Standard heterosis estimation for quality protein maize hybrids over best released and commercialized hybrids

Abstract

Maize plays an indispensable role in meeting high food demand. It is globally one of the most widely adopted and cultivated crops. Hybrid development from fixed inbred lines is one of the tactics to boost maize production. The national average maize yield in Ethiopia is low and thus, selection of promising germplasm, knowledge of combining ability, and heterotic grouping 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 hybrid checks were evaluated in two replications using alpha lattice during the 2017 cropping season at Ambo, Arsi-Negele, and Kulumsa. The objective of this study was to estimate standard heterosis for grain yield, other agronomic and morphological characters. 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. For GY, at Ambo, almost all crosses showed negative heterosis against the best check (AMH853) At Arsi-Negele 14 crosses had positive standard heterosis, from these only three crosses: L8xT1(50.8%), L8xT2 (46.6%), and L7xT1 (33.9%) showed significant difference against Jibat but at Kulumsa, the difference for standard heterosis was positive but non-significant only by two crosses: (L7xT1 (6.6%) and L19xT1 (4.7%). Based on mean grain yield and standard heterosis, L8xT2, L7xT1, L8xT1, L19xT1, L6xT2, and L18xT1 are promising. The study of the results highlighted that the breeding program was successful in generating QPM hybrids. Based on the finding we suggest that it is better to use the parents of theses hybrids s potential source materials in the breeding program for future work in the breeding program through involving them in different crosses formation.

Keywords: *cross, inbred lines, heterosis*

1. Introduction

The phenomenon of heterosis was defined by Shull (1952) as “the interpretation of increased

vigor, size, fruitfulness, speed of development, resistance to disease and to insect pests, or to climatic rigors of any kind manifested by crossbred organisms as compared with corresponding inbreeds, as the specific results of unlikeness in the constitution of the uniting parental gametes". Falconer and Mackay (1996) defined as the difference between the hybrid value for one trait and the mean value of the two parents for the same trait. According to Miranda (1999), heterosis is the genetic potential expression of the superiority of a cross in relation to its parents.

Three types of estimation of heterosis are explained in the literature; namely, mid-parent or average heterosis, which is the increased vigor of the F1 over the mean of two parents; and high-parent or better-parent heterosis, which is the increased vigor of the F1 over the better-parent (Jinks, 1983) and standard heterosis (Berhanu,2009; Beyene, 2016 and Abiy, 2017). Heterosis is usually considered to be similar with hybrid vigor (Stuber, 1994). Heterosis, or hybrid vigor, refers to the phenomena in which the offspring of two inbred parents exhibit phenotypic performance beyond the mid-parent or better-parent used to generate the hybrid (Li *et al.*, 2018). Grain yield in maize is expected to exhibit heterosis as a consequence of partial to complete dominance of genes controlling the trait (Miranda, 1999).

Maize breeders need also to determine the genetic diversity of inbreeds because it facilitates the identification of those that would produce crosses possessing high levels of heterosis (Badu-Apraku et al., 2013). The information facilitates the development of high-yielding hybrids without testing all possible hybrid combinations among the potential parents available in a hybrid program. Three major dominance theories, such as dominance, overdominance, and epistasis, as the main theories, to explain mechanisms underlying the phenomena of heterosis. However, it is generally accepted that heterosis, to a large extent, is due to over-dominance gene action (Singh, 2005). On the other hand, the expression of heterosis also depends on the level of genetic divergence between parents; i.e., differences in allele frequencies are necessary for the expression of heterosis. For that reason, expression of heterosis is expected to be lower in crosses between broad base open-pollinated populations (Miranda, 1999).

Heterosis is important in maize breeding and is dependent on the level of dominance and

differences in gene frequency (Falconer & Mackay,1996). The manifestation of heterosis depends on the genetic divergence of the two parental varieties (Hallauer; Miranda, 1988). Low grain yield heterosis is observed for crosses among genetically similar germplasm and for crosses among broad genetic base germplasm (Vasal*et al.*, 1993). Higher levels of heterosis were seen with increased divergence within a certain range, but that heterosis declined in extremely divergent crosses (Prasad and Singh, 1986). Genetic divergence of the parents is inferred from the heterotic patterns manifested in a series of crosses (Hallauer and Miranda, 1988; Miranda, 1999).

Heterosis in maize has been investigated extensively. Hallauer and Miranda (1988) reported the mid-parent heterosis ranged from -3.6% to 72.0% while high-parent heterosis ranged from -9.9% to 43.0% for maize. Maize has attained the highest levels of production in the temperate areas of the world employing modern agricultural techniques. Surprisingly, the magnitude of heterosis has not been changed during the hybrid era in the tropical areas as compared to with temperate because, in most of the tropical country's maize is grown as a rainfed crop in the hot season, under varying conditions of moisture, generally subject to periodic and erratic drought and/or excess of water at different stages of the growth cycle, without effective weed and pest control, and usually under low-fertility conditions. In general, it is grown as a subsistence crop, with very low levels of management and little inputs (Duvick, 1999), even though mean commercial maize grain yield has substantially increased during this time (Troyer, 1990). Berhanu (2009) reported estimate of heterosis ranged from 28.95 to 202.34% over mid-parent and 16.97 to 175.46 % over the better-parent for grain yield from crosses generated from LxT mating design.

The development of hybrid varieties played a great role in improving food and feed supplies. Food and feed supplies would unquestionably be greatly reduced if only non-hybrids were available to the producer (Stuber, 1994). Hybrid varieties are the first filial generations (F1) from crosses between two or more pure lines, inbreeds, open-pollinated varieties, clones or other populations that are genetically dissimilar (Singh, 2005). The development of maize hybrid began in the early 1900s (Shull,1908; East, 1908; Hallauer*et al.*, 1988; Smith *et al.*, 2017). According to Singh (2005), most of the commercial hybrid varieties are F1's from two or more inbreeds. The success of hybrid maize development depends on the capacity of the

breeding program to rapidly develop lines that combine well and identify the superior heterotic combinations to maximize the vigor of the hybrid (Kim and Ajala, 1996). An inbred is a nearly homozygous line obtained through continuous inbreeding of cross-pollinated species with selection accompanying inbreeding (Singh, 2005).

Similar to the CM, QPM hybrids proved to yield more grain than open-pollinated QPM cultivars, but mean grain yield does not differ for a single, three-way, and double-cross QPM hybrids (Pixley and Bjarnason, 2002). The broader genetic constitution of three-way and double-cross hybrids might have helped them to buffer the extreme environmental diversity of the environment better than single crosses (Pixley and Bjarnason, 2002). In a different trial, Pixley and Bjarnason (1993) also observed a QPM hybrid exceeding a normal endosperm hybrid check by an average of 14% for grain yield, 48% for Trp concentration in grain, and 60% for Trp concentration in protein. Berhanu (2009) evaluated tester crosses of white QPM and CM inbred lines and reported higher grain yield heterosis overall mid and better parents and some of the crosses over the standard checks. Similarly, Beyene (2016) reported higher heterosis from diallel crosses evaluated at Bako, Ethiopia. This study aimed to estimate the standard or economic heterosis of the crosses over the standard checks.

2. Materials and methods

2.1. Study sites

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

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

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

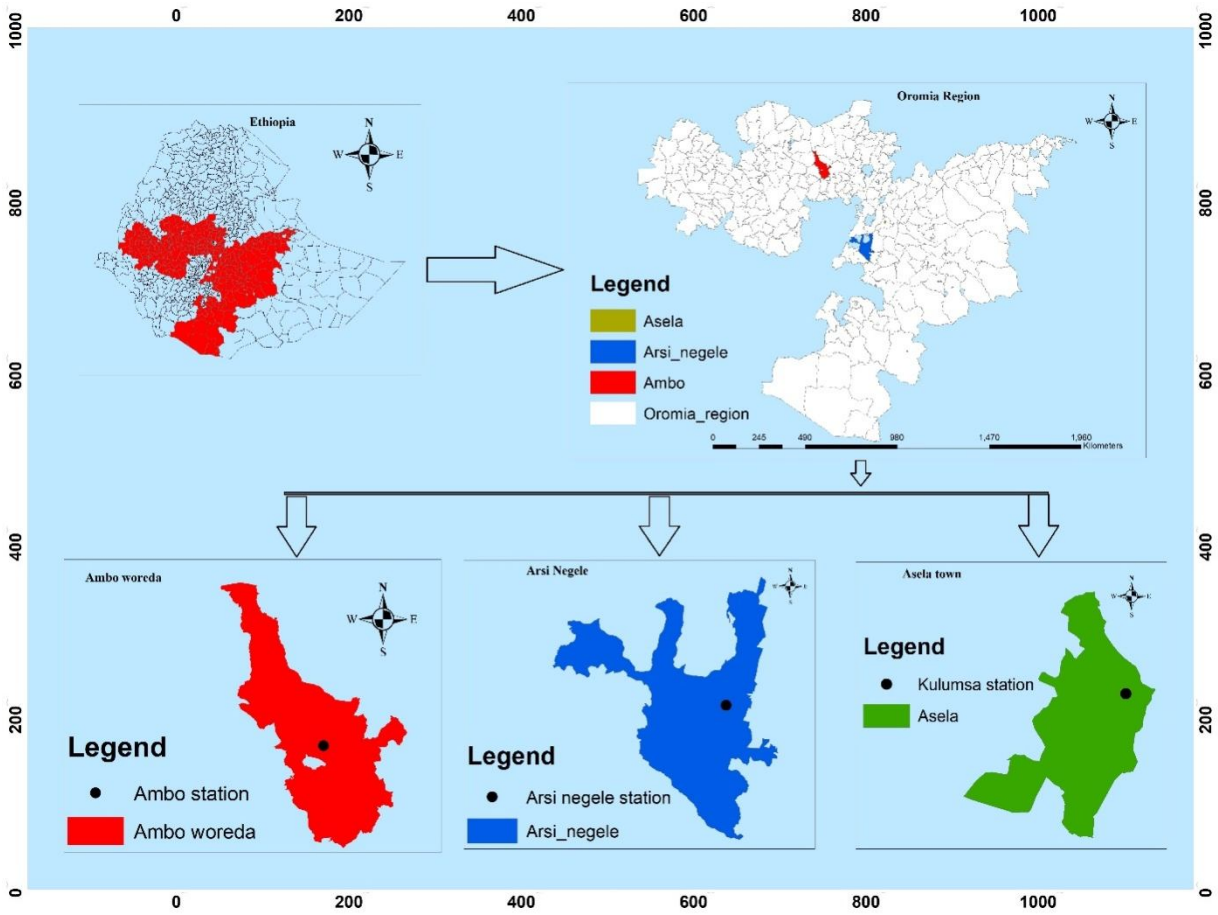

Figure 1 map of the study area

2.2. Experimental materials

From the 21 inbred lines and the two testers 42 F1 hybrids were generated at Ambo Highland Maize Breeding Program (AHMBP). The 42 F1 hybrids along with three standard checks: one QPM (AMH852Q) and two CM (Jibat and AMH853), designated as hybrid check, were tested. Each new hybrids and standard check hybrids were planted in three replication and tested at three locations during 2017 main cropping season. Each cross planted in one row plot with 0.25 and 0.75 m spacing between plants and rows, respectively which consisted of 21 plants per plot.

2.3 Statistical Analysis

Standard heterosis (STH) or economic heterosis in percent were calculated for those parameters that showed significant differences among crosses following the method suggested by Falconer and Mackay (1996).

Standard heterosis (SH), was estimated for traits that showed significant MS for cross vs best check at individual locations. In order to consider traits for combined analysis, cross x location for MPH and MPH whereas to estimate SH, genotype x location interaction should be non-significant as additional criterion. For SH, the traits which had significant check x location interaction, SH was conducted for each location.

$$\text{Standard heterosis (SH)} = \frac{F1-STV}{STV} \times 100$$ according to Berhanu (2009).

Where, F1= mean value of the cross, STV = value of the highest yielding standard variety

Test of significance of heterosis (the numerator in each equation before multiplying by 100) was determined using the t-test. The critical difference (CD) for testing the significance of SH was calculated using the following formulas:

Critical difference for heterosis over standard heterosis (SH)

$$\text{CD for SH} = \sqrt{2MSe/r} \times t$$

Where MSe is error MS, r is the number of replication and t is the Table value at 0.05, 0.01and 0.001, CD is Critical Difference, SH is standard heterosis, t -value in the formula is not included in square root. The absolute values of the relevant heterosis were tested against this critical difference.

3. Result and discussion

Analysis of Variance (ANOVA) for the hybrid trial showed a significant genotypic difference for Grain Yield (GY), Days to Tasseling (DT), Day to Silking, (DS) Plant Height (PH), Ear Height (EH), Ear Per Plant (EPP), Ear Length (EL), Kernel Per Row (KPR), Ear Diameter (ED), Thousand Seed Weight (TSW) and Biomass yield (BIOM) at each of the three locations (Table 2, 3 and 4). A similar result was also reported by (Berhanu, 2009). The genotypic difference for Gray Leaf Spot (GLS) and Leaf above uppermost Ear (LFAE) was not significant in any of the three locations. Variances due to genotype were significant only at Kulumsa for Common Leaf Rust (CLR), Leaf Angle (LANG), and Leaf Area (LFAR), while for Turcicum Leaf Blight (TLB) and Harvest Index (HI) these differences were significant only at Arsi-Negele. For Anthesis Silking Interval (ASI), Kernel Modification (MOD), Plant Aspect (PAS), and Number of Kernel Rows ear^{-1} (NKR) difference between the crosses was significant only at Ambo (Table 2). For days to maturity (MD), leaves per plant (LFPP) and leaves below the uppermost ear (LFBE) these differences were significant at two of the three locations.

Table 2. General ANOVA for grain yield and other agronomic traits of maize hybrids and lines evaluated at Ambo Agricultural Research Center, 2017.

Ambo	Mean Square										
Source of Variation	DF	GY	DT	DS	ASI	MD	PH	EH	Mod	GLS	CLR
Rep with cross	1.00	7.72**	0.43	0.19	0.05	3.86	786.29**	340.01**	1.86**	0.00	0.00
Genotype	44	5.36***	28.67***	24.38***	0.008***	3.48*	1324.9***	614.86***	0.61***	0.00	0.00
Cross	41.00	4.90***	22.97***	15.98***	4.94***	3.60*	1276.53***	606.06***	0.48*	0.00	0.00
Cross vs Checks	1.00	14.54***	201.60***	254.25***	3.05	0.26	18.57	200.80*	9.52***	0.00	0.00
Cross vs best check	1.00	20.15***	188.89***	191.64***	0.01	0.59	1978.12***	1285.72***	2.16**	0.00	0.00
Error Cross	41.00	0.71	2.92	3.17	1.44	1.83	72.40	40.84	0.24	0.00	0.00
Source of Variation	DF	TLB	EAS	PAS	EPP	EL	NKR	KPR	ED	TSW	
Rep with cross	1.00	0.00	1.31**	0.76**	0.31*	9.56	1.19	26.86	0.03	8893.28**	
Genotype	44	0.04	0.40***	0.33***	0.16**	10.37***	2.43*	34.44***	0.23***	6119.3***	
Cross	41.00	0.05	0.40***	0.34***	0.16***	9.59***	2.19	35.77**	0.24***	6373.16***	
Cross vs Checks	1.00	0.03	0.69 *	0.81**	0.278*	5.46	31.11***	35.50	0.35**	18679.10***	
Cross vs best check	1.00	0.01	0.91**	0.28	0.07	11.04	2.05	14.88	0.00	1699.22	
Error Cross	41.00	0.05	0.11	0.07	0.07	3.20	1.39	13.33	0.04	1168.31	
Source of Variation	DF	BIOM	HI	LANG	LL	LW	LFAR	LFPP	LFAE	LFBE	
Rep with cross	1.00	73.90*	2682.96***	28.58	10.71	1.11	12033.58	31.77***	0.11	38.67***	
Genotype	44	24.06*	196.57	12.45	70.53	0.60	9910.92	2.78***	0.46	1.82***	
Cross	41.00	21.75**	209.51	12.73	71.28**	0.59	9848.86	2.92***	0.47*	1.84***	
Cross vs Checks	1.00	94.74**	105.55	114.00**	1264.0***	0.01	96670.47***	0.00	7.36***	9.26***	
Cross vs best check	1.00	126.39**	43.23	11.56	1.44	0.02	562.60	0.11	0.82	0.40	
Error Cross	41.00	14.17	192.14	10.98	41.54	0.72	11302.14	1.01	0.37	0.59	

= significant at 0.05 probability level, **= significant at 0.01probabilty level and * = significant at 0.001probabilty level, DF = Degree of freedom, GxL= Genotype by location interaction, 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), GLS = Gray Leaf Spot (1-5 scoring), CLR = Common Leaf Rust (1-5 scoring), TLB = Turcicum Leaf Blight (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), HI = Harvest Index (%), 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 bellow upper most ear (number).*

Table 3 General ANOVA for grain yield and other agronomic traits of maize hybrids and lines evaluated at Arsi-Negele Agricultural Research Center, 2017.

Arsi-Negele	Mean Square									
Source of Variation	DF	GY	DT	DS	ASI	MD	PH	EH	Mod	GLS	CLR
Rep with cross	1	9.51**	36.01*	33.44	0.05	20.01***	2690.53***	762.01***	0.19	0.24	1.44*
Genotype	44	3.30***	29.92***	20.08**	0.01	3.55**	543.56***	307.03***	0.83	0.12	0.40
Cross	41	3.53***	27.13***	17.12*	4.88	3.49***	542.65***	308.64***	0.80	0.12	0.38
Cross vs Check	1	0.66	150.17***	174.57***	0.92	8.42	16.59	49.21	0.04	0.08	0.11
Cross vs Best Check	1	0.33	105.39***	84.66**	1.13	0.61	907.60***	607.24***	2.66	0.17	1.03
Error Cross	41	0.95	7.52	9.49	2.93	1.26	71.92	41.99	1.15	0.12	0.29
Source of Variation	DF	TLB	EAS	PAS	EPP	EL	NKR	KPR	ED	TSW	
Rep with cross	1	2.67***	3.44**	0.05	0.07*	14.58**	40.04***	14.86	1.66***	133.21	
Genotype	44	0.32*	0.41	0.28	0.05***	5.94***	3.11	33.12***	0.18***	5956.59***	
Cross	41	0.32*	0.43	0.30	0.04***	5.42***	2.78	29.31***	0.20***	5928.86***	
Cross vs Check	1	0.28	0.00	0.01	0.05	10.13*	31.11***	41.26	0.31*	8495.98*	
Cross vs best Check	1	0.72*	0.02	0.16	0.00	28.05***	8.00	173.95***	0.02	4992.84	
Error Cross	41	0.17	0.28	0.22	0.02	1.70	2.19	11.67	0.06	1912.74	
Source of Variation	DF	BIOM	HI	LANG	LL	LW	LFAR	LFPP	LFAE	LFBE	
rep with cross	1	9.51*	70.59	16.01	838.11**	9.33**	114635.53**	1.81	0.08	2.56	
Genotype	44	3.61**	200.01*	29.53	71.26	0.50	6890.64	0.80	0.20	0.50	
Cross	41	3.84*	208.77*	31.37	67.88	0.47	6518.12	0.80	0.20	0.52	
Cross vs Check	1	1.75	372.59	499.51**	195.25	1.17	20534.05	4.62*	1.88**	0.36	
Cross vs Best Check	1	0.50	188.04	1.36	307.17	1.50	31116.96	0.35	0.13	0.07	
Error Crosses	41	1.70	105.09	59.64	85.94	0.86	9657.96	1.01	0.20	0.64	

Table 4. General ANOVA for grain yield and other agronomic traits of maize hybrids evaluated at Kulumsa Agricultural Research Center, 2017.

Kulumsa	Mean Square									
Source of Variation	DF	GY	DT	DS	ASI	MD	PH	EH	Mod	GLS	CLR
Rep	1	7.92**	8.05	15.42*	1.19	5.25	520.01	5.25	2.50*	0.00	2.33**
Genotype	44	4.79***	41.32***	40.60***	0.00	14.40	466.46**	342.48***	0.47	0.00	0.80**
Cross	41	4.86***	28.41***	29.35***	1.25	14.99	469.42**	339.43***	0.45	0.00	0.82***
Cross vs Check	1	0.79	623.01***	552.02***	2.14	2.95	1122.00*	983.15**	0.12	0.00	1.46*
Cross vs best check	1	9.86**	367.42***	326.52***	1.21	16.35	163.72	84.66	0.19	0.00	0.23
Error cross	41	0.95	2.34	2.72	1.19	13.32	195.33	82.98	0.53	0.00	0.30
Source of Variation	DF	TLB	EAS	PAS	EPP	EL	NKR	KPR	ED	TSW	
Rep	1	0.03	0.01	0.15	0.01	13.22*	0.43	7.54	0.02	1505.53	
Genotype	44	0.05	0.37**	0.19	0.18*	7.93***	1.96	23.50*	0.20***	4558.27***	
Cross	41	0.06	0.38**	0.19	0.18*	8.06***	1.96	24.18*	0.21***	4301.81***	
Cross vs Check	1	0.03	0.31	0.64*	0.01	14.96*	4.82	15.66	0.01	22678.24***	
Cross vs best check	1	0.05	0.00	0.50	0.11	11.90*	4.97	32.22	0.18	7899.42**	
Error cross	41	0.06	0.16	0.13	0.10	2.13	1.70	13.04	0.07	971.44	
Source of Variation	DF	BIOM	HI	LANG	LL	LW	LFAR	LFPP	LFAE	LFBE	
Rep	1	35.52*	3.16	4.76	0.53	0.10	130.42	12.44***	0.03	11.19***	
Genotype	44	20.38***	134.46	50.43***	55.44***	0.93***	9290.79***	0.91**	0.25	0.52**	
Cross	41	21.41***	139.08	31.24***	54.18***	0.88**	8835.74**	0.91**	0.25*	0.54**	
Cross vs Check	1	1.90	73.25	931.43***	205.88**	0.50	26672.33**	2.11*	0.35	0.84	
Cross vs best check	1	3.42	173.46	339.06***	34.96	0.00	2370.29	1.76*	0.54	0.30	
Error cross	41	7.22	100.52	6.32	19.61	0.34	3629.30	0.40	0.14	0.24	

= significant at 0.05 probability level, **= significant at 0.01probabilty level and * = significant at 0.001probabilty level, DF = Degree of freedom, GxL= Genotype by location interaction, 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), GLS = Gray Leaf Spot (1-5 scoring), CLR = Common Leaf Rust (1-5 scoring), TLB = Turcicum Leaf Blight (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), HI = Harvest Index (%), 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 bellow upper most ear (number).*

Table 5. The general ANOVA for grain yield and other agronomic traits combined across three locations,2017.

Source of Variation	DF	Mean Square							
		GY	DT	DS	PH	EH	EPP	EL	KPR
Location	2	329.73**	2278.14**	1159.35**	123422.80**	60676.02**	4.61**	294.57*	669.62**
Genotype	44	9.34***	87.93***	71.47***	1817.37***	1067.41***	0.27***	18.31***	59.84***
Cross	41	9.67***	68.49***	50.82***	1793.51***	1068.88***	0.29***	16.89***	57.99***
Check	2	0.38	5.06	11.56	337.17	197.17	0.04	9.82*	21.86
Cross vs Check	1	13.59***	1050.80***	1038.19***	5756.21***	2748.07***	0.00	93.55***	211.59***
Cross vs best check	1	6.62**	326.52***	233.01***	3425.59***	2105.9***	0.07	24.50**	35.90
Genotype x Location	88	2.05***	6.00*	6.79	258.82***	98.48**	0.05	2.97	15.61
Cross x Location	82	1.81***	5.01	5.82	247.55***	92.63**	0.05	3.09	15.64
Check x Location	4	4.85*	13.06	12.81	510.58	243.33	0.11*	0.65	8.26
pooled error crosses	123	0.87	4.26	5.13	113.21	55.27	0.06	2.34	12.68
pooled error genotypes	132	0.93	4.22	5.05	118.95	62.94	0.05	2.42	12.81
pooled error checks	6	0.67	4.39	3.61	278.89	182.28	0.02	4.70	18.93

Source of Variation	DF	Mean Square			DF	Mean Square				
		ED	TSW	BIOM		ASI†	MD†	EAS†	LFPP†	LFBE†
Location	2	8.57*	235157.73**	1475.99**	1	352.80***	22826.27***	8.45	1.04	73.69
Genotype	44	0.50***	13595.74***	26.23***	44	7.08***	4.30***	0.57***	1.70	1.18
Cross	41	0.53***	13699.93***	27.02***	41	7.27***	4.34	0.57**	1.75	1.23
Check	2	0.06	1039.38	8.17	2	6.33*	2.25	0.19	1.15	0.77
Cross vs Check	1	0.08	34436.88***	29.82*	1	0.63	7.23*	1.27**	0.48	0.06
Cross vs Best Check	1	0.00	15592.55***	42.01*	1	4.69	9.43*	1.34**	0.72	0.00
Genotype x Location	88	0.06	1519.21	10.91*	44	2.64	2.73*	0.21*	1.99***	1.17***
Cross x Location	82	0.07	1451.95	9.99	41	2.54	2.76**	0.22*	2.09***	1.16***
Check x Location	4	0.03	2948.70*	12.96	2	0.33	3.25	0.06	0.26	0.77
pooled error crosses	123	0.05	1350.83	7.7D	82	2.18	1.54	0.13	0.70	0.41
pooled error genotypes	132	0.05	1320.95	7.35	88	2.11	1.58	0.13	0.69	0.41
pooled error checks	6	0.07	630.48	3.49	4	1.33	0.92	0.04	0.78	0.41

3.1 Standard Heterosis

Tables 6,7, and 8 presents Standard heterosis (SH) for five traits (GY, PH, EH, MOD and EAS) at Ambo, four traits (GY, PH, EH, and TLB) at Arsi-Negele, and three traits (GY, LFANG, and LFPP) at Kulumsa. For the combined data, the standard heterosis is presented in Table 5. The traits that had non-significant MS for cross vs best check were not included in estimating standard heterosis. The best checks used for calculating SH were Jibat at Arsi-Negele and Kulumsa and AMH853 at Ambo.

3.1.1 Standard heterosis at an individual location

At Ambo, all crosses did not show any SH over the best check (AMH853) for GY (Table 6). At Arsi-Negele, 13 crosses showed positive SH and three of them showed significant differences. SH ranged from -46.25% (L2xT2) to 50.81% (L8xT1) (Table 7). At Kulumsa, only two crosses (L7xT1 and L19xT1) had positive SH over Jibat but were not statistically significant. At this location, SH ranged from -55.52% (L13xT1) to 6.57% (L7xT1) (Table 8) which is in line with the result of Abiy (2017). He reported SH ranged -30.42% to 10.10% from highland maize hybrids tested at Ambo and Kulumsa but none of the crosses had significantly different SH.

AT Ambo, all crosses had negative and significant SH, except three crosses (L7xT1, L8xT1, and L8xT2) which had positive and non-significant SH over CM best check (AMH853), for PH and EH. These three crosses were the highest grain yielder next to the standard check. SH ranged from -38.54% (L1xT1) to 2.89% (L8xT1) for PH and from -42.91% (L2xT2) to 3.72% (L8xT1) for EH (Table 6). Similarly, at Arsi-Negele, two crosses (L7xT1) and L8xT1) showed positive and non-significant SH for PH. The crosses showed positive SH but only SH from L7xT1 showed statistically significant. At Arsi-Negele SH ranged from -31.64% (L2xT2) to 8.76% (L7xT1) for PH and from -44.38 (L3xT1) to 16.85 (L7xT1) for EH (Table 7). The result of this study is in line with the negative SH reported by Berhanu (2009) and Patil*et al.* (2017). At Kulumsa, the orthogonal contrast of cross-vs- check was non-significant due to this, the estimation of SH was not done.

All crosses had positive SH for MOD except, L2xT1 at Ambo. This cross had zero SH for MOD indicating, its ability to produce well-modified endosperm than other crosses. Out of

42 crosses, 24 showed significant SH over AMH853 (Table 6). The highest (150.0%) SH was recorded by L20xT2 indicates this cross was the poorest for MOD. A lower magnitude of SH is desirable with regard to this trait.

At Arsi-Negele, most of the crosses manifested by negative heterosis over the best check (Jibat) except, three crosses of which one had positive SH and the other zero SH for TLB. Ten crosses showed significant negative SH for TLB which indicates that these crosses tolerate TLB better than the standard check

Table 6. Standard heterosis (SH) for traits that were not included in the across location heterosis determination of the 42 F1hybrids obtained by LxT and evaluated at Ambo in 2017 (best check was AMH853).

Code	%GY	%PH	%EH	%MOD	%EAS	Code	%GY	%PH	%EH	%MOD	%EAS
L1xT1	-78.18***	-38.54***	-35.47***	83.33*	77.78***	L13xT1	-76.64***	-33.33***	-37.16***	83.33*	77.78***
L1xT2	-30.59**	-17.15***	-22.64***	50.00	0.00	L13xT2	-49.12***	-23.12***	-34.79***	66.67*	11.11
L2xT1	-49.56***	-21.19***	-29.39***	0.00	11.11	L14xT1	-44.85***	-10.41**	-14.53**	50.00	11.11
L2xT2	-72.15***	-36.61***	-42.91***	50.00	66.67***	L14xT2	-28.51**	-7.32*	-14.86**	116.67***	22.22
L3xT1	-45.50***	-17.73***	-24.32***	33.33	44.44**	L15xT1	-25.22**	-11.95**	-15.20**	100.00**	44.44**
L3xT2	-11.84	-12.72**	-17.23***	33.33	11.11	L15xT2	-41.67***	-7.51*	-16.89***	100.00**	22.22
L4xT1	-70.83***	-35.65***	-38.51***	83.33*	66.67***	L16xT1	-40.90***	-14.45***	-23.65***	33.33	22.22
L4xT2	-45.83***	-18.69***	-29.39***	50.00	22.22	L16xT2	-37.83***	-18.67***	-34.79***	50.00	22.22
L5xT1	-36.18***	-9.83**	-15.54**	83.33*	55.56***	L17xT1	-26.53**	-5.20	-4.73	16.67	33.33*
L5xT2	-28.84**	-17.15***	-24.66***	116.67***	22.22	L17xT2	-7.79	-10.79**	-19.26***	100.00**	11.11
L6xT1	-26.64**	-2.12	1.01	66.67*	22.22	L18xT1	-14.14	-0.39	-1.01	83.33*	22.22
L6xT2	-18.86*	-6.55	-5.41	83.33*	33.33*	L18xT2	-48.03***	-9.63*	-18.92***	100.00**	22.22
L7xT1	-23.25*	2.50	2.03	66.67*	44.44**	L19xT1	-43.31***	-7.51*	-18.24***	33.33	44.44**
L7xT2	-19.52*	-8.29*	-13.51**	50.00	22.22	L19xT2	-36.07***	-9.25*	-24.66***	100.00**	22.22
L8xT1	-22.37*	2.89	3.72	116.67***	33.33*	L20xT1	-36.18***	-3.28	-6.08	116.67***	22.22
L8xT2	-3.40	1.16	2.03	100.00**	22.22	L20xT2	-38.16***	-11.56**	-18.24***	150.00***	44.44**
L9xT1	-12.50	-10.21**	-13.51**	83.33*	0.00	L21xT1	-33.66***	-8.67*	-5.41	33.33	33.33*
L9xT2	-22.59*	-7.32*	-12.50*	16.67	22.22	L21xT2	-29.38**	-9.44*	-19.93***	66.67*	22.22
L10xT1	-36.51***	-9.25*	-12.50*	83.33*	55.56***	Minimum	-78.18	-38.54	-42.91	0.00	0.00
L10xT2	-25.33**	-8.09*	-10.14*	83.33*	44.44**	Maximum	-3.40	2.89	3.72	150.00	77.78
L11xT1	-39.47***	-12.52**	-14.86**	83.33*	55.56***	CD,0.05	1.65	18.99	13.85	0.97	0.66
L11xT2	-26.65**	-11.37**	-17.57***	33.33	22.22	CD,0.01	2.20	25.36	18.51	1.29	0.88
L12xT1	-34.65***	-7.72*	-5.07	50.00	11.11	CD,0.001	2.89	33.22	24.24	1.69	1.15
L12xT2	-40.24***	-10.41**	-23.31***	50.00	0.00						

Table7. Standard heterosis (SH) for traits that were not included in the across location heterosis determination of the 42 F1hybrids obtained by LxT and evaluated at Arsi-Negele in 2017 (best check was Jibat).

Code	%GY	%PH	%EH	%TLB	Code	%GY	%PH	%EH	%TLB
L1xT1	-40.22*	-30.79***	-40.45***	16.67	L13xT1	-32.25*	-31.36***	-44.38***	-25.00
L1xT2	-9.77	-17.23***	-29.21***	-25.00	L13xT2	-17.10	-21.47***	-40.45***	-8.33
L2xT1	-22.48	-25.99***	-41.01***	0.00	L14xT1	1.95	-1.41	-5.62	-8.33
L2xT2	-46.25**	-31.64***	-39.88***	8.33	L14xT2	-23.45	-15.25**	-21.91**	-16.67
L3xT1	-11.40	-15.54**	-25.28***	8.33	L15xT1	-26.22	-16.67**	-28.65***	-8.33
L3xT2	-15.31	-10.73*	-19.10*	-16.67	L15xT2	-1.14	-11.86*	-21.91**	-16.67
L4xT1	-31.76*	-25.99***	-34.83***	-25.00	L16xT1	1.95	-7.34	-11.24	0.00
L4xT2	-8.96	-24.58***	-41.57***	-33.33*	L16xT2	-20.36	-25.42***	-42.13***	-16.67
L5xT1	25.90	-8.76	-17.42*	-16.67	L17xT1	-10.59	-9.60	-8.43	-16.67
L5xT2	5.70	-11.86*	-24.16**	-25.00	L17xT2	-14.33	-20.05***	-27.52***	-16.67
L6xT1	-18.57	-1.41	-5.62	-8.33	L18xT1	14.50	-5.93	-9.55	-33.33*
L6xT2	1.79	-10.45*	-10.11	-25.00	L18xT2	-1.63	-13.56**	-28.09***	-25.00
L7xT1	33.88*	8.76	16.85*	-33.33*	L19xT1	26.38	-3.95	-6.18	-25.00
L7xT2	1.47	-9.60	-16.29*	-33.33*	L19xT2	-4.07	-5.08	-17.98*	-25.00
L8xT1	50.81**	5.93	5.06	-41.67**	L20xT1	5.54	-1.98	-2.81	-16.67
L8xT2	46.58**	-1.69	-0.56	-33.33*	L20xT2	-23.62	-12.59*	-24.719**	-25.00
L9xT1	-16.29	-6.21	-7.87	-16.67	L21xT1	-18.73	-10.73*	-15.17*	-25.00
L9xT2	-7.82	-7.91	-14.60*	-16.67	L21xT2	-14.98	-12.15*	-23.03**	-41.67**
L10xT1	-15.47	-9.60	-21.35**	-33.33*	Minimum	-46.25	-31.64	-44.38	-41.67
L10xT2	12.21	-8.47	-15.73*	-25.00	Maximum	50.81	8.76	16.85	16.67
L11xT1	-44.46**	-12.99**	-20.22**	-25.00	CD,0.05	1.93	17.16	12.79	0.85
L11xT2	5.05	-11.58*	-18.54*	-33.33*	CD,0.01	2.57	22.93	17.09	1.14
L12xT1	-3.75	-7.63	-5.06	-25.00	CD,0.001	3.37	30.02	22.38	1.49
L12xT2	-13.84	-9.04	-25.28***	-41.67**					

Table 8. Standard heterosis (SH) for traits that were not included in the across location heterosis determination of the 42 F1hybrids obtained by LxT and evaluated at Kulumsa in 2017 (best check was Jibat).

Code	%GY	%LFANG	%LFPP	Code	%GY	%LFANG	%LFPP
L1xT1	-47.11***	-33.33***	1.13	L13xT1	-55.52***	-21.05**	-3.53
L1xT2	-21.19*	-29.83***	2.33	L13xT2	-19.78*	-36.84***	3.53
L2xT1	-17.86	-29.83***	-3.53	L14xT1	-18.04	-31.58***	11.71**
L2xT2	-48.34***	-22.80***	5.86	L14xT2	-16.73	-14.04*	3.53
L3xT1	-43.78***	-40.36***	9.38*	L15xT1	-14.62	-24.57***	8.19
L3xT2	-23.99*	-40.36***	9.38*	L15xT2	-5.78	-19.31**	5.86
L4xT1	-50.08***	-21.05**	2.33	L16xT1	-20.05*	-26.32***	8.19
L4xT2	-21.28*	-35.09***	1.13	L16xT2	-24.34*	-22.80***	-1.20
L5xT1	-13.92	-49.12***	7.06	L17xT1	-15.41	-26.32***	11.71**
L5xT2	-19.44*	-43.85***	12.91**	L17xT2	-32.49**	-22.80***	7.06
L6xT1	-13.05	-17.54**	10.58*	L18xT1	-16.64	-21.05**	15.24***
L6xT2	-4.20	-33.33***	5.86	L18xT2	-12.43	-29.83***	4.66
L7xT1	6.57	-21.05**	8.19	L19xT1	4.73	-24.57***	9.38*
L7xT2	-23.38*	-38.59***	-2.40	L19xT2	-17.43	-24.57***	8.19
L8xT1	-4.38	-24.57***	15.24***	L20xT1	-21.19*	-24.57***	10.58*
L8xT2	-2.01	-31.58***	4.66	L20xT2	-26.97**	-29.83***	8.19
L9xT1	-22.85*	-17.54**	9.38*	L21xT1	-12.43	-17.54**	7.06
L9xT2	-8.32	-31.58***	10.58*	L21xT2	-5.52	-8.78	9.38*
L10xT1	-23.21*	-33.33***	5.86	Minimum	-55.52	-49.12	-3.53
L10xT2	-18.56	-31.58***	3.53	Maximum	6.57	-8.78	15.24
L11xT1	-24.43*	-21.05**	11.71**	CD,0.05	2.22	5.91	1.23
L11xT2	-22.42*	-24.57***	1.13	CD,0.01	2.96	7.90	1.64
L12xT1	-17.78	-29.83***	5.86	CD,0.001	3.88	10.35	2.14
L12xT2	-9.81	-36.84***	14.11				

The other crosses with zero value of SH are also good for TLB providing their stability and other agronomic traits are better than the standard check. The high yielder crosses (L8xT1 and L8xT2) showed significant tolerance to TLB than the standard check. The highest (16.67%) and lowest (-41.67%) SH for TLB was scored by L1xT1 and L21xT2, respectively (Table 7). In contrast to this result, Beyene (2016) reported positive and significant heterosis over the standard check. Berhanu (2009) also reported positive and negative SH over the check.

At Ambo, positive SH was obtained from all crosses for EAS. There were also crosses (L1xT2, L9xT1, and L12xT2) with zero SH for EAS which indicates these crosses were

good for EAS compared with the rest of the crosses. Positive and significant SH was obtained from 16 crosses which shows that about 38%of the crosses had poor EAS. Most crosses with significant SH were crossed that have T1 as one of their parents implying that T1 was a poor EAS combined towards improving EAS than T2 (Table 6). The result of EAS in this study was in line with the report of Beyene (2016). He reported positive and significant heterosis over the best check.

At Kulumsa, all crosses had negative with highly significant SH for LFANG. This implies that all crosses had a narrow-leaf angle compared to the standard check (Jibat). Duvick (2005) also reported as leaves became more upright in the 1970s era in a comparison of single crosses representing U.S. corn belt hybrids of three eras:1930s, 1950s, and 1970s. The narrowest (-49.12%) was recorded by L5xT1 but L21xT2, which manifested the highest SH to the negative direction with the value of -8.78% for LFANG had relatively wider LFANG (Table 8). Varieties with narrow leaves can help to economize the space and to exposed leaves found at the lower side of the plant and due to this greater number of leaves can access solar radiation. Due to LFANG reduction, leaf area can be increased and the higher leaf area ultimately can increase photosynthesis which is the heart of efficient utilization of resources by the plant (Huanga e*t al.,* 2017). Almost all crosses showed positive SH for LFPP except, for four crosses with negative but non-significant SH. Fourteen crosses showed positive and significant heterosis. The highest (15.24%) and lowest (-3.53%) SH were shown by L18xT1 and L2xT1, respectively (Table 8). Similarly, Berhanu (2009) reported positive and negative SH over the check.

3.1.2 Standard heterosis across locations

In the combined analysis, SH estimation was computed for five traits which showed significant MS for cross vs best check (AMH853). The estimated SH is presented in Table 9.

The highest SH of 20.8 % (1.67 t ha^{-1} grain yield advantage over AMH853) for GY was obtained from L8xT2, even though the difference was not significant (Table 9). This cross can be released after carrying out further evaluation across locations. SH standard heterosis ranged from -52.6% (L13xT1) to 20.8% (L8xT2) for GY. The five high-yielding crosses across the three locations were L6xT2 (8.20), L7xT1 (9.13), L8xT1(9.09), L8xT2 (9.67), and L19xT1 (8.30) (data not shown). Similarly, Beyene (2016) and Abiy 2017 reported non-

significant SH. The two authors reported SH THAT ranged from -44.07% to -9.72% and from -30.42 to 10.1, respectively. Berhanu (2009) obtained SH ranging between -28.17% to 20.33% and was able to identify one cross with significant SH.

For DT, almost all crosses had positive and significant SH except, L16xT2 (-0.19%) which recorded negative SH. Similarly, most crosses had positive and significant SH for DS which indicates the crosses were late in flowering compared with standard check variety for both DS and DT. The value of SH ranged from -0.19% (L16xT2) to 16.10% (L1xT1) DT and from 0.71% (L16xT2) to 13.57% (L1xT1) for DS (Table 9). In contrast to the current finding, Berhanu (2009), Abiy (2017) and Patil*et al*. (2017) reported negative and significant SH for DT and DS.

Only four crosses had positive SH for EL but none of them were significantly different. These crosses were, L6xT1 (3.06%), L7xT1 (1.36%), L9xT1 (0.34%) and L9xT2 (6.80%). The value of SH for EL ranged from -35.4% (L1xT1) to 6.8% (L9xT2). The other crosses showed negative SH and a few of them showed significant differences. The result agrees with the previous works of Berhanu (2009) and Beyene (2016). These authors reported SH that ranged from -26.4% to 1.47% and from -16.76% -6.8%, respectively.

Only four crosses (L15xT2, L16xT2, L17xT2, and L21xT2) showed positive SH for TSW across locations but all were not statistically significant. SH ranged from -40.82 % (L3xT1) to 17.46 % (L17xT2) (Table 9). In contrast to the current finding, Berhanu (2009) and Patil*et al*. (2017) reported crosses with a positive and significant difference. Berhanu reported SH ranging from -29.32% to 10.87%. Patil*et al.* (2017) also reported SH ranging from 30.24% to 64.15% for 100 seed weight.

Table 9. Standard heterosis (SH) for traits that were included in the across location heterosis determination of the 42 F1hybrids obtained by LxT and evaluated at Ambo, Arsi-Negele, and Kulumsa in 2017 (best check was AMH853).

Code	%GY	%DT	%DS	%EL	%TSW	Code	% GY	%DT	%DS	%EL	%TSW
L1xT1	-51.25***	16.10***	13.57***	-35.4***	-38.9***	L13xT1	-52.6***	14.98***	12.32***	-28.57**	-38.9***
L1xT2	-13.06	8.61***	6.60**	-17.01	-9.70	L13xT2	-21.29	6.92**	5.00*	-15.99	-10.39
L2xT1	-21.94**	7.11**	6.42**	-15.99	-12.37	L14xT1	-13.94	12.17***	9.64***	-20.40*	-20.6*
L2xT2	-51.08***	13.85***	11.96***	-26.70**	-38.4***	L14xT2	-13.61	7.11**	6.96**	-19.72*	-0.80
L3xT1	-29.84*	11.61***	8.92***	-21.08*	-40.82***	L15xT1	-12.07	9.92***	7.85***	-28.6**	-18.38
L3xT2	-8.68	6.74**	4.82*	-6.63	-16.12	L15xT2	-7.67	5.99*	4.64	-7.82	5.02
L4xT1	-47.73***	13.85***	11.96***	-33.3***	-37.8***	L16xT1	-13.42	4.86*	3.93	-14.96	-10.25
L4xT2	-18.67	6.36**	5.17*	-20.40*	-10.19	L16xT2	-20.04	-0.19	0.71	-13.61	3.34
L5xT1	-2.57	12.73***	11.07***	-15.99	-28.13**	L17xT1	-8.97	10.30***	7.32**	-11.90	-14.08
L5xT2	-7.58	8.05***	6.60**	-8.84	-11.07	L17xT2	-10.93	4.12**	3.04	-7.99	17.46
L6xT1	-9.93	9.55***	6.78**	3.06	-20.20*	L18xT1	1.59	6.17**	4.64	-13.61	-15.18
L6xT2	2.46	6.36**	5.71*	-3.40	-7.56	L18xT2	-13.42	5.24*	5.17***	-17.69	-8.72
L7xT1	14.11	8.98***	6.78**	1.36	-26.70**	L19xT1	3.71	8.05***	5.89***	-7.82	-11.73
L7xT2	-7.00	3.93	1.97	-8.16	-4.71	L19xT2	-11.90	2.06	1.79	5.44	-0.62
L8xT1	13.60	9.73***	7.14**	-9.52	-18.99	L20xT1	-11.28	10.48***	10.35***	-12.41	-8.83
L8xT2	20.82	4.87*	3.57*	0.00	-3.25	L20xT2	-22.18	6.74**	7.67**	-7.31	-1.19
L9xT1	-8.62	10.67***	7.67**	0.34	-25.44*	L21xT1	-12.37	11.98***	7.67**	-21.76*	-21.8*
L9xT2	-3.38	4.86*	4.82*	6.80	-8.77	L21xT2	-6.44	7.30**	6.25*	-4.76	5.89
L10xT1	-17.72	10.86***	8.57***	-0.34	-22.85*	Minimum	-52.62	-0.19	0.71	-35.37	-40.82
L10xT2	-4.19	3.93	2.68	-5.27	-8.81	Maximum	20.82	16.10	13.57	6.80	17.46
L11xT1	-26.86*	9.55***	7.50**	-15.99	-19.76	CD=0.05	1.91	4.06	4.45	3.08	71.89
L11xT2	-8.33	2.62	1.79	-2.38	-3.27	CD=0.01	2.52	5.37	5.87	4.07	94.99
L12xT1	-11.39	15.73***	11.78***	-23.29*	-24.58*	CD=0.001	3.13	6.67	7.29	5.05	117.97
L12xT2	-12.33	11.23***	8.92***	-18.19	-10.54						

4. Conclusion

The analysis of variance showed significant difference among tested genotypes for grain yield, yield related, phenological, agronomic and morphological traits at individual locations. In combined analysis across location, the result showed very highly significant difference among genotypes for most of the traits considered in the study. The highly significant difference observed for genotype by location and cross by location interaction highlights that the performance of the genotypes is inconsistent across location. This indicates that these new hybrids which performed good but with unstable performance across location should be consider for their suitability for specific location by doing further investigation. Based on the mean grain yield pooled over the three locations six crosses: L8xT2, L7xT1, L8xT1, L19xT1, L6xT2, and L18xT1 were found to be superior to the best check (AMH853) by 20.82, 13.60, 14.11, 3.71, 2.46, and 1.59 %, respectively. Generally, this study identified crosses that have a noticeable level of heterosis above the recently released standard variety (AMH853). This study indicates the existence of better newly developed crosses that are nutritionally balanced compared with the standard commercialized check varieties. We recommend these well-performed crosses to be considered for release following the remain steps need to be followed for varieties release.

Authors' contributions

GMM collected the data, performed the analysis, and developed the manuscript. ATC reviewed and made editorial comments on the draft manuscript.

Authors' information

GMM is a plant breeder with more than 10 years of experience who has been involved in the development of maize germplasm development with the national maize breeding program.

ATC(Ph.D.) is a senior scientist currently working in CIMMYT-Ethiopia and taking over the leading research works that have been planned and implemented on maize improvement. He was a crop process leader at the Ethiopian Institute of Agriculture Research.

YMS is one of maize breeder in the national research system. Currently he continues working as maize breeder in the system.

Funding

Funding – Funding was provided by CIMMYT and the Ethiopian Institute of Agriculture Research (EIAR). The lion's share of funding was CIMMYT.

Availability of data and materials

Availability of data and materials – data can be requested from the first author.

Ethics approval

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

Competing interests

The authors declare that they have no competing interests.

355
356
357
358
359
360
361

Reference

363
364 Abiy BG (2017). Combining ability of highland maize (Zea Mays L.) inbred lines using line
365 x tester analysis. M.Sc. Thesis. College of Agriculture, Hawassa University, Hawassa,
366 Ethiopia.121 p.

367 Badu-Apraku M, Oyekunle M, Fakorede AB, Vroh I, Akinwale RO, Aderounmu M (2013).
368 Combining ability, heterotic patterns and genetic diversity of extra-early yellow inbreeds
369 under contrasting environments. Euphytica, DOI 10.1007/s10681-013-0876-4.

370 Berhanu T (2009). Heterosis and combining ability for yield, yield-related parameters, and
371 stover quality traits for food-feed in maize (Zea Mays L.) adapted to the mid-altitude
372 agroecology of Ethiopia. MSc.Thesis. Haramaya University, , Haramaya, Ethiopia.199 p.

373 Beyene A (2016). Heterosis and combining ability of mid-altitude quality protein maize (*Zea*
374 *Mays L.*) inbred lines at Bako, Western Ethiopia. MSc. Thesis, Haramaya University,
375 Haramaya, 158 p.

376 Duvick DN (1999). Commercial strategies for exploitation of heterosis. In: J.G. Coors and S.
377 Pandey (Eds.). The Genetics and Exploitation of Heterosis in Crops. ASA, CSS, and SSSA,
378 Madison, Wisconsin, USA, 19-29 pp.

379 Duvick DN (2005). The contribution of breeding to yield advances in maize (Zea mays L.).
380 Iowa State University Ames, Iowa 50011.
381 East EM (1908). Inbreeding in corn. Rep. Conn. Agric. Exp. Stn,, 419-428 pp.

382 Falconer DS and Mackay TFC (1196). Introduction to quantitative genetics.4th ed. Longman,
383 London, UK.

384 Hallauer AR and JMiranda JB (1988). Quantitative Genetics in Maize Breeding. 2nd ed. Iowa State
385 University Press, Iowa, Ames. USA.

386 Hallauer AR and Miranda JB (1998). Quantitative Genetics in Maize Breeding. 2nd ed.
387 Iowa State University Press, Iowa, Ames. USA.

388 Huanga S, Gaoa Y, Lia Y, Xub L, Taoa H, Wanga P (2017). Influence of plant architecture
389 on maize physiology and yield in the Heilonggang River valley. The crop journal, 5, 52-62.
390 Jinks JL (1983). Biometrical genetics of heterosis. In: Frankel R. (Eds.). Heterosis:
391 Reappraisal of Theory and Practice. Springer-Verlag, Berlin, Heidelberg, Germany, pp. 1-46.

392 Kim SK and Ajala SO (1996). Combining ability of tropical maize germplasm in west Africa
393 II.Tropical vs temperate x tropical origins. Maydica, 41: 135-141.

394 Li Z, Coffey L, Garfin J, Miller MD, White MR, Spalding EP, Leon ND, Kaepple SM,
395 Schnable SP, Springer NM and Hirsch1 CN (1918). Genotype-by environment interactions
396 affecting heterosis in maize.PLoS ONE 13(1): e0191321. https://doi.org/

10.1371/journal.pone.0191321.

Miranda JB (1999). Inbreeding depression. In: J.G. Coors & S. Pandey (Eds.). The Genetics and Exploitation of Heterosis in Crops. ASA, CSS, and SSSA, Madison, Wisconsin, USA, 69-80 pp.

Patil BS, Ahamed ML and Babu DR (2017). Heterosis studies for yield and yield component characters in maize (*Zea mays L.*). IJAEB, 10(4): 449-455. DOI: 10.5958/2230-732X.2017.00056.0.

Pixley KV and Bjarnason MS (1993). Combining ability for yield and protein quality among modified endosperm opaque-2 tropical maize inbreeds. Crop Science 33: 1229-1234.

Pixley KV and Bjarnason MS (2002). Stability of grain yield, endosperm modification, and protein quality of hybrid and open-pollinated quality protein maize cultivars. Crop Science, 42: 1882-1890.

Prasad SK and Singh TP (1986). Heterosis in relation to genetic divergence in maize (Zea mays L.). Euphytica, 35: 919-924.

Shull GH (1908). The composition of a field of maize. Am. Breed. Assoc. Rep. 4: 296-301.

Shull GH (1952). Beginnings of the heterosis concept. In: Gowen J.W. (Eds.). Heterosis. Iowa State University Press, Iowa, Ames, USA, pp. 14-48.

Singh BD (2005). Plant breeding: Principles and methods. 7th ed. Kalyani Publishers, New Delhi, India.

Smith JS, Grandner CAC and Costich DE (2017). Ensuring the genetic diversity of maize and its wild relatives.

Stuber CW (1994). Heterosis in plant breeding. Plant Breeding Reviews, 1994, 12: 227-251.

Troyer AF (1990). A retrospective view of corn genetic resources heredity, 81: 17-24.

Vasal SK (1993). Srinivasan G, Pandey HS, Gonzalez F, Crossa J. and Beck DL. Heterosis and combining ability of CIMMYT's quality protein maize germplasm: I. Lowland tropical. Crop Science, 33: 46-51.