NKR, LANG, LFAR, LFPP, LFAE, and LFBE showed non-significant MS (data not shown) implies testers' consistent performance across locations. The MS for DS, EPP, EL, KPR, ED, and TSW (Table 6), DT, MD, MOD, GLS, CLR, NKR, HI, LANG, LFAR, and LFAE, showed a non-significant difference for line GCA x location interaction whereas line GCA significantly interacted with a location for GY, ASI, PH, EH, TLB, EAS, PAS, BIOM, LFPP and LFBE (data not shown). The SCA x location was significant for GY, PH, EH, LFPP, and LFBE (data not shown) which is in line with the report of Birhanu (2009). DT, DS, ASI, MD, MOD, GLS, CLR, TLB, EAS, PAS, EPP, EL, NKR, KPR, ED,

TSW, BIOM, HI, LANG, LFAR, and LFAE had non-significant MS for SCA x location interaction. Demissew (2014) also reported significant MS for line GCA x location for yield-related, phenological, and agronomic traits. He also reported significant MS for SCA x location for most traits except grain yield-related traits. Generally, for traits that showed significant MS for the source of variations by location interaction, the performance was not consistent across the location.

The existence of significant MS for line GCA ($P < 0.05$), testers GCA ($P < 0.001$), and SCA ($P < 0.001$) for DS agrees with Beyene (2016) who reported significant differences for GCA and SCA. Gudeta *et al.* (2015) also reported significant MS for tester GCA and line GCA for DS. In contrast, Gudeta *et al.* (2015) reported non-significant MS for SCA. Other authors also reported the importance of both additive and non-additive gene action in the control of these traits (Demissew, 2014; Amare *et al.*, 2016; Abiy, 2017). For DS, the greatest share of variability observed in crosses was contributed by the GCA of both lines and testers accounted together (79.63%) for the total sum of squares. Similarly, Abiy (2017) observed a higher proportion (64.11%) of GCA sum square contribution from the hybrids tested at Kulumsa for DS, and Birhanu (2009) also reported similar information regarding DS.

For EPP, tester GCA and SCA had significant MS at ($P < 0.001$) but not for line GCA. The MS of line GCA, tester GCA, and SCA were significant at ($P < 0.01$) for EL. Significant tester GCA and SCA ($P < 0.001$) and line GCA at ($P < 0.05$) were observed for ED whereas the MS of line GCA was non-significant ($P > 0.05$) difference for EPP (Table 6). Similar results were reported by (Birhanu, 2009; Demissew, 2014; Beyene, 2016; Abiy, 2017). Amare *et al.* (2016) and Beyene (2016) reported non-significant MS for SCA of ED which disagrees with this study. Amare also reported significant MS for line GCA which contrasts with the non-significant MS of GCA obtained in this study for ED. EPP MS was significant for tester GCA and SCA but non-significant for line GCA. The result of this study disagrees with what was reported by Gudeta *et al.* (2015) and Amare *et al.* (2016) for testers GCA and LxT SCA. They also reported significant MS for line GCA which is in line with the finding of this study. The contribution of the GCA sum square accounted for 79.27, 80.13, and 78.46% of the total sum square of the cross for EPP, EL, and ED, respectively. This indicates the greater contribution of additive genetic variance for the total variation observed in the

crosses for these traits, though both additive and non-additive gene action were responsible for the variation in crosses. Several investigators reported the importance of both additive and non-additive gene actions in the inheritance of EPP, EL, KPR, and ED (Birhanu, 2009; Amare *et al.*, 2016). Gudeta *et al.* (2015) also reported the higher contribution of GCA sum square than SCA to the total sum square of the cross for EPP.

The higher contribution of GCA over SCA in the current study disagrees with the report of Abiy (2017) reported a lower contribution of GCA sum square than SCA to the total sum square of the cross for ED. For TSW significant ($P < 0.001$) tester GCA and SCA MS were obtained but line GCA MS was non-significant and disagrees with the report of Amare *et al.* (2016). He reported significant MS for line GCA and non-significant differences for tester GCA and SCA. Gudeta *et al.* (2015) reported significant MS for line GCA and SCA but non-significant MS for tester GCA for TSW. Shah *et al.* (2015) reported significant MS for line GCA, tester GCA, and SCA for TSW. In this study, the significant MS obtained for tester GCA and SCA for TSW is in line with the significant MS GCA and SCA reported by (Birhanu, 2009; Demissew, 2014; Shah *et al.*, 2015; Beyene, 2016; Abiy, 2017). These authors reported significant MS for tester GCA and SCA for TSW. The sum square contribution of GCA was 79.10% which is greater than the contribution of SCA to the total sum square of the cross for TSW.

For KPR, highly significant MS ($P < 0.01$) was observed for MS line GCA which agrees with the report of Demissew (2014), Amare *et al.* (2016), and Beyene (2016). The MS of tester GCA was non-significant ($P > 0.05$) which disagrees with what Demissew (2014); Amare *et al.* (2016) and Beyene (2016) reported. The non-significant MS of SCA for KPR is in line with the findings of Amare *et al.* (2016). The sum square contribution of GCA was higher (80.0%) and agrees with the report of Birhanu (2009) and Amare *et al.* (2016). They reported 67.08 and 82.07 % sum square contribution by GCA, respectively to the total sum square for KPR. Even though line GCA was not significant, the percent sum square contribution of GCA was higher for TSW. Based on this, both the additive and non-additive gene effects were found to be important for the control of TSW but the MS of tester GCA and SCA was highly significant. The higher sum square contribution was due to the GCA sum of lines and testers (79.0.9%) (while that of SCA was (20.91 %) of the total sum square of cross.

Table 6. Combined ANOVA for combining ability and proportional contribution of GCA and SCA sum of squares in LxT crosses evaluated at three locations in, 2017.

Source of Variation	DF	MS					
		DS	EPP	EL	KPR	ED	TSW
Location	2	1159.35**	4.61**	294.57*	669.62**	8.57*	235157.73**
Cross	41	50.82***	0.29***	16.89***	57.99***	0.53***	13699.93***
Line (L gca)	20	50.74*	0.18	24.65**	95.06**	0.62*	10496.97
Tester (T gca)	1	644.48***	5.99***	61.01**	4.15	4.81***	234328.15***
Line x Tester (L x T sca)	20	21.22***	0.12***	6.92**	23.61	0.23***	5871.48***
Cross x Location	82	5.82	0.05	3.09	15.64	0.07	1451.95
L gca x Location	40	5.03	0.05	3.10	16.12	0.08	1966.55
T gca x Location	2	25.86**	0.32**	8.42*	15.04	0.16	309.46
LxTsca x Location	40	5.60	0.04	2.82	15.19	0.05	994.47
pooled error crosses	123	5.13	0.06	2.34	12.68	0.05	1350.83
(%) SS line (GCA)		48.70	30.21	71.19	79.96	56.67	37.38
(%) SS Tester (GCA)		30.93	49.06	8.81	0.17	21.79	41.72
(%) SS LxT (SCA)		20.37	20.73	20.01	19.86	21.54	20.91
GCA/SCA Ratio		3.91	3.82	4.00	4.04	3.64	3.78

*= significant at 0.05 probability level, **= significant at 0.01 probability level, *** = significant at 0.001 probability level, DF = Degree of freedom SS = Sum Square, DS = Days to Silking, EPP = Ear Per Plant, EL = Ear Length, KPR = Kernels Per Row, ED = Ear Diameter, TSW = Thousand Seed Weight

3.2.3 General combining ability (GCA) effect of lines

4.2.2.1. General combining ability (GCA) effects of lines at an individual location

At Ambo, GCA effects for GY ranged from -2.52 to 2.03 t ha⁻¹. Of the 21 lines, five (L6, L7, L8, L9, and L17) showed a highly significant positive GCA effect. L3 had a significant GCA effect at (P<0.05) a GCA effect of 0.59 t ha⁻¹, indicating their ability to combine well for GY. GCA effects of: 1.14, 1.26, 2.03, 1.16, and 1.64 t ha⁻¹ were obtained for L6, L7, L8, L9, and L17, respectively. The lines with a significant negative GCA effect and with a significant difference were L1 (-1.74 t ha⁻¹), L2 (-2.33 t ha⁻¹), L4 (-2.10 t ha⁻¹), and L13 (-2.52 t ha⁻¹) (Table 7). Crosses involving lines that had a significant negative GCA effect also showed lower GY than the mean of crosses (5.91 t ha⁻¹) except for, L1xT2 (6.33 t ha⁻¹) (data not shown). At Arsi-Negele, L5, L7, L8, L18, and L19 showed significant positive GCA effects. The value of the effect was 1.38 (L5), 1.49 (L7), 3.40 (L8), 0.80 (L18), and 1.09 t ha⁻¹(L19). L1, L2, L4, L11, L13, and L21 showed significant negative GCA effects for GY. The GCA effect ranged from -1.69 to 3.40 t ha⁻¹ considering both GCA effect directions (Table 8).

At Kulumsa, 11 lines showed positive GCA effects. From these lines, six of them (L6, L7, L8, L15, L19, and L21) had a significant effect. Ten lines showed negative GCA effects of which five (L1, L2, L3, L4, and L13) had a significant effect (Table 8). L8 and L7 had consistently higher positive GCA for GY at all three locations with significant effects (Figure 1). In the combined analysis, L8, L7, L6, L19, L5, L18, and L9 showed relatively higher positive GCA effects (Figure 2). Therefore, these lines could be nominated as potential testers in the breeding program to study other sets of new material for their combining ability, classify newly developing inbred lines into different heterotic groups, and identify of best single crosses. Moreover, the single cross hybrid composed of these good combiner lines can be used for the identification of the best three-way crosses for direct release. Similarly, Birhanu (2009), Shushay (2014), Amare *et al.* (2016), and Abiy (2017) reported significant negative and positive GCA effects on grain yield.

The GCA effect of EH ranged from -27.84 cm to 29.90 cm at Ambo, -20.11 to 19.63 cm at Arsi-Negele, and -20.91 to 17.08 cm At Kulumsa. For PH, the GCA effect ranged from -43.17

to 37.07cm at Ambo, -29.44 to 25.30 at Arsi-Negele, and -34.09 to 20.15 cm at Kulumsa (Tables 7 and 8)

Table 7. Estimates of general combining ability (GCA) effects of lines and testers for traits at Ambo are not included in the combined analysis.

Code	Ambo					
	GY	ASI	EH	PH	MOD	LFBE
L1	-1.74***	-1.07	-17.34***	-40.42***	-0.05	-0.05
L2	-2.33***	-0.07	-27.84***	-43.17***	-0.68	-0.67*
L3	0.59*	-1.32	-5.09*	-7.67*	-0.55	-0.55
L4	-2.10***	0.18	-24.59***	-38.67***	-0.05	-1.67***
L5	0.25	0.68	-4.09	-3.18	0.45	-1.92***
L6	1.14**	-0.07	22.40***	20.57***	0.07	-1.04**
L7	1.26***	-0.82	17.15***	24.32***	-0.18	-0.42
L8	2.03***	-0.32	29.90***	37.07***	0.57	-0.17
L9	1.61***	-1.07	6.40*	9.07**	-0.30	-0.05
L10	0.39	-1.32	8.90**	9.32**	0.20	0.33
L11	0.20	-0.32	1.65	0.82	-0.18	0.57*
L12	-0.20	-1.57	4.65*	8.32*	-0.30	0.95**
L13	-2.52***	-0.07	-27.59***	-41.42***	0.07	0.70*
L14	-0.14	0.43	3.90	8.82**	0.20	-0.05
L15	0.17	0.18	1.90	6.57*	0.45	0.20
L16	-0.38	2.93*	-17.59***	-11.17**	-0.43	-0.17
L17	1.64***	0.18	7.90**	11.07**	-0.18	0.57*
L18	0.38	0.18	10.90***	18.82***	0.32	0.70*
L19	-0.41	-0.32	-6.09*	10.07**	-0.05	0.70*
L20	-0.18	3.43**	7.65**	12.57***	0.95	1.07**
L21	0.34	0.18	6.90**	8.32*	-0.30	0.95**
SE (line)	0.42	0.60	3.20	4.25	0.24	0.38
SEd (gi-gj) line	0.57	0.85	4.67	5.79	0.35	0.54
T1	-0.34	-0.76	3.92	0.37	-0.07	-0.01
T2	0.34	0.76	-3.92	-0.37	0.07	0.01
SE (tester)	0.13	0.19	0.99	1.31	0.08	0.12
SEd (gi-gj) tester	0.18	0.26	1.44	1.79	0.11	0.17

. Six lines (L1, L2, L3, L4, L13, and L16) commonly showed significant negative GCA effects for EH and PH. L19 had negative and significant GCA effects at Ambo (Table 7). At Arsi-Negele, L1, L2, L4, L13, and L16 showed negative and significant GCA effects for EH and PH in common. L15 also had a negative and significant GCA effect for EH at Arsi-Negele. At

Kulumsa, L4 and L13 showed negative and significant GCA effects for EH and PH in common but considering only EH, three lines (L1, L2, and L5) had negative and significant GCA effects at Kulumsa (Table 8) indicates that these lines significantly contributed to reduction of plant stature. On the other hand, L6, L7, L8, L9, L10, L12, L17, L18, L20, and L21 showed positive and significant GCA effects for both EH and PH at Ambo (Table 7). At Arsi-Negele, L6, L7, L8, L9, L10, L12, L14, L19, and L20 showed positive and significant GCA effects for EH and PH (Appendix 9). At Kulumsa, L12 and L20 had positive and significant GCA effects for EH and PH. L6 and L8 showed positive and significant GCA effects for EH indicating that these lines contributed to high plant stature for their crosses. Regarding the testers, the GCA effect was non-significant at Ambo and Arsi-Negele but at Kulumsa, the tester's GCA effect showed a significant difference for EH whereas for PH no testers had a significant GCA effect at all three locations (Table 7 and 8). But Birhanu reported positive and negative GCA effects of testers with significant effects for both traits.

At Ambo for ASI, L16 and L20 showed positive and significant GCA effects of 2.93 and 3.43 days, respectively (Table 7). This implies that these lines contributed more to the existence of a wide gap between male and female flowering by the cross. The mean of ASI was 5.5 days for L20xT2 and L20xT1, 3 days for L16xT1, and 7 days for L16xT2 (data not shown). Of the 21 lines tested in this study, 12 lines had a negative GCA effect for ASI even though the effects were non-significant. The negative GCA effect for ASI is desirable because it has its role in narrowing down the day's gap between male and female flowering. None of the lines showed significant negative GCA effects but there were only two lines that had positive GCA with significant effect. The number of lines that showed a positive GCA effect for ASI obtained in his study is fewer than those reported by other authors (Demissew, 2014 Beyene, 2016).

All lines at Ambo showed a non-significant GCA effect for MOD (Table 7). Of the 21 lines, 11 showed a negative GCA effect even if the effect was non-significant. This indicates the opportunity available to improve kernel modification (reduction of chalkiness) which is the challenge in QPM breeding. In contrast to this study result, Demissew (2014) reported significant positive and negative GCA effects for MOD.

At Arsi-Negele, none of the lines and testers showed a significant GCA effect for HI. Implies that these lines didn't contribute significantly to crosses in the role of conversion of biomass into grain yield. Similarly, Abiy (2017) reported no lines which had a significant GCA effect. A relatively higher positive GCA effect was shown by L5 (13.67%), L7 (10.56%), L8 (9.14%), and L16 (11.91%). Crosses formed by crossing L5, L7, L8, and L6 with T1 showed better yield than those crossed with T2. This indicates that the contribution of L5, L7, and L8 (lines with positive and significant GCA for GY) (Table 8) was higher for conversion of biomass into grain yield from crosses formed from lines with T1 compared with the same lines crossed with T2 (data not shown). In contrast to this study output, Birhanu (2009) and Abiy (2017) reported significant GCA effects in the negative and positive directions for some lines. There were also lines: L1, L3, and L21 which are manifested by a negative GCA effect (Table 8) had also lower grain yield by crosses formed from these lines with testers (data not shown).

Table 8. Estimates of general combining ability (GCA) effects of lines and testers for traits at Arsi-Negele and Kulumsa which are not included in the combined analysis in 2017.

Code	Arsi-Negele				Kulumsa		
	GY	EH	PH	HI	GY	EH	PH
L1	-1.1**	-13.36***	-20.94***	-10.19	-1.65**	-14.91**	-13.60
L2	-1.69***	-18.36***	-29.44***	-4.82	-1.53**	-11.41*	-4.85
L3	-0.41	-2.12	-1.70	-8.66	-1.62**	1.83	-1.10
L4	-0.84*	-16.36***	-23.19***	-4.25	-1.83***	-12.91**	-30.09***
L5	1.38***	-0.87	3.30	13.67	0.34	-9.16*	-12.60
L6	-0.11	10.63***	11.05**	-2.71	1.25*	17.08***	13.40
L7	1.49***	17.88***	20.80***	10.56	1.28*	6.08	-2.10
L8	3.40***	19.63***	25.30***	9.14	1.88***	11.33*	6.65
L9	-0.33	7.63**	9.05**	2.39	0.47	5.83	10.65
L10	0.31	1.13	5.55*	0.35	-0.14	4.08	6.15
L11	-0.79*	0.38	-0.20	-2.60	-0.43	-2.67	-1.60
L12	-0.13	4.13	6.80*	-5.50	0.67	10.83*	20.15**
L13	-1.10**	-20.11***	-25.19***	-3.87	-2.05***	-20.91**	-34.09***
L14	-0.24	5.38*	6.80*	-5.41	0.26	3.08	7.40
L15	-0.43	-4.86*	-3.70	-2.34	1.08*	0.83	-0.10
L16	-0.15	-6.11*	-7.44*	11.91	-0.29	-8.67	-5.10
L17	-0.36	1.63	-4.70	-1.29	-0.49	1.08	10.15
L18	0.80*	0.88	4.30	1.92	0.58	5.08	5.65
L19	1.09**	6.88**	13.55***	7.84	1.52**	-5.17	4.15
L20	-0.14	5.38*	8.65**	2.72	-0.51	13.58**	19.15**

L21	-0.62*	0.63	1.30	-8.87	1.21*	5.08	1.65
SE (line)	0.49	3.24	4.24	5.13	0.49	4.55	6.99
SEd (gi-gj) line	0.69	4.58	6.00	7.24	0.69	6.44	9.88
T1	0.03	3.68	3.08	-1.89	-0.15	5.05***	1.49
T2	-0.03	-3.68	-3.08	1.89	0.15	-5.05***	-1.49
SE (tester)	0.15	1.00	1.31	1.58	0.15	1.41	2.16
SEd (gi-gj) tester	0.18	1.44	1.77	2.24	0.21	1.99	3.05

LFBE showed significant MS for line GCA at Ambo (Table 3). The other morphological traits did not show significant line GCA MS even if the MS was significant for the cross at Ambo and Kulumsa (Tables 3 and 5). The effect of GCA ranged from -1.92 to 1.07 leaves. Out of the 21 lines, only four showed negative and significant GCA effects. The other eight lines showed positive and significant GCA effects. Of the lines that produced high yielding crosses (L3xT2, L8xT1, and L17xT2) (data not shown), L3 and L8 had negative GCA while L17 had positive and significant GCA for LFBE. These lines (L3, L8, and L17) had positive and significant GCA effects for GY (Table 7).

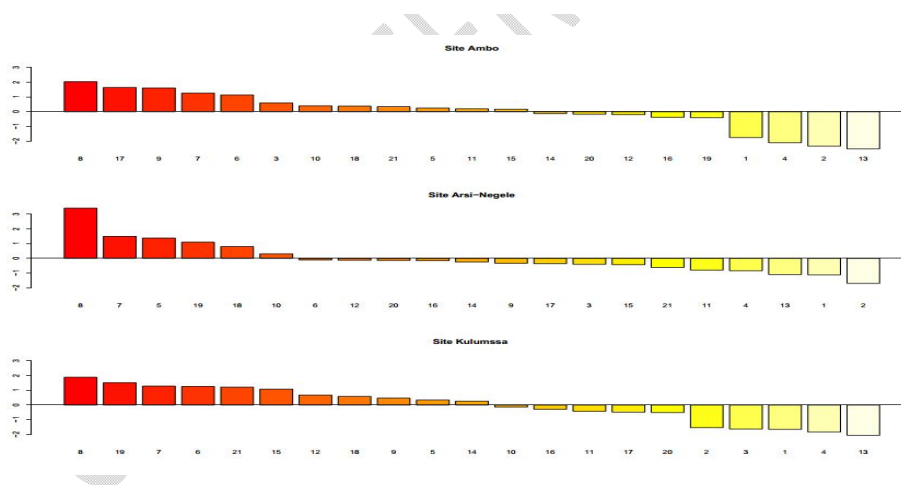


Figure 1. GCA (General Combining Ability) effects of 21 highland quality protein maize inbred lines for grain yield at individual location level (Ambo, Arsi-Negele, and Kulumsa) in 2017.

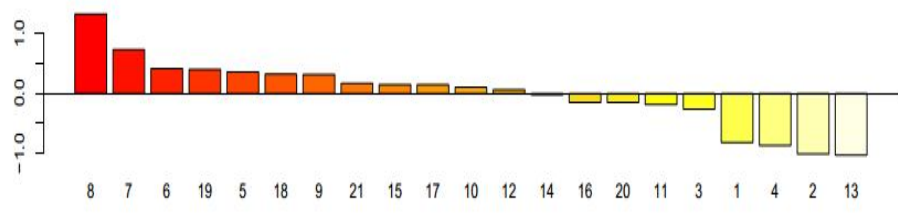
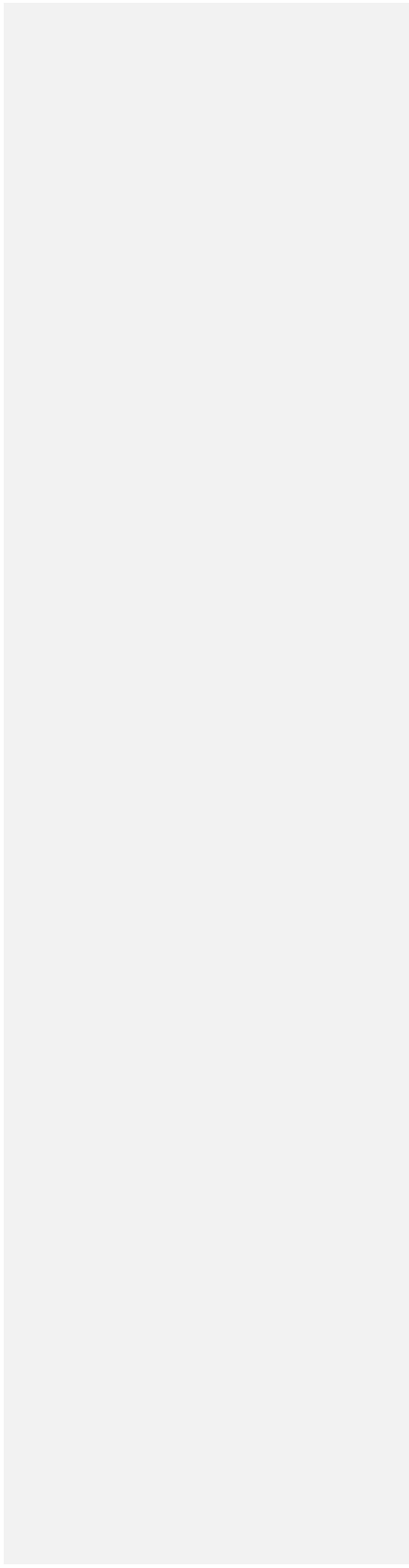


Figure 12. GCA (General Combining Ability) effects of 21 highland quality protein maize inbred lines for grain yield measured combined across three locations in 2017.

UNDER PEER REVIEW



3.2.4 General combining ability (GCA) effect of lines across locations

Under this sub section, only traits showed significant MS for crosses, line GCA, and/or tester GCA but non-significant MS for factor by location interaction was discussed. Based on this DT, DS, EL, ED, and KPR were the traits that fulfilled the criteria.

L16 and L19 showed significant negative GCA effects with the value of -5.38 days and -2.96 days for DT, respectively. This indicates that these lines were the contributor to the earliness of the crosses they formed. On the other hand, L1 and L12 showed positive and significant GCA effects with values of 3.53 and 4.53 days, respectively. These lines contributed to late tasseling for the crosses they served as parents. For DS, L16 also showed significant negative GCA effects (-4.13 days). L12 showed a significant GCA effect of 3.36 days (Table 9). Generally, in this study relatively few numbers of lines showed significant GCA for phenology traits than what was reported compared to the previous studies (Demissew, 2014; Beyene, 2016) for DT and Birhanu (2009); Amare *et al.* (2016) for DT and DS.

From grain yield-related traits only L9 had a positive value and showed a significant ($P < 0.05$) GCA effect (2.62 cm) for EL implying that this line contributed to the increase of EL for the crosses where this line was involved as a parent. In the cross-location combining ability analysis, none of the lines had significant GCA effects for ED and KPR. In contrast, Dagne (2008) and Demissew (2014) reported significant negative and positive GCA effects for EL, ED, and KPR.

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Table 9. Estimates of general combining ability (GCA) effect of lines and testers for phenological and yield-related traits in the combined analysis (Ambo, Arsi-Negele, and Kulumsa), 2017.

Code	DT	DS	EL	KPR	ED
L1	3.53*	3.11	-2.23	-4.32	-0.08
L2	1.86	2.28	-1.44	-3.41	-0.16
L3	0.70	0.11	-0.22	1.48	-0.33
L4	1.53	1.69	-2.34	-5.89	-0.02
L5	1.78	1.94	0.02	2.11	0.39
L6	-0.38	-0.47	2.02	1.97	-0.21
L7	-1.71	-2.22	1.49	4.27	-0.29
L8	-0.96	-1.31	1.27	4.36	-0.03
L9	-0.54	-0.47	2.62*	4.03	-0.23
L10	-0.88	-1.06	1.59	0.64	-0.24
L11	-2.04	-1.97	0.54	0.20	-0.24
L12	4.53**	3.36*	-1.34	0.09	0.22
L13	2.28	1.78	-1.59	-4.22	-0.17
L14	1.11	1.44	-1.23	-2.18	0.38
L15	-0.38	-0.47	-0.93	-0.89	0.16
L16	-5.38***	-4.13*	-0.29	-1.01	0.07
L17	-1.04	-1.47	0.42	0.22	0.27
L18	-2.38	-1.72	-0.51	1.25	0.10
L19	-2.96*	-2.72	1.85	1.06	0.03
L20	0.20	2.11	0.43	1.09	0.34
L21	1.11	0.19	-0.12	-0.86	0.02
SE (line)	1.42	1.59	1.24	2.75	0.20
SEd (gi-gj) line	2.01	2.24	1.76	2.52	0.28
T1	2.09	1.60	-0.49	-0.13	-0.14
T2	-2.09	-1.60	0.49	0.13	0.14
SE (tester)	2.21	3.60	2.05	0.13	0.29
SEd (gi-gj) tester	3.11	5.09	2.90	0.78	0.40

* = significant at 0.05 probability level, **= significant at 0.01 probability level, *** = significant at 0.001 probability level. DT= Days for Tasseling, DS= Days for Silking, EPP = Ear Per Plant, EL= Ear Length, KPR = Kernel Per Row, ED = Ear Diameter, TSW = Thousand Seed Weight.

3.3 Specific combining ability (SCA) effect

3.3.1 Specific combining ability (SCA) effects of crosses at the individual location

Specific combining ability is used to designate deviations of certain crosses from expectations based on the average performance (GCA effects) of the lines involved (Sprague and Tatum, 1942). SCA effect is also the basis for grouping germplasms into different heterotic groups, specifically combining ability (SCA) effects for grain yield (Gurung et al., 2009; Fan et al., 2009). Specific combining ability is controlled by non-additive gene action (Gowen, 1964; Kambal and Webster, 1965). Therefore, SCA is an important criterion in the evaluation of hybrids.

Estimates of SCA effects for GY and other agronomic traits for the hybrids computed for each location are presented in Tables 10, 11 and 12. In this study, all single crosses showed non-significant SCA effects for GY both in a negative and positive directions at Ambo and Arsi-Negele which is in line with the report made by Amare et al. (2016). Pavan et al. (2011) also reported a non-significant SCA effect on grain yield and yield-related traits. At Kulumsa, however, five crosses (L2xT1, L4xT2, L7xT1, L13xT2, and L19xT1) showed positive and significant SCA effects. Five other crosses (L2xT2, L4xT1, L7xT1, L13xT1, and L19xT1) showed negative and significant SCA effects. Other authors also reported significant positive and negative SCA effects for GY (Birhanu, 2009; Demissew, 2014). At Ambo the SCA effect for GY ranged from -1.37 (L2xT2) to 1.37 t ha⁻¹ (L2xT1), at Arsi-Negele ranged from -1.55 (L11xT1) to 1.55 t ha⁻¹ (L11xT2) and at Kulumsa between -1.89 (L2xT2) to 1.89 t ha⁻¹ (L2xT1) (Table 10, 11 and 12). The highest yielding cross (L7xT1) had the 3rd highest SCA effect (1.86 t ha⁻¹) after L2xT1 (1.89 t ha⁻¹) and L13xT2 (1.88 t ha⁻¹), respectively. The female parent of the cross L7xT1 showed positive and significant GCA at Kulumsa (data not shown), Ambo, and Arsi-Negele (Tables 7 and 8). This cross (L7xT1) had the highest GY not only at Kulumsa but also at Ambo and Arsi-Negele (data not shown). The crosses: L2xT1, L4xT2, L13xT2, and L19xT1 showed significant SCA effects but the female parents of these crosses showed negative and significant GCA effects at Kulumsa except, L19 which had positive and significant GCA effects (Table 8). Cross (L19 xT1) had higher GY at Kulumsa due to the positive and significant GCA effect of the female parent (Tables 8 and 11). L7xT1

exhibited the highest GY at Kulumsa due to the female parent's high GCA and its significant interaction effect with the tester which was manifested in a positive and significant SCA effect. This also indicates the increased concentration of favorable alleles from the parents. Vasal et al. (1992c) argued that positive SCA effects indicate that lines are in opposite heterotic groups while negative SCA effects indicate that lines are in the same heterotic group.

For MD, none of the crosses showed a significant SCA effect both in the positive and the negative direction. The value of the SCA effect ranged from -1.88 (L17xT2) to 1.88 days (L17xT1) at Arsi-Negele (Table 11).

Even though taller varieties are not desired in most cases due to their susceptibility to lodging and excessive vegetative growth, such types of hybrids are desirable in maize livestock mixed farming systems where the livestock mostly feed on crop residues after harvesting (Birhanu, 2009). But breeding programs should make an effort to reduce the ear placement and improve the feed quality of the hybrids. In this study, some crosses had negative and positive magnitude with significant SCA effects consistently for PH and EH. For EH, nine crosses at Ambo, seven crosses at Arsi-Negele, and one cross (L6xT2) at Kulumsa had negative value and significant SCA effect implying the lines and testers contributed less to EH increment. Similarly, nine crosses at Ambo, seven crosses at Arsi-Negele, and one (L6xT1) cross at Kulumsa had positive and significant SCA effects for EH. The SCA effect for EH ranged from -13.41 (L1xT1) to 13.41 cm (L1xT2) at Ambo, from -11.07 (L7xT2) to 11.07 cm (L7xT1) at Arsi-Negele and -14.44 (L6xT2) to 14.44 cm (L6xT1) at Kulumsa (Table 10,11, and 12). For PH, eight crosses at Ambo and five crosses at Arsi-Negele had negative and significant SCA effects indicating the parents had good synergy towards decreasing PH (Tables 10 and 11). Significant positive and negative SCA effects were reported from QPM crosses for PH (Birhanu, 2009; Demissew, 2014 Natol, 2017) but in contrast, Zakiullah et al. (2018) reported non-significant SCA effects in the positive and negative direction for PH. The value of the SCA effect varied between -22.36 cm (L4xT1) to 22.36 cm (L4xT2) at Ambo whereas, at Arsi-Negele, the value was between -13.17 cm (L7xT2) to 13.17 cm (L7xT1).

Table 10. Estimates of specific combining ability (SCA) effect of line x testers for traits at Ambo which are not included in the combined analysis in 2017.

Code	Ambo						Code	Ambo					
	GY	EH	PH	PAS	LL	LFPP		GY	EH	PH	PAS	LL	LFPP
L1xT1	-1.83	-13.41**	-28.11***	0.48	-7.07*	-0.05	L12xT1	0.59	9.58*	3.13	-0.39	1.92	0.04
L1xT2	1.83	13.41**	28.11***	-0.48	7.07*	0.05	L12xT2	-0.59	-9.58*	-3.13	0.39	-1.92	-0.04
L2xT1	1.37	6.08*	19.63**	-0.64	-2.16	1.20	L13xT1	-0.90	-5.67	-13.61**	0.36	1.42	-0.30
L2xT2	-1.37	-6.08*	-19.63***	0.64	2.16	-1.20	L13xT2	0.92	5.67	13.61**	-0.36	-1.42	0.30
L3xT1	-1.20	-9.16*	-6.87	0.11	-0.08	-0.88	L14xT1	-0.40	-3.67	-4.37	-0.14	-5.74*	0.20
L3xT2	1.20	9.16*	6.87	-0.11	0.08	0.88	L14xT2	0.41	3.67	4.37	0.14	5.74*	-0.20
L4xT1	-0.80	-10.66**	-22.36***	0.11	3.71	1.62*	L15xT1	1.09	-2.67	-6.12	-0.02	0.96	0.79
L4xT2	0.80	10.66**	22.36***	-0.11	-3.71	-1.62*	L15xT2	-1.09	2.67	6.12	0.02	-0.96	-0.79
L5xT1	0.00	2.83	9.13*	-0.27	5.54*	0.62	L16xT1	0.20	4.33	5.13	-0.02	7.12*	-0.13
L5xT2	0.00	-2.83	-9.13*	0.27	-5.54*	-0.62	L16xT2	-0.20	-4.33	-5.13	0.02	-7.12*	0.13
L6xT1	-0.02	0.83	5.38	0.23	-10.99**	-0.38	L17xT1	-0.52	6.83*	6.88	0.36	2.84	-1.05
L6xT2	0.02	-0.83	-5.38	-0.23	10.99**	0.38	L17xT2	0.52	-6.83*	-6.88	-0.36	-2.84	1.05
L7xT1	0.17	7.58*	13.63**	-0.14	-0.83	-0.55	L18xT1	1.88	9.33*	11.63*	-0.27	-7.74*	-1.05
L7xT2	-0.17	-7.58*	-13.63*	0.14	0.83	0.55	L18xT2	-1.88	-9.33*	-11.63*	0.27	7.74*	1.05
L8xT1	-0.53	-2.67	1.88	0.11	-0.33	-0.80	L19xT1	0.00	0.83	1.88	0.11	-1.20	-0.55
L8xT2	0.53	2.67	-1.88	-0.11	0.33	0.80	L19xT2	0.00	-0.83	-1.88	-0.11	1.20	0.55
L9xT1	0.80	-4.67	-4.12	-0.39	2.34	1.37	L20xT1	0.43	5.08	10.38*	0.11	4.67	0.54
L9xT2	-0.80	4.67	4.12	0.39	-2.34	-1.37	L20xT2	-0.43	-5.08	-10.38*	-0.11	-4.67	-0.54
L10xT1	-0.17	-5.67	-1.87	0.11	5.67*	-0.38	L21xT1	0.14	6.83*	0.63	-0.02	-2.00	0.04
L10xT2	0.17	5.67	1.87	-0.11	-5.67*	0.38	L21xT2	-0.14	-6.83*	-0.63	0.02	2.00	-0.04
L11xT1	-0.25	-1.92	-1.87	0.23	1.96	-0.30	SE (LxT)	0.60	4.52	6.02	0.19	4.56	0.71
L11xT2	0.25	1.92	1.87	-0.23	-1.96	0.30	SEd (Sji-Skl)	0.84	6.39	8.51	0.26	6.45	1.00

At Ambo no crosses showed a significant SCA effect for PAS in the negative and positive directions (Table 10). For PAS, EAS, MOD, and disease parameters, a negative SCA effect is desirable. Only one cross (L2xT1) had a negative and significant ($P < 0.05$) SCA effect for CLR with the magnitude of -0.92 at Kulumsa. There were also other crosses that showed a negative SCA effect indicating that LxT interaction makes good synergy to reacting with this disease or may it cause suppression of deleterious genes (Table 12). Birhanu (2009) also reported significant negative and positive SCA for CLR.

For BIOM, none of the crosses showed a significant SCA effect neither in the negative nor in the positive direction at Arsi-Negele and Kulumsa. In contrast to this result, Shushay (2014) and Abiy (2017) reported a relatively high number of crosses with significant positive and negative SCA effects for BIOM. For HI, all crosses showed a non-significant SCA effect at Arsi-Negele in both directions (positive and negative). Relatively high SCA effect was obtained from L9xT1 (10.83 %), L10xT2 (17.42 %), and L11xT2 (15.62%) in magnitude even if the SCA effects of each cross were non-significant. These crosses had an intermediate performance for GY indicating the crosses were relatively good in converting biomass into the GY (Table 11). In contrast to the result of this study, Birhanu (2009) and Abiy (2017) reported a high number of crosses that showed significant and positive SCA effects for hybrids adapted to mid-altitude and highland areas, respectively.

For LANG, none of the crosses showed a significant SCA effect at Kulumsa (Table 12). The negative SCA effect is desirable for LANG because it can help to narrow the leaf angle. While the leaf angle becomes narrow, it can help to expose the leaves found on the lower side of the plant to the sunlight and this photosynthesis can improve the performance of the plant in converting inputs into the final sinks. The size and distribution of leaf area determine light interception in a crop canopy and influence overall photosynthesis and yield increase up to 5% due to the consequence of improved plant architecture in the top and middle canopy layers (Huang *et al.*, 2017). For LFPP, the SCA effect was non-significant by the crosses to the negative and positive direction at Ambo and Kulumsa (Tables 10 and 12). Similarly, for LFBE, the SCA effect was non-significant in both directions at Kulumsa (Table 12). For LFAR, only one cross (L13xT2) had a positive and significant SCA effect implying that the parents were complementing each other to increase leaf area. The value of SCA effect ranged

from -113.60 cm^2 (L13xT1) to 113.60 cm^2 (L13xT2) (Table 12). Regarding this trait, Birhanu (2009) reported a relatively high number of single crosses that showed a significant negative and positive SCA effects. Similar to the result of this study, Zakiullah *et al.* (2018) reported a non-significant SCA effect from crosses formed using the diallel method.

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Table 11. Estimates of specific combining ability (SCA) effect of line x testers for traits at Arsi-Negele which are not included in the combined analysis in 2017.

Code	Arsi-Negele						Code	Arsi-Negele					
	GY	MD	EH	PH	BIOM	HI		GY	MD	EH	PH	BIOM	HI
L1xT1	-0.96	-0.37	-8.67*	-15.07**	-1.56	0.42	L12xT1	0.28	0.13	5.32	-1.83	-0.38	6.75
L1xT2	0.96	0.37	8.67*	15.07**	1.56	-0.42	L12xT2	-0.28	-0.13	-5.32	1.83	0.38	-6.75
L2xT1	0.70	0.38	-4.18	1.92	0.39	6.81	L13xT1	-0.49	0.13	-5.43	-11.82**	-0.59	-1.67
L2xT2	-0.70	-0.38	4.18	-1.92	-0.39	-6.81	L13xT2	0.49	-0.13	5.43	11.82**	0.59	1.67
L3xT1	0.09	-1.37	-6.42*	-7.33	-0.55	7.08	L14xT1	0.75	-0.62	3.57	9.17*	0.51	4.87
L3xT2	-0.09	1.37	6.42*	7.33	0.55	-7.08	L14xT2	-0.75	0.62	-3.57	(-9.17*	-0.51	-4.87
L4xT1	-0.73	0.13	-0.67	-4.33	-0.75	-2.89	L15xT1	-0.80	-0.12	-6.67*	-7.33	-0.91	-2.74
L4xT2	0.73	-0.13	0.68	4.33	0.75	2.89	L15xT2	0.80	0.12	6.67*	7.33	0.91	2.74
L5xT1	0.59	0.88	-0.68	-0.33	0.18	6.85	L16xT1	0.66	1.63	10.07**	12.92**	0.02	7.61
L5xT2	-0.59	-0.88	0.68	0.33	-0.18	-6.85	L16xT2	-0.66	-1.63	-10.07**	-12.92**	-0.02	-7.61
L6xT1	-0.65	-0.37	-1.68	4.92	-0.41	-3.84	L17xT1	0.09	1.88	4.82	6.17	-0.36	4.61
L6xT2	0.65	0.37	1.68	-4.92	0.41	3.84	L17xT2	-0.09	-1.88	-4.82	-6.17	0.36	-4.61
L7xT1	0.97	0.88	11.07**	13.17**	1.51	-3.53	L18xT1	0.47	-1.37	4.57	3.67	1.48	-7.48
L7xT2	-0.97	-0.88	-11.07**	-13.17**	-1.51	3.53	L18xT2	-0.47	1.37	-4.57	-3.67	-1.48	7.48
L8xT1	0.11	-0.37	-1.17	3.67	0.55	-2.66	L19xT1	0.91	1.13	1.57	-2.08	0.98	1.23
L8xT2	-0.11	0.37	1.18	-3.67	-0.55	2.66	L19xT2	-0.91	-1.13	-1.57	2.08	-0.98	-1.23
L9xT1	-0.29	0.38	-0.68	-1.58	-1.51	10.83	L20xT1	0.86	0.13	6.07*	6.32	1.07	-0.26
L9xT2	0.29	-0.38	0.68	1.58	1.51	-10.83	L20xT2	-0.86	-0.13	-6.07*	-6.32	-1.07	0.26
L10xT1	-0.88	-1.87	-6.17*	-4.08	1.04	-17.42	L21xT1	-0.14	-0.87	-0.18	-1.83	-0.23	1.06
L10xT2	0.88	1.87	6.17*	4.08	-1.04	17.42	L21xT2	0.14	0.87	0.18	1.83	0.23	-1.06
L11xT1	-1.55	-0.37	-4.43	-4.33	-0.48	-15.62	SE (LxT)	0.69	0.79	4.58	6.00	0.92	7.25
L11xT2	1.55	0.37	4.43	4.33	0.48	15.62	SEd (Sji-Skl)	0.84	1.49	6.60	8.09	1.44	10.25

Table 12 Estimates of specific combining ability (SCA) effect of line x testers for traits at Kulumsa which are not included in the combined analysis in 2017.

Code	Kulumsa									
	GY	EH	CLR	BIOM	LANG	LL	LW	LFAR	LFPP	LFBE
L1xT1	-1.32	-5.56	0.20	-2.98	-1.43	-5.50	-0.33	-68.87	-0.23	-0.27
L1xT2	1.32	5.56	-0.20	2.98	1.43	5.50	0.33	68.87	0.23	0.27
L2xT1	1.89**	-12.06	-0.92*	4.02	-2.26	8.32*	0.51	101.69	-0.81	-0.60
L2xT2	-1.89**	12.06	0.92*	-4.02	2.26	-8.32*	-0.51	-101.69	0.81	0.60
L3xT1	-0.97	-5.31	-0.05	-0.95	-0.60	-1.84	0.59	24.38	-0.15	-0.10
L3xT2	0.97	5.31	0.05	0.95	0.60	1.84	-0.59	-24.38	0.15	0.10
L4xT1	-1.49*	-3.06	0.20	-1.08	2.74	-3.84	-0.58	-69.71	-0.06	0.06
L4xT2	1.49*	3.06	-0.20	1.08	-2.74	3.84	0.58	69.71	0.06	-0.06
L5xT1	0.47	0.19	-0.30	1.75	-1.85	3.91	0.59	74.34	-0.56	-0.35
L5xT2	-0.47	-0.19	0.30	-1.75	1.85	-3.91	-0.59	-74.34	0.56	0.35
L6xT1	-0.35	14.44*	0.08	2.75	3.15	-1.50	0.01	-9.52	0.19	0.15
L6xT2	0.35	-14.44*	-0.08	-2.75	-3.15	1.50	-0.01	9.52	-0.19	-0.15
L7xT1	1.86**	8.94	-0.42	2.13	3.57	2.41	0.01	20.86	0.60	0.23
L7xT2	-1.86**	-8.94	0.42	-2.13	-3.57	-2.41	-0.01	-20.86	-0.60	-0.23
L8xT1	0.02	2.69	0.08	1.34	1.07	3.58	-0.08	26.04	0.60	0.40
L8xT2	-0.02	-2.69	-0.08	-1.34	-1.07	-3.58	0.08	-26.04	-0.60	-0.40
L9xT1	-0.68	-2.31	0.58	-1.21	2.74	-1.50	0.01	-11.79	-0.23	-0.44
L9xT2	0.68	2.31	-0.58	1.21	-2.74	1.50	-0.01	11.79	0.23	0.44
L10xT1	-0.11	-1.56	0.45	-0.15	-1.01	0.75	-0.58	-29.23	0.02	-0.27
L10xT2	0.11	1.56	-0.45	0.15	1.01	-0.75	0.58	29.23	-0.02	0.27
L11xT1	0.04	-4.81	-0.05	0.71	0.24	-0.50	-0.49	-34.73	0.60	0.23
L11xT2	-0.04	4.81	0.05	-0.71	-0.24	0.50	0.49	34.73	-0.60	-0.23
L12xT1	-0.30	5.69	-0.55	-0.61	1.07	-0.59	-0.16	-14.91	-0.73	-0.52
L12xT2	0.30	-5.69	0.55	0.61	-1.07	0.59	0.16	14.91	0.73	0.52

Table 12 (Continued)

Code	Kulumsa									
	GY	EH	CLR	BIOM	LANG	LL	LW	LFAR	LFPP	LFBE
L13xT1	-1.88**	-3.56	0.33	-2.33	3.15	-8.67**	-0.58	-113.60*	-0.65	-0.35
L13xT2	1.88**	3.56	-0.33	2.33	-3.15	8.67**	0.58	113.60*	0.65	0.35
L14xT1	0.08	-0.56	0.58	-2.94	-4.76	4.83	0.67	81.38	0.44	0.23
L14xT2	-0.08	0.56	-0.58	2.94	4.76	-4.83	-0.67	-81.38	-0.44	-0.23
L15xT1	-0.35	-2.31	0.58	-2.30	-1.85	-5.25	-0.33	-67.85	0.02	0.40
L15xT2	0.35	2.31	-0.58	2.30	1.85	5.25	0.33	67.85	-0.02	-0.40
L16xT1	0.40	12.19	-0.30	-2.21	-1.43	0.66	0.09	11.27	0.52	0.40
L16xT2	-0.40	-12.19	0.30	2.21	1.43	-0.66	-0.09	-11.27	-0.52	-0.40
L17xT1	1.13	7.94	-0.05	3.07	-1.43	1.16	0.42	34.86	0.19	0.31
L17xT2	-1.13	-7.94	0.05	-3.07	1.43	-1.16	-0.42	-34.86	-0.19	-0.31
L18xT1	-0.09	-10.56	-0.05	2.58	1.49	-3.84	0.34	-11.89	0.60	0.56
L18xT2	0.09	10.56	0.05	-2.58	-1.49	3.84	-0.34	11.89	-0.60	-0.56
L19xT1	1.41*	-0.81	0.08	-0.68	-0.60	4.58	0.46	71.38	-0.06	0.31
L19xT2	-1.41*	0.81	-0.08	0.68	0.60	-4.58	-0.46	-71.38	0.06	-0.31
L20xT1	0.48	-0.06	-0.05	-0.14	0.65	1.08	-0.41	-16.35	0.02	-0.19
L20xT2	-0.48	0.06	0.05	0.14	-0.65	-1.08	0.41	16.35	-0.02	0.19
L21xT1	-0.24	0.44	-0.42	-0.80	-2.68	1.75	-0.16	2.23	-0.31	-0.19
L21xT2	0.24	-0.44	0.42	0.80	2.68	-1.75	0.16	-2.23	0.31	0.19
SE (LxT)	0.69	6.44	0.39	1.90	1.78	3.13	0.41	42.60	0.45	0.35
SEd (Sji-Skl)	0.98	9.11	0.54	2.69	2.51	4.43	0.58	60.24	0.63	0.49

3.3.2. Specific combining ability (SCA) effects of crosses across locations

Estimates of specific combining ability (SCA) effects for traits included in the combined analysis of the hybrids trial are presented in Table 13. For EPP, all crosses showed non-significant SCA effects, indicating the lines and the testers were not good at complementing each other to produce good heterosis by their crosses to the possible high number of ears per plant. Other authors also reported significant positive and negative SCA effects (Birhanu, 2009; Beyene 2016) for maize hybrids adapted to mid-altitude areas. Demissew (2014) also reported similar results for highland QPM materials.

L2xT1 had a negative and highly significant SCA effect ($P < 0.01$ or $P < 0.05$) for both DT and DS (Table 13) indicating female and male parents complemented each other to generate crosses with early flowering. But this cross performance had low GY at all locations. On the contrary, L2xT2 had a positive and significant SCA effect for both DT and DS which indicates that this cross was characterized by late flowering (Table 13). Compared to the previous studies (Amare et al., 2016 and Beyene, 2016) the number of crosses showed that significant SCA effects in this study were fewer in number.

For EL, none of the crosses showed a significant SCA effect in the positive and negative directions but the magnitude of the SCA effect is varied for each cross. Similarly, Natol (2017) reported a non-significant SCA effect from single crosses but in contrast, Shah *et al.* (2015) reported a significant SCA effect for this trait. The positive SCA effect is desirable for EL. Even though cross (L2xT1) had a high SCA effect (1.37 cm), it was non-significant. The same cross showed a positive and significant ($P < 0.01$ or $P < 0.05$) SCA effect for ED and TSW with the highest SCA effect in the magnitude of 0.42 cm and 77.56 g, respectively (Table 13). L8xT2 had high GY and showed a positive SCA effect at three locations. But the effect was not significant for EL and ED. The high yielding cross (L8xT2) had a negative and non-significant SCA effect on TSW. Likewise, Birhanu (2009) and Demissew (2014) reported a higher number of lines that had positive and negative SCA effects for GY-related traits. Natol (2017) found a high number of crosses with a significant SCA effect for TSW.

Table 13. Estimates of specific combining ability (SCA) effects for phenological and yield-related traits in the combined analysis of 42-line x tester cross-tested across three locations (Ambo, Arsi-Negele, and Kulumsa) in 2017.

Code	DT	DS	EPP	EL	ED	TSW	Code	DT	DS	EPP	EL	ED	TSW
L1xT1	1.24	1.65	-0.08	-1.01	-0.22	-22.43	L12xT1	-0.09	-0.27	0.05	0.08	-0.06	5.10
L1xT2	-1.24	-1.65	0.08	1.01	0.22	22.43	L12xT2	0.09	0.27	-0.05	-0.08	0.06	-5.10
L2xT1	-5.09**	-4.18*	-0.23	1.37	0.42**	77.56**	L13xT1	1.49	1.82	-0.12	-0.54	-0.10	-21.13
L2xT2	5.09**	4.18*	0.23	-1.37	-0.42**	-77.56**	L13xT2	-1.49	-1.82	0.12	0.54	0.10	21.13
L3xT1	0.07	0.32	0.07	-0.69	-0.09	-14.17	L14xT1	0.15	-0.35	0.17	0.44	0.08	-5.28
L3xT2	-0.07	-0.32	-0.07	0.69	0.09	14.17	L14xT2	-0.15	0.35	-0.17	-0.44	-0.08	5.28
L4xT1	1.24	1.57	0.02	-0.56	-0.16	-19.53	L15xT1	-0.34	-0.10	0.08	-1.20	0.02	-11.83
L4xT2	-1.24	-1.57	-0.02	0.56	0.16	19.53	L15xT2	0.34	0.10	-0.08	1.20	-0.02	11.83
L5xT1	-0.01	0.48	-0.03	-0.09	-0.02	-0.37	L16xT1	0.15	-0.10	0.14	0.38	0.16	5.91
L5xT2	0.01	-0.48	0.03	0.09	0.02	0.37	L16xT2	-0.15	0.10	-0.14	-0.38	-0.16	-5.91
L6xT1	-0.67	-1.10	-0.05	1.02	0.06	7.64	L17xT1	0.65	0.40	0.00	0.17	-0.18	-26.54
L6xT2	0.67	1.10	0.05	-1.02	-0.06	-7.64	L17xT2	-0.65	-0.40	0.00	-0.17	0.18	26.54
L7xT1	0.15	0.65	-0.02	1.27	0.14	-9.28	L18xT1	-1.67	-1.85	0.09	0.83	0.08	18.82
L7xT2	-0.15	-0.65	0.02	-1.27	-0.14	9.28	L18xT2	1.67	1.85	-0.09	-0.83	-0.08	-18.82
L8xT1	0.07	0.07	-0.16	-0.29	-0.05	2.03	L19xT1	0.57	0.32	0.15	-0.59	0.02	10.39
L8xT2	-0.07	-0.07	0.16	0.29	0.05	-2.03	L19xT2	-0.57	-0.32	-0.15	0.59	-0.02	-10.39
L9xT1	0.49	-0.27	-0.01	-0.04	-0.05	0.35	L20xT1	-0.42	-0.35	-0.06	0.08	0.10	16.69
L9xT2	-0.49	0.27	0.01	0.04	0.05	-0.35	L20xT2	0.42	0.35	0.06	-0.08	-0.10	-16.69
L10xT1	0.99	1.15	-0.09	0.89	-0.03	5.09	L21xT1	-0.01	-0.93	0.06	-0.90	-0.02	-19.70
L10xT2	-0.99	-1.15	0.09	-0.89	0.03	-5.09	L21xT2	0.01	0.93	-0.06	0.90	0.02	19.70
L11xT1	0.99	1.07	0.02	-0.62	-0.09	0.68	SE (LxT)	1.70	1.67	0.14	1.19	0.16	22.30
L11xT2	-0.99	-1.07	-0.02	0.62	0.09	-0.68	SEd (Sji-Skl)	2.40	2.37	0.20	1.68	0.22	31.54

Conclusion

In the combined ANOVA over the three locations, MS due to GCA of lines and SCA (LxT interaction) were significant for DT, DS, EL, and ED. This indicates that both additive and non-additive genetic variances were important in the control of these traits. However, the proportion of GCA sum of squares was higher than that of SCA for all traits indicating the preponderance of additive gene action controlling these traits. For EPP and TSW even if the MS of SCA was significant and the GCA of the line was non-significant, the proportion sum squares of GCA was higher than SCA meaning that the additive gene effect also played a role in addition to the non-additive for the inheritance. For KPR, only MS of line GCA was significant. MS due to GCA of testers was significant for DT, DS, EPP, EL, ED, and TSW. For GY, LxT (SCA) MS was significant at three locations whereas line GCA MS was significant at Ambo and Arsi-Negele. While considering testers' GCA MS, it was non-significant at the three locations for GY. Generally, based on the sum square contribution of GCA, yield and yield-related traits inheritance were controlled by additive gene action.

The combining ability analysis showed that L7 and L8 were good general combiners for grain yield at all three locations consistently. For days to anthesis and silking L16 was the best general combiner followed by L19. Also, they have significant negative GCA indicating that these lines have favorable allele frequency for early maturity. Across locations, L16 and L19 for DT, L16 for DS, L9 for EL, L7, and L8 for KPR, and L16 and L17 for TSW were the best general combiner. Based on mean grain yield performance and combining ability, L8xT2, L7 xT1, L8 xT1, L19xT1, L6 xT2, and L18 xT1 were promising crosses that should be advanced for further evaluation in the maize breeding program.

This study also identified inbred lines with good GCA and cross combinations with desirable SCA for important traits. This indicates the possibility of developing desirable cross combinations and synthetic varieties through the crossing of the inbred lines with desirable traits of interest. Furthermore, promising cross combinations identified in this study could be utilized for future breeding work as well as for direct release after rigorous testing in multilocation trials. The information provided in this study can be useful for the researchers to develop high-yielding hybrids and/ or synthetic varieties.

Declarations

Ethics approval and consent to participate

The researchers have obtained permission from funding institutions CIMMYT and EIAR. Accordingly, the information under this article had been developed in collaboration with CIMMYT, Ethiopian Institute of agriculture research investigators, and university instructors.

Consent for publication

Consent for publication – all authors have read and approved the publication of this paper.

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