



Research article

Combining ability and genetic distance analysis of mid altitude sub-humid agroecology adapted maize inbred lines for high grain yield

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ABSTRACT

Understanding the combining ability effects, heterosis, and genetic relationships between parental lines would be helpful in the maize breeding program to develop high-yielding and genetically stable maize varieties for various contrasting environments. Hence, the objective of this study was to estimate combining ability effects, heterosis, genetic distance (GD) and associations for grain yield and other agronomic traits. Forty-five F₁ diallel crosses, four commercial checks, and ten inbred lines were evaluated at Bako and Jima Agricultural Research Centers, Ethiopia. Significant differences were observed among environments, genotypes and genotype by environment interaction for grain yield and almost all studied agronomic traits. Combining ability analysis showed both additive and non-additive gene effects significantly controlled grain yield and all other studied traits. The preponderance of general combining ability (GCA) effects indicates the importance of additive gene action inheriting most agronomic traits. Lines L2, L7, and L9 were the best combiners for grain yield, whereas lines L3 and L4 had desirable GCA values to improve days to flowering and plant height. Among the top ten crosses, L6 × L9, L6 × L7 and L4 × L9 were good specific combiners and had 18.8 %, 17.2 % and 16.2 % grain yield advantage over the best check, BH546. These hybrids also had high mid and better-parent heterosis compared with other crosses. The associations of GD with mean of F₁ and SCA effects were positive and highly significant for grain yield and some other traits. In contrast, correlations of GD with mid and better parent heterosis were non-significant for grain yield and most other traits. The results of this study are particularly useful for breeders who envisage combining conventional and molecular methods.

1. Introduction

Maize (*Zea mays* L.) is one of the most important strategic cereal crops for improving the food security and economic well-being of millions of people in Ethiopia [1]. It is grown in a broader range of environmental conditions than any other cereal crop in the country. Currently, maize is cultivated on around 2.5 million hectares (ha) of land, with mean annual production of approximately 10.7 million tons (t) with a national productivity of 4.2 t ha⁻¹ [2]. It is the second most widely cultivated crop after Tef (*Eragrostis tef* (Zucc.)

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Trotter) and the first highest-yielding cereal crop in the country [3]. Even though the production and productivity of maize have shown significant progress in the country [1,2], the national average yield is still low compared to the world average of 5.9 t ha⁻¹. It is far below the developed countries' average productivity, like USA (11.1 t ha⁻¹), Australia (6.7 t ha⁻¹), Canada (10.0 t ha⁻¹), Germany (10.3 t ha⁻¹) and China (6.3 t ha⁻¹) [2]. The low productivity of maize in Ethiopia is attributed to different factors, including inadequate farmers' access to improved maize varieties, erratic rainfall distribution, shortage and unavailability of critical inputs like fertilizers on time, and the emergence of new insect pests and diseases [4,5]. Therefore, efforts are required to develop high-yielding and stress-resilient maize hybrids to tackle these challenges and expedite the rate of maize productivity gain in Ethiopia.

Hybrid breeding is one of the most important research tools for maize production improvement, especially in areas facing a wide range of challenges in terms of biotic and abiotic stresses. Hybrid breeding requires selection of the best-inbred lines based on their genetic structure and combining ability effects [6–8]. Combining ability divided into general and specific combining abilities [9]. General combining ability (GCA) is the average performance of a line in different cross-combinations [10]. It indicates the additive gene effects in the expression of traits. In contrast, specific combining ability (SCA) shows the performance of a hybrid that is relatively better or worse than the parents involved and indicates the non-additive gene actions, mainly a function of dominance and epistatic gene action effects [11]. Several combining ability studies have been conducted so far; some of them showed additive gene action is more important in the expression of the studied traits [6,12–14], while others revealed the preponderance of non-additive gene effects in the inheritance of grain yield and some agronomic traits [10,15,16]. These kinds of studies indicated that the type of gene action mainly depend on the type of inbred lines used in the study. This indicates that it is necessary to estimate the gene action effects of newly developed and introduced inbred lines every time.

Moreover, manipulating the genetic diversity of inbred lines through morphological and molecular markers is an essential step in the maize breeding program, which provides the basis for the analysis of combining ability and exploiting heterosis in a hybrid breeding program [17,18]. However, morphological markers cannot easily detect the difference among closely related lines because most characters are influenced by environmental conditions, low polymorphism, and dominant and late expression [7,19]. Relying more on molecular markers is more effective than morphological markers in detecting genotype differences efficiently without being influenced by environmental conditions [19]. Different types of molecular markers are available to assess the genetic diversity in crops. However, with the advancement of molecular technology, scientists have shifted to single nucleotide polymorphism (SNP) markers, a more recent and popular marker for fine-mapping heritable traits in maize [20]. This marker is currently the most preferred marker and is available cheaply with high throughput. SNP markers have been used for genotyping a wide range of maize genotypes [17,20]. In addition, estimating the associations of genetic distance with heterosis and SCA effects for grain yield and other traits would help to design a breeding strategy and predict hybrid performance [21].

The correlation of genetic distance with hybrid performance, heterosis, and SCA has been studied in different markers. Legesse et al. [19] confirmed the existence of a low correlation in amplified fragment length polymorphism (AFLP) measured genetic distance with hybrid performance and mid-parent heterosis. Wegary et al. [21] reported the magnitude of correlation values of simple sequence repeats (SSR) markers with mid-and high-parent heterosis, and the SCA of grain yield and agronomic traits were too low except for plant height. On the other hand, Makumbi et al. [22] manifested the presence of a significant correlation among SCA, GD, and heterosis for F₁ hybrid grain yield under stress and optimum management conditions. Although SNP markers are most popular in the fine mapping of heritable traits in maize, limited information exists on the associations between SNP marker's genetic distance with heterosis, SCA, and F₁ mean performance for grain yield and other agronomic traits in Ethiopia.

In maize breeding program, development of high yielding F₁ hybrids with good agronomic performance gives a considerable attention to provide desirable varietal options for farm communities. Best inbred lines and hybrids may be selected based on combining ability analysis, heterosis and with desirable mean performance. In addition, the information generated in this study would be very important to the breeders in defining a maize breeding strategy and may use the selected inbred lines as a germplasm source for further breeding purpose. Even though, some genetic studies on commercial maize inbred lines have been done so far [13,14,23,24], determination of heterosis and combining ability effects of the newly developed inbred lines is a never-ending process in the maize breeding program. Therefore, the objective of this study was to estimate combining ability effects, heterosis, genetic distance (GD) and associations for grain yield and other agronomic traits.

2. Materials and methods

2.1. Testing sites' description

The trials were conducted during 2015 and 2016 in the main cropping seasons of Ethiopia at two testing sites, namely Bako (9°06'

Table 1
Description of the study locations.

Location	Geographical location			Annual rainfall (mm)	Temperature (°C)		Soil type
	Latitude (N)	Longitude (E)	Elevation (masl)		min	max	
Bako	9°06'	37°09'	1650	944.4	12.3	29.8	Nitosol
Jima	7°40'	36°	1753	1572	11	26.3	Eutric Nitosol

Masl = meters above sea level, Min = minimum, max = maximum.

N, 37°09' E, altitude 1650 m above sea level (masl), Nitosol soil) and Jima (7°40'N, 36°E, altitude 1753 masl, Eutric Nitosol). The locations represent mid-altitude sub-humid maize growing agroecology of Ethiopia which is the major maize production areas. Detailed description of the study locations is presented in Table 1.

2.2. Experimental materials, design, and management

Ten inbred elite lines were used to generate forty-five single cross hybrids by using a half-diallel crossing scheme at Bako National Maize Research Center (BNMRC). Of these inbred lines, eight were locally developed and two were introduced inbred lines (Table 2). Forty-five F₁ single cross progenies and four commercial checks (BH540, BH543, BH546, and BH547) were planted using 7 × 7 alpha-lattice design with three replications. The distance between rows, plants within the row, and plot length was 0.75 m, 0.3 m, and 5.1 m, respectively. Each plot had two rows. The second trial involving ten parental inbred lines was planted adjacent to the hybrid trials on the same day to avoid biases resulting from inter-plot competition between inbred lines and the hybrids [25]. Inbred lines were planted in a randomized complete block design (RCBD) with three replications. One border row was used at each end of the replication/blocks to minimize the border effect. All agronomic management, such as fertilizer application, weeding, and insect pest management, was done based on the recommendations for both locations.

2.3. Phenotypic data

Data were recorded for grain yield and other agronomic traits on each plot. List of all collected data abbreviation, measurement unit and description are indicated in Table 3.

2.4. Genotypic data

The inbred lines used in this study are a subset of 265 inbred lines previously reported by Ertiro et al. [17]. The procedures for DNA extraction and genetic distance calculation were described in detail by Ertiro et al. [17]. Briefly, DNA was extracted from a bulked leaf sample collected from 10 seedlings using a modified version of CIMMYT's high throughput mini-prep Cetyl Trimethyl Ammonium Bromide (CTAB) method [26]. DNA concentration was measured using the Quant-iT™ PicoGreen® dsDNA assay kit (Invitrogen™, Paisley, UK) and the Tecan Infinite F200 Pro Plate Reader (Grödig, Austria), and normalized to 50 ng μL⁻¹ [17]. The extracted DNA quality was measured as described in Ertiro et al. [27] and shipped to the Institute of Biotechnology at Cornell University (<http://www.biotech.cornell.edu/brc/genomics-facility>). Samples were genotyped with 955,120 genotyping by sequencing (GBS) SNP markers at the Institute of Biotechnology, Cornell University. After filtering based on minor allele frequency (MAF) of 0.05 and a minimum count of 80 % of the sample size, 220,787SNP markers were used to estimate genetic distance between inbred lines using TASSEL v.5.2.24 software [28]. The association between genetic distance with mid and better parent heterosis, SCA, and mean values of hybrids were done using Pearson's correlation coefficients.

2.5. Data analysis

Grain yield and other agronomic traits data analysis of variance (ANOVA) was done using a mixed model procedure of SAS statistical packages [29]. Entry was considered a fixed factor, whereas environment, replication, and incomplete block within replications were considered random factors. Levene's test was used to test the homogeneity of variances before analyzing the combined data [30]. The means were separated using Least Significant Difference (LSD) [31]. Combining ability analysis was done using the Diallel-SAS procedure [32] following Griffing's [33] Method IV and Model I (fixed model).

Table 2

The genotype name, origin, and seed source of parental lines used to make diallel crosses and checks.

Inbred line code	Pedigree	Origin	Source
L1	MM0010022-3-1-1	BNMRC	BNMRC
L2	MM0010003-91-1-1-1-1-1	BNMRC	BNMRC
L3	CML444	CIMMYT	BNMRC
L4	MM0010002-126-3-2-2-1-1	BNMRC	BNMRC
L5	MM0010001-5-1-1-1-1-1	BNMRC	BNMRC
L6	CML197	CIMMYT	BNMRC
L7	MM0010004-9-1-1-1-1-1	BNMRC	BNMRC
L8	MM0010043-B-7-2-1-1	BNMRC	BNMRC
L9	MM0010001-7-1-1-1-2-1-1	BNMRC	BNMRC
L10	MM1110003-56-2-1-2-1-1	BNMRC	BNMRC
Checks			
1	BH540	BNMRC	BNMRC
2	BH543	BNMRC	BNMRC
3	BH546	BNMRC	BNMRC
4	BH547	BNMRC	BNMRC

BNMRC= Bako National Maize Research Center.

Table 3

List of traits with their abbreviation and description.

No	Abbreviation	Trait	Unit	Description of data collection
1	GY	Grain yield	tons per hectare (t ha ⁻¹)	Calculated from field weight of all ears harvested from each plot taking shelling percentage of 80 % and adjusted in to 12.5 % moisture content to estimate grain yield per hectare.
2	DA	Days to anthesis	days	Number of days from planting to the day when 50 % of the plants in a plot started pollen shedding
3	DS	Days to silking	days	Number of days from planting to the day when 50 % of plants emerged 2–3 cm long silk
4	ASI	Anthesis silking interval	days	The interval between days to silking and anthesis (DS-DA)
5	PH	Plant height	cm	The mean height of five randomly taken plants from each plot and measured from the ground level to the first tassel branch
6	EH	Ear height	cm	The mean height of five randomly taken plants from each plot and measured the ground level to insertion point of the top useful ear
7	EP	Ear to plant height ratio	ratio	Calculated as the ratio of the ear height to the plant height
8	EPP	Number of ears per plant	number	Calculated by dividing the total number of ears to the total number plants harvested in each plot

Mid and better parent heterosis were estimated based on the formula suggested by Falconer and Mackay [34].

Mid parent heterosis (%) = $\frac{F_1 - MP}{MP} * 100$; Better parent heterosis (%) = $\frac{F_1 - BP}{BP} * 100$, Where, F1 = Mean of the crosses; MP = Mean of the two parents; BP = Mean of better parent

3. Results

3.1. Mean performance of parents and hybrids

Combined analysis of variance (ANOVA) for inbred lines showed significant difference for all studied traits. Year effect on the performance of parents showed significant difference for grain yield and most of the studied traits except anthesis silking interval (ASI) and number of ears per plant. The interaction effect of parental lines with year also showed significant difference for all traits (Table 4). Inbred lines, L1 and L5, showed the highest yield of 6.33 t ha⁻¹ and 6.11 t ha⁻¹, respectively, followed by L7 (4.14 t ha⁻¹), while L8 and L10 had the lowest grain yield, 2.34 and 2.13 t ha⁻¹, respectively (Table 4).

Mean days to anthesis ranged from 78 to 86 days, with a grand mean of 83.03 days, while mean days to silking ranged from 80.33 to 88.67, with the grand mean of 83.38 days. The shortest days to anthesis and silking were recorded on L1, L3, L4, and L5 parental lines. Mean days to ASI ranged from 1.25 to 3.75, with an overall mean of 2.35 days. Inbred lines L1, L3, L5, and L7 recorded less than two days to ASI. The grand mean of plant and ear height was 181.69 and 86.72 cm, ranging from 153.08 to 226.17 cm and 71.67–105.5 cm,

Table 4

Mean squares and mean values of grain yield and agronomic traits for ten maize inbred lines.

Lines	GY	DA	DS	ASI	PH	EH	EP	EPP	
L1	6.33	78.5	80.3	1.83	188	90.1	0.48	1.29	
L2	3.28	81.5	83.5	2.00	168.5	92.3	0.55	1.04	
L3	4.72	79.8	81.3	1.50	189.5	87	0.45	1.16	
L4	3.2	78.0	80.5	2.42	161.7	79.1	0.49	1.11	
L5	6.12	79.5	80.8	1.25	188.7	87.8	0.46	1.19	
L6	3.22	83.0	85.8	2.92	198.2	105.5	0.55	1.39	
L7	4.15	82.5	84.0	1.42	187.7	86.1	0.47	1.23	
L8	2.35	80.7	84.3	3.75	155.8	71.7	0.46	1.09	
L9	3.53	80.8	84.5	3.67	226.2	95.7	0.41	1.29	
L10	2.12	86.0	88.7	2.75	153.1	72.3	0.49	0.86	
Mean	3.9	81.03	83.38	2.35	181.7	86.7	0.48	1.16	
Maximum	6.33	86	88.67	3.75	226.2	105.5	0.55	1.39	
Minimum	2.12	78	80.33	1.25	153.1	71.7	0.41	0.86	
CV	10.97	1.17	1.19	38.67	4.81	5.22	7.54	9.21	
LSD	0.5	1.11	1.16	1.06	10.28	5.3	0.04	0.13	
Source of variation	Df	Mean square							
		GY	DA	DS	ASI	PH	EH	EP	EPP
Year (Y)	1	2.56**	290.40**	277.35**	0.15	17544.60**	4250.42**	0.0068*	0.0004
Rep/y	4	0.37	8.08**	1.93	2.65*	362.93**	189.12**	0.0034	0.0374
Line	9	12.43**	33.66**	43.19**	4.91**	2994.60**	645.56**	0.0104**	0.1348**
Line × Year	9	1.90**	22.88**	21.87**	6.27**	613.97**	225.60**	0.0150**	0.0885**
Error	36	0.18	0.9	0.99	0.83	76.34	20.52	0.0013	0.0115

*P ≤ 0.05, **P ≤ 0.01, LSD = Least Significant Difference, Df = degree of freedom, CV = Coefficient of variation, Rep = Replication, GY = Grain yield, DA = Days to anthesis, DS = Days to silking, ASI = Anthesis silking interval, PH = Plant height, EH = Ear height, EP = Ear position, EPP = Number of ears per plant.

respectively. Lines L2, L4, L8, and L10 recorded the shortest plant and ear height compared to others. The mean number of ears per plant was recorded 1.16 with a range of 0.87–1.39. The highest number of ears per plant was recorded from L1 (1.29), L6 (1.39), and L7 (1.23) parental lines.

In the combined ANOVA of hybrid trials, environment, genotype, hybrid, genotype \times environment interaction, and hybrid \times environment interaction effects were significant for grain yield and all studied traits except genotype \times environment and hybrid \times environment interaction effects for grain yield and ASI (Table 5). The mean values of the top ten hybrids, including standard checks, are presented in Table 6. The highest grain yield was recorded from the cross, L6 \times L9, followed by L6 \times L7, L4 \times L9, L7 \times L10, L3 \times L9 and L2 \times L9 crosses. The mean grain yield of these top crosses depicted greater than 10 % yield advantage over the high-yielding check, BH546 (8.2 t ha⁻¹). Minimum and maximum days to anthesis and silking were 71.3 and 80.4 days, and 73.7 and 82.3 days, with means of 76 days and 78.4 days, respectively. Among the top ten crosses, L4 \times L9 was early as well as high yielder compared to other hybrids. All top-yielding hybrids showed shorter days to anthesis silking interval than the best hybrid check BH546, and ranged from 1 to 3 days with a mean of 2.5 days. Plant height ranged from 216.9 cm to 281.8 cm with a mean value of 254.7 cm, while ear height varied from 111.22 cm to 159.7 cm with a mean value of 132.6 cm. Ear to plant height ratio (Ear position) ranged from 0.47 to 0.58, with the mean of 0.52. Number of ears per plant varied from 0.9 to 1.5, with overall mean of 1.16 ears per plant. Among the ten top-yielding hybrids, L6 \times L9, L6 \times L7 and L4 \times L9 showed higher number of ears per plant than the best check, BH546.

3.2. Mid and better parent heterosis

Percentage of mid-parent heterosis (MPH) for grain yield ranged from 23.8 % (L5 \times L6) to 282.6 % (L6 \times L10) (Table 7). Highly significant and positive MPH was shown for almost all crosses. Similarly, the highest better parent heterosis (BPH) was recorded at 261.7 % from the cross L8 \times L10, while the lowest was -5.5 % expressed from the L5 \times L6 cross, and most crosses showed positively significant BPH. The lowest percentage of MPH for days to anthesis was -9.9 %, whereas BPH was -11.6 %. Most of the crosses showed negatively significant mid and better parent heterosis for days to anthesis. The MPH and BPH for days to silking ranged from -9.0 % to -2.0 % and -8.5 %–1.7 %, respectively. Out of forty-five crosses, more than half of them expressed negatively significant MPH and BPH for days to silking. MPH and BPH for plant height ranged from 12.1 % to 64.1 % and 9.4 %–62.7 %, respectively (Table 8). MPH and BPH for ear height also ranged from 15.1 % to 85.4 % and 5.4 %–83.6 %, respectively. Almost all crosses expressed positive MPH and BPH.

3.3. Combining ability

The analysis of variance for general combining ability (GCA), GCA \times environment, specific combining ability (SCA), and SCA \times environment is presented in Table 5. GCA and SCA showed significance for all studied traits except the anthesis-silking interval for SCA. The interaction of GCA with environment showed significance except for anthesis-silking. In contrast, SCA \times environment interaction showed non-significance for all studied traits.

The GCA effects of lines for grain yield ranged from -0.77 t ha⁻¹ (L4) to 1.06 t ha⁻¹ (L9) (Table 9). Line, L9 was observed to be high

Table 5
Mean squares for grain yield and agronomic traits for diallel crosses of 10 selected inbred lines.

Source of variation	Df	Mean square							
		GY	DA	DS	ASI	PH	EH	EP	EPP
Environment(E)	2	210.01**	113.92**	439.32**	106.67**	30938.07**	16594.93*	0.054**	1.608**
Rep/E	6	9.32**	51.09**	41.12**	1.24	3517.49**	1886.09**	0.005**	0.082**
Bloc (Rep \times E)	54	2.41	5.73*	5.15**	1.71	268.58	163.81	0.001	0.040**
Genotype (G)	48	10.43**	35.14**	34.02**	2.40**	1586.77**	780.46**	0.005**	0.088**
G \times E	96	2.80	6.12**	5.95**	1.67	365.33**	205.03**	0.002**	0.042**
Hybrids	44	11.23**	45.61**	44.52**	2.08*	1868.68**	997.68**	0.007**	0.106**
Hybrids \times E	88	3.12	6.59**	6.99**	1.62	404.86**	176.68*	0.001*	0.038*
GCA	9	24.17**	193.78**	188.57**	4.25**	5632.96**	2259.98**	0.021**	0.326**
SCA	35	7.90**	7.51**	7.47**	1.52	900.72**	673.09**	0.003**	0.050**
GCA \times E	18	4.93**	15.81**	19.84**	2.22	804.79**	287.14**	0.002*	0.075
SCA \times E	70	2.66	4.22	3.69	1.46	302.03	148.28	0.001	0.028
Pooled error G	234	2.17	4.07	3.67	1.32	213.08	129.28	0.001	0.025
Pooled error hybrids	264	2.30	4.36	3.89	1.49	228.14	131.31	0.001	0.028
%GCA SS	44.0	86.9	86.0	86.0	41.8	61.7	46.3	65.8	62.9
%SCA SS	56.0	13.1	14.0	58.2	38.3	53.7	34.2	34.2	37.1
Mean	8.67	76.0	78.4	2.5	254.7	132.6	0.52	1.16	
Maximum	10.7	80.4	82.3	3.6	281.8	159.7	0.58	1.5	
Minimum	5.0	71.3	73.7	1.3	216.9	111.2	0.47	0.9	
CV (%)	16.99	2.66	2.44	46.85	5.73	8.57	6.37	13.62	

* $P < 0.05$.

** $P < 0.01$, GCA = General combining ability, SCA=Specific combining ability, SS = sum of squares, Df = Degrees of freedom, Rep = Replication, GY = Grain yield, DA = Days to anthesis, DS = Days to silking, ASI = Anthesis-silking interval, EH = Ear height, PH=Plant height, EP = Ear position, EPP=Number of ears per plant.

Table 6Mean performance of top-yielding F₁ hybrids and four checks for grain yield and agronomic traits.

Entry	Hybrids	% GY over best check (BH546)	GY	AD	SD	ASI	PH	EH	EP	EPP
38	L6 × L9	18.8	10.7	77.4	80.6	3.1	277.78	153.22	0.55	1.47
36	L6 × L7	17.2	10.5	77.3	79.7	2.3	266.00	139.89	0.53	1.28
29	L4 × L9	16.2	10.5	73.7	75.7	2.0	265.89	133.00	0.50	1.28
42	L7 × L10	14.4	10.3	79.4	80.9	1.4	261.00	134.11	0.51	1.17
23	L3 × L9	13.2	10.2	74.9	77.1	2.2	270.33	133.44	0.49	1.21
16	L2 × L9	11.2	10.0	77.2	79.7	2.4	281.78	147.22	0.52	1.18
12	L2 × L5	7.3	9.7	76.2	79.1	2.9	256.78	138.56	0.54	1.19
41	L7 × L9	7.2	9.6	76.1	78.4	2.3	272.11	127.11	0.47	1.17
15	L2 × L8	5.9	9.5	77.3	79.8	2.4	251.33	136.11	0.54	1.12
39	L6 × L10	5.6	9.5	79.4	81.9	2.4	274.44	159.67	0.58	1.22
46	BH540		7.1	73.0	75.3	2.3	248.89	129.11	0.51	1.08
47	BH543		8.0	76.3	79.6	3.2	249.67	138.78	0.55	1.14
48	BH546		9.0	74.0	77.6	3.6	262.44	127.11	0.49	1.26
49	BH547		8.7	75.6	78.2	2.7	246.89	135.22	0.55	1.12
	Mean		8.7	76.0	78.4	2.5	254.7	132.6	0.5	1.2
	LSD		1.37	1.87	1.78	1.07	13.56	10.56	0.03	0.15

GY (t ha⁻¹) = Grain yield, DA = Days to anthesis, DS = Days to silking, ASI = Anthesis-silking interval, EH = Ear height, PH = Plant height, EP = Ear position, EPP = Number of ears per plant, LSD = Least Significant Difference.

Table 7

Mid-and better parent heterosis below and above diagonal, respectively for grain yield of diallel crosses of ten maize inbred lines.

Inbred Lines	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10
L1		48.2*	42.4*	27.4	53.2**	60.1**	26.6	35.9	56.7**	22.7
L2	95.3**		105.5**	172.9**	75.7**	160.7**	109.6**	199.3**	186.1**	160.2**
L3	63.2**	142.5**		65.6*	54.4*	93.2**	128.8**	85.7**	124.6**	85.0**
L4	69.3**	176.2**	97.4**		1.0	123.6**	99.6**	110.4**	217.3**	144.3**
L5	55.8**	128.7**	74.4**	32.7		-5.5	48.7**	46.0*	57.1**	50.9**
L6	112.2**	163.1**	129.6**	124.3**	23.8		165.5**	138.6**	236.2**	217.3**
L7	53.0 ^a	134.2**	143.5**	125.4**	77.2**	199.0**		133.7**	125.7**	154.6**
L8	98.2**	248.7**	148.0**	142.6**	110.9**	175.9**	198.5**		164.4**	261.7**
L9	101.2**	196.6**	157.0**	232.8**	99.3**	251.6**	143.9**	217.5**		168.2**
L10	83.8**	216.0**	155.4**	193.9**	124.1**	282.6**	237.1**	280.3**	235.1**	

* P ≤ 0.05.

** P ≤ 0.01.

Table 8

Maximum and minimum MPH and BPH for grain yield and some agronomic traits of diallel crosses of ten maize inbred lines.

Traits	Mean	Mid parent heterosis (MPH)			Better parent heterosis (BPH)		
		Max	Min	SE(m)	max	min	SE(m)
Grain yield	8.7	282.6	23.8	0.44	261.7	-5.5	0.71
Days to anthesis	76.0	-1.9	-9.9	0.60	-3.9	-11.6	0.98
Days to silking	78.4	-2.0	-9.0	0.57	1.7	-8.5	0.93
Plant height	254.7	64.1	12.1	4.36	62.7	9.4	7.12
Ear height	132.6	85.4	15.1	3.31	83.6	5.4	5.40
Ear position	0.52	17.4	-1.7	0.01	14.7	-7.1	0.01
Number of ears per plant	1.16	16.5	-15.4	0.05	10.2	-23.3	0.08

SE(m) = Standard error of the mean, Max = Maximum, Min = Minimum.

general combiner, while L4 was poor general combiner for the trait. Lines L2, L7, and L9 exhibited positive and significant GCA effects for grain yield, whereas L4, L5, and L8 showed highly significant negative effects for the same trait. Lines L1, L3, and L4 showed highly significant and negative GCA effects for days to anthesis and silking while L2, L6, and L10 depicted highly significant and positive GCA effects in the same trait. In the case of plant height, L4 and L8 inbred lines showed negatively significant GCA effects, while L9 and L10 observed positively significant GCA effects. For ear height, L3, L4, L7, and L8 inbred lines showed negative significant GCA effects while L2, L6, L9, and L10 exhibited positive significant GCA effects. Inbred lines, L3, L7, and L9 showed negative significant GCA effects for ear position while L2 and L6 lines showed positive significant GCA effects. Lines L6 and L9 showed positive significant GCA effects for number of ears per plant and were considered good combiners, whereas L2, L4 and L10 showed negative significant GCA effects and poor combiners. Estimating specific combining ability (SCA) effects for grain yield and other agronomic traits showed considerable difference in some crosses (Table 10). For grain yield, L1 × L6, L4 × L9, L6 × L7, and L6 × L9 crosses were the best specific combiners with positively significant SCA effects while L1 × L7, L4 × L5, L5 × L6, and L9 × L10 crosses were poor specific

Table 9
General combining ability effects of ten inbred lines for grain yield and other agronomic traits.

Lines	Traits							
	GY	AD	SD	ASI	PH	EH	EP	EPP
L1	-0.21	-1.89**	-1.45**	0.44**	-2.92	-1.53	0.000	-0.009
L2	0.50*	1.06**	1.03**	-0.03	1.49	6.14**	0.022**	-0.044*
L3	0.15	-1.84**	-1.66**	0.19	-2.89	-5.10**	-0.014**	0.014
L4	-0.77**	-2.47**	-2.82**	-0.35*	-14.51**	-7.78**	-0.001	-0.103**
L5	-0.60**	0.36	0.40	0.04	-3.33	-3.04	-0.006	0.007
L6	-0.23	1.43**	1.57**	0.13	-1.27	5.89**	0.024**	0.102**
L7	0.54*	0.36	0.00	-0.37*	4.61*	-3.40*	-0.023**	0.008
L8	-0.53*	0.43	0.39	-0.05	-6.39**	-3.78*	-0.001	-0.003
L9	1.06**	-0.19	-0.09	0.11	19.01**	4.44*	-0.021**	0.106**
L10	0.08	2.74**	2.64**	-0.10	6.20*	8.15**	0.019*	-0.078*
SE(g)	0.06	0.20	0.25	0.03	10.06	3.59	0.00002	0.001
SE (gi-gj)	0.14	0.44	0.55	0.06	22.36	7.98	0.00005	0.002

* $P \leq 0.05$.

** $p \leq 0.01$, GY = Grain yield, DA = Days to anthesis, DS = Days to silking, ASI = anthesis – silking interval, PH=Plant height, EH = Ear height, EP = Ear position, EPP = number of ears per plant, SE (gi) = Standard error of general combining ability effects, SE (gi-gj) = standard error of the difference of general combining ability effect.

combiners with negatively significant SCA effects.

3.4. Genetic distance and its association with phenotypic traits

Pair-wise, SNP genetic distances between two parental inbred lines ranged from 0.08 to 0.125 (Table 10). Relatively, the largest genetic distance was observed between L1 and L5 lines followed by L1 and L6, L6 and L9, L3 and L5, L1 and L7, L1 and L9, and L3 and L6 lines. On the other hand, the shortest genetic distance was recorded between L4 and L5 lines, followed by L4 and L6 and L5 and L6 lines. Pearson's correlation coefficients were computed for different parameters with SNP marker genetic distance (Table 11). Genetic distance had strong and significant correlation with mean values of grain yield (0.61), ASI (0.361), plant height (0.595) and ear height (0.478). The association of genetic distance with SCA effects were significant and positive for grain yield, plant and ear height, and ear position. The associations of genetic distance with MPH for ASI and ear position were positive and significant while negative and significant for days to anthesis, and non-significant for all other traits. BPH was positive and significant with genetic distance only for ear height, and ear position.

4. Discussion

In this study, the effect of genotype was significant for grain yield and other agronomic traits for both inbred lines and hybrids, indicating significant variation among lines and hybrids. This allows the possibility of selecting good hybrids suitable for mid-altitude maize growing in Ethiopia's agroecology. In addition, hybrid interaction with the environment was significant for grain yield and most other traits, indicating that the performance of hybrids was different across environments. Most of the inbred lines used in this study depicted good grain yield and agronomic performance. These inbred lines with the desirable grain yield and agronomic performance help to develop single cross hybrids that have high yielding and desirable agronomic performance. Almost all top ten hybrids showed 71–80 days to anthesis. These kinds of hybrids are important in the mid-altitude sub-humid agroecology of Ethiopia, which receives rainfall for more than five consecutive months [24]. On the other hand, almost all top ten hybrids showed 1–3 days to ASI, i.e., the crosses had an acceptable range between anthesis and silking days. It is a desired character to improve silking and anthesis synchronization problems during the flowering period for good seed setting [35]. Most top-yielding hybrids showed tall plant height and these hybrids may be more selective in resource-poor farm communities in Ethiopia who used maize residues for animal feed and a fuel sources [36,37].

Estimating GCA and SCA is important to assess the gene effects on grain yield and other agronomic traits [10]. This study showed significant GCA effects for all studied traits and SCA effects for most traits, indicating that both additive and non-additive gene effects contribute to the expression of the traits. The percentage sum square of GCA was greater than that of SCA in all studied traits except grain yield, ASI and ear height, indicating that additive gene action played a greater role in the expression of most agronomic traits. Similar to this study, Yu et al. [38] for normal maize and Mebratu et al. [39] and Tilahun et al. [14] for quality protein maize (QPM) reported the preponderance of additive gene action in the expression of most agronomic traits. On the contrary, Elmyhun et al. [8] stated higher SCA variances for plant and ear height, days to anthesis and silking than GCA variances, indicating a preponderance of non-additive gene action in controlling the traits. The result of this study stated that non-additive gene effects influence the grain yield performance of genotypes. Wegary et al. [40,41] reported similar results with this study working under optimum and stressed conditions. Chiuta and Mutengwa [10] also reported that non-additive genetic effects were responsible for grain yield inheritance under heat-stressed conditions.

Inbred lines L2, L7, and L9 had positive and significant GCA effects for grain yield, indicating that these lines contributed desirable genes to improve grain yield potential in their crosses. Similar results were reported by Wolde et al. [42] for non-QPM inbred lines and

Table 10
SNP genetic distance (below diagonal) and specific combining ability for yield (upper diagonal) of ten maize inbred lines.

Inbred Lines	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10
L1		0.09	-0.09	0.04	1.03	1.21*	-1.26*	0.03	-0.17	-0.88
L2	0.115		0.12	0.40	1.04	-0.71	-1.01	0.85	-0.26	-0.51
L3	0.119	0.116		0.06	0.38	-0.25	-0.03	0.02	0.27	-0.48
L4	0.12	0.115	0.12		-1.10*	-0.45	0.09	-0.62	1.45**	0.14
L5	0.125	0.117	0.123	0.103		-2.88**	0.04	0.59	0.02	0.88
L6	0.125	0.118	0.122	0.093	0.08		1.53**	-0.56	1.15*	0.95
L7	0.121	0.116	0.119	0.12	0.121	0.123		0.34	-0.66	0.97
L8	0.117	0.113	0.116	0.091	0.118	0.118	0.116		-0.69	0.05
L9	0.122	0.114	0.121	0.121	0.112	0.125	0.119	0.117		-1.11*
L10	0.118	0.11	0.117	0.117	0.12	0.121	0.103	0.113	0.116	

* $P \leq 0.05$.** $P < 0.01$.**Table 11**
Pearson's correlation between genetic diversity with mean value of crosses, specific combining ability and heterosis.

Traits	GD with Mean	GD with SCA	GD with MPH	GD with BPH
Grain yield ($t\ ha^{-1}$)	0.61**	0.545**	0.114	0.107
Days to anthesis	-0.2	-0.246	-0.321*	-0.192
Days to silking	-0.124	-0.139	-0.141	-0.214
Anthesis silking interval	0.361*	0.238	0.331*	0.234
Plant height (cm)	0.595**	0.636**	0.156	0.131
Ear height (cm)	0.478*	0.615**	0.243	0.3*
Ear position	0.092	0.459**	0.358*	0.298*
Number of ears per plant	0.236	0.146	0.097	0.142

* $P \leq 0.05$.** $p \leq 0.01$, GCA = General combining ability, SCA=Specific combining ability, MPH = Mid parent heterosis, BPH =Better parent heterosis, GD = genetic distance.

Mebratu et al. [39] and Tilahun et al. [14] for QPM inbred lines. Inbred lines L1, L3 and L4 had desirable GCA effects for days to anthesis and silking, suggesting that these inbred lines could be a potential source of favorable alleles to decrease days to flowering in their crosses. Early maturing types of genotypes are important in areas that receive low precipitation. In the case of plant height, inbred lines L4 and L8 showed negatively significant GCA effects. At the same time, L7, L9 and L10 exhibited positively significant GCA effects, indicating the existence of divergence among inbred lines to improve this trait. The inbred lines with significant negative GCA effects were good combiners to reduce plant and ear height; short plants are less exposed to lodging [24,41]. Crosses that showed significant SCA effects were performed better or poorer than the expected parents' average performance [12,41]. Crosses, L4 \times L9, L6 \times L7, and L6 \times L9 showed the best specific combiners for grain yield. These cross combinations involved L4 and L6 parents having negative GCA effects, with L7 and L9 parents having positive GCA effects for grain yield. This indicated that the existence of high dominant gene effects on these crosses. In general, SCA effects on grain yield can help to exploit the best cross combinations for commercialization and identify heterotic groups of newly developed maize inbred lines [10,24].

Almost all crosses showed positive and significant MPH and BPH for grain yield. Maximum MPH and BPH for grain yield were scored up to 282.6 % and 261.7 %, respectively, and some crosses recorded more than 200 % MPH. Different investigators reported related results; Berhanu [43] noted all crosses showed positive and significant MPH and BPH for grain yield and estimated 202.3 % and 175.5 % average levels of MPH and BPH for mid-altitude adapted maize inbred lines for grain yield, respectively. Wegary et al. [21], in diallel crosses among 15 QPM inbred lines evaluated at Harare, Zimbabwe, and Bako, Ethiopia, reported most of the hybrids had positive mid and better parent heterosis for grain yield with recorded up to 229.2 % and 221.4 % heterosis, respectively. Abera [44] reported that out of 81 crosses, thirty-three hybrids displayed positive MPH up to 250 %, and thirty-three crosses displayed positive BPH up to 235 % for grain yield. Nepir et al. [12] indicated that all crosses showed positively significant heterosis over the mid-parents, while most of the crosses revealed positively significant heterosis over the better parents, and they showed maximum MPH (315.9 %) and BPH (281.8 %). In the case of days to anthesis and silking, almost all crosses showed negatively significant mid and better parent heterosis. The result agrees with Wegary et al. [21]. Almost all crosses depicted positively significant MPH and BPH for plant and ear height. This result agreed with the findings of Nepir et al. [12], who reported positive MPH and BPH for plant and ear height in most crosses. Wegary et al. [21] also reported that positive MPH for both plant and ear height.

The choice of suitable parental lines for hybrid breeding is dependent on the degree of genetic difference among parental inbred lines [45]. The genetic variation determines the extent to which heterosis may be exploited. The more divergent parents, the higher the heterosis and vice-versa [46]. The pair-wise genetic distance generated by the SNP marker showed less genetic divergence among inbred lines and ranged from 0.08 to 0.125. This might be because the inbred lines share a common genetic background. Correlation coefficients between genetic distance with the mean value of F_1 and genetic distance with SCA effects for grain yield were positive and highly significant, indicating the potential of molecular markers to predict hybrid performance. Similar findings were reported by

Wegary et al. [21] and Makumbi et al. [22] showed positively significant correlations between genetic distance with F1 hybrid performance and SCA effects of grain yield in maize. Significant positive correlation was observed between genetic distance with the mean values of plant and ear height, consistent with findings reported by Wegary et al. [21] that showed a positively significant correlation between plant height and molecular genetic distance. The association between genetic distances with MPH and BPH of grain yield showed non-significant. This indicated that the heterosis for grain yield and most agronomic traits were influenced less by the genetic distance of parental inbred lines [19,21].

5. Conclusions

In the present study, some inbred lines had desirable GCA effects for yield and other agronomic traits. Among the inbred lines, L2, L7, and L9 were good general combiners to improve grain yield and other agronomic traits. Crosses, L4 × L9, L6 × L7, and L6 × L9 were good specific combiners and the best-performed single cross hybrids compared to the standard checks. These crosses were generated relatively from parents that had high genetic distance, indicating the possibility of identifying high-yielding single cross hybrids. In this research, several crosses also revealed high MPH and BPH. The association between SNP markers based on genetic distance with SCA and F₁ values of grain yield and most agronomic traits was highly significant. In contrast, MPH and BPH showed nonsignificant correlations with most of the studied traits, suggesting that the GD had limited value in predicting the performance of F₁ hybrids. In general, the information generated in this study would be helpful for the national maize breeding program of Ethiopia in developing desirable cross combinations and identification of high yielding hybrids and inbred parents for their registration and release.

Data availability statement

Data will be made available on request.

CRediT authorship contribution statement

Bitew Tilahun Engida: Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Dagne Wegary:** Writing – review & editing, Visualization, Validation, Supervision, Conceptualization. **Tolera Keno:** Writing – review & editing, Visualization, Validation, Data curation. **Tesfaye Walle Mekonnen:** Writing – review & editing, Validation, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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