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Combining Ability of Tropical Maize Inbred Lines Under Optimum and Low Nitrogen Conditions

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Abstract: Combining ability and trait heritability are critical parameters for developing maize hybrids with stable performance under variable production environments. This study evaluated 19 elite female and 4 male maize inbred lines crossed in a North Carolina Design II mating scheme, generating 76 hybrids along with two standard checks. The hybrids were tested in an alpha-lattice design under both optimum and low-nitrogen (N) conditions. Analysis of variance revealed that both additive and non-additive gene actions significantly influenced grain yield and associated agronomic traits. Notably, inbred line L7 exhibited consistently positive and significant general combining ability (GCA) effects for grain yield across both N regimes, underscoring its potential as a key parental line. Grain yield heritability ranging from 49% under low-N to 51% under optimum N, suggesting that genetic improvement through hybridization and selection are feasible under contrasting fertility conditions. The identification of superior female and male lines highlights valuable parental resources for breeding maize hybrids with enhanced tolerance to N stress. These findings provide a basis for developing resilient and high-yielding hybrids suited to diverse production systems, particularly in low-input environments.

Keywords: Additive; General combining ability; Gene action; heritability; specific combining ability

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1. Introduction

Maize (*Zea mays* L.) is one of the most important cereal crops globally, cultivated for food, feed, and industrial purposes (Kamara et al., 2020). Together with wheat and rice, it provides about 42% of the world's food calories and 37% of protein intake (FAOSTAT, 2021). Global maize production increased from 313 million metric tons in 1971 to 1,162 million metric tons in 2020 (FAOSTAT, 2024).

In sub-Saharan Africa (SSA), maize is the most widely grown and consumed staple crop, providing dietary energy to more than 300 million people while also serving as livestock feed and raw material for agro-industries (Cairns et al., 2021). In Ethiopia, maize contributes the largest share (35%) of total grain production (CSA, 2022). Despite its significance, the national average yield of 4.2 t ha^{-1} lags behind the global mean of 5.8 t ha^{-1} (USDA, 2021). This yield gap is largely attributed to low-input farming systems characterized by inadequate fertilizer use, limited pesticide application, and scarce irrigation facilities (Badu-Apraku et al., 2017).

Among production constraints, low soil nitrogen (N) is recognized as the most critical factor limiting maize productivity in SSA (Ribeiro et al., 2020). Although fertilizer application of 90-120 kg N ha^{-1} is recommended for optimum productivity (Sadou et al., 2018), resource-poor smallholder farmers rarely achieve this level due to high fertilizer costs and limited access. Consequently, maize yields are reduced by 10-50% annually under low-nitrogen (low-N) conditions (Ribeiro et al., 2020; Mukhtar et al., 2025). Developing low-N tolerant maize hybrids is therefore critical for sustainable production and food security.

The choice of breeding strategy and program design is dependent on trait heritability and genetic architecture. Hybrid breeding relies heavily on information about heterosis and combining ability, which provide insights into the genetic potential of parental lines and guide the development of superior hybrids (Dosho et al., 2021). Combining ability analysis is a classical and widely used tool in hybrid breeding programs, as it partitions the genetic contribution of parental lines based on progeny performance (Allard, 1960). General combining ability (GCA) is associated with additive gene effects, while specific combining ability (SCA) reflects non-additive gene actions such as dominance and epistasis (Sprague & Tatum, 1942). Both types of gene action are relevant in maize

breeding. Several studies have demonstrated that additive effects tend to play a more prominent role in governing yield and related traits (Woldu et al., 2020; Fortunate et al., 2022). However, under stress environments such as low-N, non-additive effects may become more important in determining grain yield (Bedassa et al., 2021).

Although nitrogen-use efficiency is essential for maize productivity in SSA, few studies have evaluated the combining ability and heritability of newly developed tropical maize inbred lines under both optimal and low-N conditions, especially in Ethiopian highland germplasm, yet it is critical for identifying promising parental lines and designing strategies to develop high-yielding, low-N tolerant hybrids for smallholder farming systems.

We hypothesized that additive effects would predominate for most agronomic traits under both nitrogen regimes, while non-additive effects would contribute more strongly to grain yield under low-N stress, and that these traits would show moderate to high heritability, enabling genetic improvement through selection and crossing. Accordingly, the objectives were to (i) estimate the general and specific combining ability effects of grain yield and related agronomic traits under optimum and low-N conditions, and (ii) determine the heritability to guide breeding strategies for improving maize productivity in nitrogen-limited environments.

2. Materials and Methods

2.1. Soil analysis and plant materials

Soil samples were collected before planting from the low-N experimental field at Ambo Agricultural Research Center (AARC), from the optimal-N fields at Holetta Agricultural Research Center (HARC) and Adet Agricultural Research Center. Composite samples were taken diagonally across pots with an auger at 0-30 cm depth and analyzed at the HARC soil laboratory (Table 1). Planting materials included four maize inbred lines as male parents and 19 inbred lines as female parents. Crosses were made using the North Carolina Design II (Comstock and Robinson, 1952) at AARC in 2020, producing 76 single-cross hybrids. Two commercial checks (AMH851 and AMH853) were included. Parental lines are listed in Table 2.

Table 1. Soil properties under low- N and optimal condition of 2021 cropping season

Field	pH	OC%	P PPM	Mg PPM	Ca PPM	K PPM	Na PPM	N%
AARC	7.98	1.13	6.93	0.84	2.37	0.77	0.14	0.07
HARC	6.23	1.49	12.26	2.99	6.31	0.09	0.14	0.10

pH= power of hydrogen, OC =organic content, P PPM= phosphorus, Mg= magnesium, Ca = calcium, K = potassium, Na = sodium, N= nitrogen, ppm = parts per million.

Table 2. Description of maize inbred lines used in the North Carolina Design II

Group of lines	*Code*	*Pedigree*
Male group	L1	HLF0005
	L2	MH9907013-1-2-2-2-#-#-B
	L3	HLF0012
	L4	HLF0009
Female group	L1	MH1500562-14-1-2-3-B-B
	L2	MH1500708-30-1-1-1-B
	L3	MH1500525-10-2-2-1-B-B
	L4	MH1500702-20-2-2-1-B
	L5	MH1500485-28-3-1-2-B-B
	L6	MH1500684-5-2-3-1-B
	L7	MH1500475-4-2-1-2-B-B
	L8	MH1500696-16-2-1-1-B
	L9	MH1500470-4-1-2-1-B-B
	L10	MH1500524-10-2-1-2-B-B
	L11	MH1500477-4-2-2-2-B-B
	L12	MH1500679-2-1-1-1-B
	L13	MH1500692-12-1-2-1-B
	L14	MH1500617-24-2-2-2-B-B
	L15	MH1500829-15-2-B-B
	L16	MH1500703-24-1-1-1-B
	L17	MH1500680-2-2-1-1-B
	L18	MH1500693-14-1-2-1-B
	L19	MH1500603-23-3-1-3-B-B
Checks	1	JIBAT (AMH851)
	2	KOLBA (AMH853)

L=Lines

2.2. Study sites and trial management

Field trials were conducted in 2021 at three Ethiopian Institute of Agricultural Research centers: AARC ((8°57′ N, 38°07′ E; 2225 m. a. s. l.; 1018 mm annual rainfall), HARC (9°03′ N, 38°30′ E; 2400 m. a. s. l; 1144 mm annual rainfall), and Adet ARC (11°16′ N, 37°29′ E; 2216 m. a. s. l.; 1250 mm annual rainfall). An alpha-lattice (0,1) design with two replications was used (Patterson and Williams, 1976). The low-N trial at AARC was conducted on a field depleted by continuous maize cultivation with residue removal. Optimum-N trials were conducted at HARC and Adet ARC with urea and NPS

fertilizers applications. Plots consisted of four rows, 5.25 m long, with 0.75 m row spacing and 0.25 m plant spacing.

2.3. Data collection

Data on grain yield and other important agronomic traits was collected as follows: Days to anthesis (DA): The number of days from emergence to when 50% of the plants in a plot started shedding pollen. Days to silking (DS): The number of days from plant emergence to when 50% of the plants in a plot have grown 2 to 3 cm long silks. Grain yield (GY): Field weight from all the ears of each experimental unit was measured and used to calculate grain yield (expressed in tons ha^{-1} and adjusted to 12.5% moisture content). Ear Length (EL): The length of the ear from the base to the tip in centimeter; it was measured as the average length of five randomly sampled ears from each experimental unit. Ear diameter (ED): This was measured mid-way along the ear length as the average diameter of five sampled ears. Number of kernels per row (KPR): This was recorded as the average number of kernels per row from five randomly selected ears. Number of rows per ear (RPE): This was recorded as the average number of kernel rows per ear from five randomly sampled ears. Thousand kernel weights (TKW): After shelling, random kernels from the bulk of shelled grain in each experimental unit were taken and a thousand kernels were counted and weighed in grams and then adjusted to 12.5% grain moisture.

2.4. Statistical analysis

Analysis of variance (ANOVA) was performed in R version 4.3.2 (R Core Team, 2023). In the analysis, locations, blocks and replications were considered random effects because they represent a sample of environments and experimental units drawn from a broader population. Genotypes were considered fixed effects since the primary objective of the study was to evaluate and compare the performance of specific genotypes under investigation. This model structure allowed appropriate estimation of variance components and subsequent calculation of heritability. Model assumptions, including normality of residuals, homogeneity of variance, and independence of observations, were checked using Shapiro-Wilk and Levene's tests and by inspecting residual plots. All assumptions were met. Significance was declared at $\alpha = 0.05$. Mean separation among genotypes was performed

using Duncan's multiple range test following ANOVA, and the results are interpreted as descriptive comparisons among genotype means. General combining ability effects, specific combining ability effects and genetic variance components were estimated using AGD-R software (Rodriguez et al., 2018) following Griffing's method (Griffing, 1956) for a North Carolina design II (NC II) mating scheme. The general linear model used for the NC II design (Suza et al., 2023) was:

$$yijk = \mu + mi + fij + mfij + rk + eijk$$

Where: *yijk* is the observed value, μ is the general mean, *mi* is the male effect, *fj* is the female effect, *mfij* is the interaction effect of female j when crossed to male *i, rk* is the replication effect and eijk is the residual error.

Narrow-sense heritability (h^2) was computed as:

$$h^2 = \sigma^2a/\sigma^2p$$

where, σ^2a = additive genetic variance (Singh 1993) and σ^2p denotes phenotypic variance.

Relative reduction in grain yield and agronomic traits under low-N was calculated as Banziger et al. (1997), using the formula (1 - MV low- N / MV optimal N), where MV low- N represents the mean trait value acquired in the experiment under low- N and MV optimum N represents the mean trait value obtained in the experiment under optimum N conditions.

3. Results

3.1. Combining ability analysis for grain yield and related traits

Combined analysis of variance across environments revealed highly significant ($P < 0.01$) effects of genotypes, sites, genotype x site interaction, female and male GCA, SCA, and site x female, and site x male interactions for grain yield (GY, t ha^{-1}). The genotype x site interaction was particularly significant for days to anthesis (DA, days), GY, and thousand kernel weight (TKW, g). Male and female GCA effects were significant ($P < 0.01$) for most of the traits, underscoring the contribution of both parental groups. The male x female interaction was also highly significant for GY and TKW. In

the combined analysis, SCA contributed more than GCA to the total genetic variance for GY (Table 3.1), confirming the importance of non-additive effects.

Under optimum conditions**,** significant ($P < 0.01$) effects were observed for site, genotype, and male GCA for GY. Site x genotype and site x female interactions were significant ($P < 0.01$) for DA and days to silking (DS, days**)** (Table 3.2), indicating that these traits were mainly influenced by site, genotypes, and male GCA effects.

Under low-N conditions, highly significant differences ($P < 0.01$) were observed for genotype, female GCA, and male GCA for most traits. For GY specifically, genotype effects were non-significant, whereas female GCA remained significant (Table 3.3). This indicates that additive parental effects contributed more to yield variation than overall hybrid differences under stress. The non-significant genotype effect further highlights the importance of exploiting heterosis to enhance yield stability under low-N conditions. These results indicate that both additive and non-additive gene actions contribute to trait expression across nitrogen regimes; however, additive effects were more pronounced under low-nitrogen conditions, where SCA effects were non-significant. Such patterns are common under stress environments, where reduced phenotypic variability may mask underlying genetic differences.

Table 3. Analysis of variance for grain yield and other traits at combined, optimum N and low-N environments

Table 3.1. Combined environments		Mean squares							
Source of variation	DF	DA	DS	GY	EL	ED	KPR	RPE	TKW
Site	2	1066**	3231**	616**	110**	208**	362**	2	305186**
Block (Rep x Site)	3	0.69	0.81	3.17**	0.69	1.35	10.63**	0.59**	1170**
Genotypes	75	19.80**	24.31**	2.63**	3.17**	42.9**	24.46**	3.89**	4637**
Male GCA	3	18.43	22.8	15.61**	25.23**	585.3**	208.78**	8.26**	37395**
Female GCA	18	47.37**	64.09**	2.85**	3.06*	59.3**	28.80**	11.2**	6175
Male x Female SCA	54	10.58	11.04	1.85**	1.93	7.27	12.70*	1.21	2359**
Site x Genotypes	150	12.61**	11.75	2.14**	2.03	7.53	8.97	1.26	2776**
Site x Male	6	14.75	16.44	3.44**	2.11	30.75**	5.47	3.01*	14408
Site x Female	36	14.82**	17.21**	3.09**	2.17	5.03	12.44	2.68**	2413
Site x Male x Female	108	11.82*	9.72	1.74*	2.02	7.22	8.09	0.7	2223
Error	219	8.7	9.8	1.33	1.67	6.54	8.47	0.95	2044
%GCA female	-	57.64	63.44	25.94	32.19	33.1	28.32	69.01	32
%GCA male	-	3.74	3.76	23.66	23.44	54.69	34.21	8.5	32
% SCA	-	38.63	32.8	50.39	44.38	12.23	37.47	22.48	36
SE m		0.57	0.56	0.09	0.10	0.3	0.17	0.05	0.8
CV%		9.68	8.8	14.23	7.75	10.3	6.11	5.22	4.2
Table 3.2. Optimum N									
Site	1	3673.1**	5930**	2135.6**	25	21	36	32	25
Block (Rep x Site)	2	1.60*	0.81	10.43**	1.08	480	17.50*	0.49	2678*
Genotypes	75	17.80**	18.16**	3.44**	2.00**	24.67**	13.85**	3.37**	5036**
Male GCA	3	22.37	24.96	22.11**	7.77**	295.72**	97.82**	8.43**	33863**
Female GCA	18	33.66**	37.45**	3.23*	2.86**	32.29**	19.20**	10.2**	5269*
Male x Female SCA	54	12.14	11.21	2.48	1.39**	7.07*	7.4	0.82	3357
Site x Genotypes	75	15.53**	13.59	3.21**	45	35	56	2.3	231

Site x Male	3	26.22	28.06*	1.01	21	5.6	23	1.3	213
Site x Female	18	14.78**	18.11*	5.29**	12	21	5.9	1.5	217
Site x Male x Female	54	15.32*	11.42	2.63*	201	32	9.2	0.9	205
Error	146	10.26	10.38	1.86	1.22	4.62	6.37	0.62	2925
% GCA female	-	45.5	49.8	22.5	34.4	31.4	33.3	72.4	25.1
% GCA male	-	5.1	5.5	25.7	15.53	48	28.3	10	26.9
% SCA	-	49.4	44.71	52	50	20.6	38.4	17.6	48
Table 3.3. Low-N									
Block (Rep x Site)	1	0.14	1.11	0.01	0.14	1.44	2.98	0.07	0.9
Genotypes (Geno)	75	12.18**	16.5**	0.38	3.20**	26.25**	19.60**	1.76	51.4*
Male GCA	3	2.92	3.7	0.65	19.39**	332.82**	116.01**	2.7	328.3**
Female GCA	18	29.44**	42.68**	0.59**	2.39	31.66**	22.13**	3.63**	55.7*
Male x Female SCA	54	6.94	7.85	0.29	2.57	7.41	13.4	1.09	34.6
Error	73	5.59	8.65	0.28	2.13	8.35	10.57	1.28	32.1
%GCA female	-	58	63.8	37.6	18	29	27.1	49.4	26
%GCA male	-	1	1	6.85	24.2	50.7	23.68	6	25.5
% SCA	-	41	35.2	55.57	57.8	20.3	49.22	44.5	48.5

**=Significant at the 0.01 probability level, *=Significant at the 0.05 probability level, DA = days to anthesis (day), DS = days to silking (day), GY= grain yield (t ha^{-1}), EL= ear length (cm), ED= ear diameter (cm), KPR=number of kernels per row (number), RPE= number of rows per ear (number), TKW=thousand- kernel weight (g)

3.2 Variance components and heritability under optimum and low-N

Across combined environments**,** additive variance exceeded dominance variance for most traits, except for GY, where dominance variance was higher and SCA variance surpassed GCA variance (Table 4). This indicates that non-additive gene action plays a major role in governing GY across environments, whereas additive effects are more important for other traits.

Under optimum nitrogen conditions**,** moderate heritability estimates were observed for most traits, with number of rows per ear (RPE, number) showing comparatively higher values. Genotypic variance was relatively high for RPE and number of kernels per row (KPR, number), suggesting good potential for selection under favorable growing conditions.

Under low-N conditions, additive variance exceeded dominance variance for all traits except ear length (EL, cm). Female variance components were higher for GY, DA, DS, and RPE, whereas genotypic variance was more pronounced for GY, DA, and ear diameter (ED, cm). Environmental variance contributed substantially to most traits under stress, reflecting the influence of low-N conditions on trait variability. These patterns suggest that selection based on both parental GCA and overall genetic variance could effectively improve performance under both optimum and low-N environments.

Table 4. Variance components and heritability at optimum N (OP) and low-N (LN)

	δ^2g		δ^2 male		δ^2 Female		δ^2gca		δ^2sca	
Traits	OP	LN	OP	LN	OP	LN	OP	LN	OP	LN
DA	1.86	3.23	0.14	0.01	1.35	2.81	0.47	0.67	0.81	1.52
DS	1.92	3.7	0.18	0.02	1.64	4.35	0.21	0.04	1	2.38
GY	0.4	0.52	0.26	0.01	0.05	0.04	0.16	0.08	0.14	0.03
EL	0.39	0.54	0.17	0.44	0.18	0.02	0.09	0.22	0.18	0.18
ED	2.78	8.95	1.93	8.56	0.98	3	0.38	0.02	1.4	5.4
KPR	3.74	4.52	2.38	2.70	1.48	1.09	0.51	1.87	1.87	1.8
RPE	1.37	0.24	0.2	0.04	1.18	0.31	0.1	0.02	0.74	0.2
TKW	268	9.68	200	7.73	68.23	2.63	50.31	1.29	126.76	4.88

	δ^2A		δ^2 D		δ^2e		h^2	
Traits	OP	LN	OP	LN	OP	LN	OP	LN
DA	3.24	6.09	1.88	2.69	5.2	2.79	0.5	0.75
DS	3.98	9.53	0.84	0.01	4.2	4.33	0.53	0.67

GY	0.56	0.11	0.63	0.03	1.14	0.14	0.51	0.49
EL	0.71	0.73	0.34	0.89	0.61	1.06	0.63	0.6
ED	5.59	21.9	1.51	0.05	5.72	4.17	0.55	0.84
KPR	7.5	7.21	2.05	5.28	3.19	5.28	0.75	0.71
RPE	3	0.78	0.41	0.51	0.31	1.87	0.92	0.55
TKW	507	19.54	201.22	5.12	902.12	16.03	0.44	0.61

DA = days to anthesis (day), DS = days to silking (day), GY= grain yield (t ha^{-1}), EL= ear length (cm), ED= ear diameter (cm), KPR=number of kernels per row (number), RPE= number of rows per ear (number), TKW=thousand-kernel weight (g). δ^2g= genotypic variance, δ^2gca and δ^2sca= general and specific combining ability variances, respectively; δ^2A and δ^2D= additive and dominance genetic variances respectively, δ^2e= environmental variance h^2 = narrow-sense heritability.

3.3. General combining ability effects under contrasting environments

Several inbred lines showed significant GCA effects for GY and related traits (Table 5). Under both the optimum and low-N conditions, inbred line L7 consistently displayed positive and significant ($P < 0.05$) GCA effects for GY (Figure 1) and contributed positively to TKW, confirming its stability and strong additive value across low-N and optimum conditions. Other lines also contributed differently to trait expression. For example, L10 showed contrasting GCA effects for phenology, while L19 expressed GCA effects for kernel traits under optimum conditions (Table 6). These patterns are useful for identifying superior lines and clarifying which parents contribute favorable additive effects toward improving grain yield and associated traits. Under low-N conditions, inbred lines L6 and L12 showed positive and significant GCA effects for phenology (Table 6), suggesting that these parents contribute additive gene effects that delay maturity.

Table 5. General combining ability effects across locations for grain yield and other related traits

	Lines	DA	DS	GY	EL	ED	KPR	RPE	TKW
Female Lines	L1	-1.73	-1.97	-0.01	-0.06	-2.40	-1.19	-0.75	-9.60
	L2	0.28	-0.18	0.59	-0.68	-0.60	-0.40	0.64	-12.46
	L3	0.03	-0.45	-0.05	-0.54	-1.13	0.39	-0.06	-14.41
	L4	-0.99	-1.44	0.10	0.93*	-1.35	2.24	-0.08	9.75
	L5	0.57	1.11	-0.17	-0.18	-0.38	-0.99	0.10	14.37
	L6	1.83	1.91	-0.52	0.17	-0.36	2.26	0.70	-37.00*
	L7	-1.70	-2.01	0.67*	-0.47	2.61	-2.34	-0.64	30.67*
	L8	0.46	-0.52	-0.08	0.41	0.70	1.39	0.66	-11.54
	L9	-1.57	-0.79	0.12	-0.08	1.13	-0.77	0.54	2.94
	L10	-3.07*	-2.82	0.25	0.33	-1.52	-0.05	-1.41	3.92

	L11	-0.39	-0.25	0.36	-0.39	2.59	-2.44*	-0.30	17.56
	L12	2.06	1.82	0.24	-0.05	1.44	0.67	0.69	-7.28
	L13	1.88	1.78	-0.15	0.03	1.47	-0.25	0.91	-0.01
	L14	-0.13	0.25	-0.24	-0.71	-0.86	-0.49	-0.83	1.77
	L15	0.48	-0.29	-0.63	0.32	-1.14	0.70	-1.34	-8.79
	L16	1.79	2.62	-0.34	0.52	1.10	1.90	0.78	-3.58
	L17	0.22	0.69	-0.30	0.16	1.22	0.60	0.74	-9.97
	L18	1.04	2.49	0.32	0.33	2.01	-0.32	1.07	0.20
	L19	-1.12	-2.15	-0.05	0.07	-5.24**	-0.49	-1.46	31.67*
Male	L1	-0.04	0.10	-0.03	-0.05	-1.25	1.09	0.36	-18.07
Lines	L2	0.11	0.64	-0.43	0.85	-3.15	1.84	-0.42	-13.98
	L3	0.45	0.88	0.48	-0.35	3.29	-1.30	-0.06	13.90
	L4	-0.54	-1.71	0.01	-0.42	0.96	-1.55	0.11	17.77

**=Significant at the 0.01 probability level, *=Significant at the 0.05 probability level, DA = days to anthesis (day), DS = days to silking (day), GY= grain yield (t ha^{-1}) EL= ear length (cm), ED= ear diameter (cm), KPR=number of kernels per row (number), RPE= number of rows per ear (number), TKW=thousand kernel weight (g).

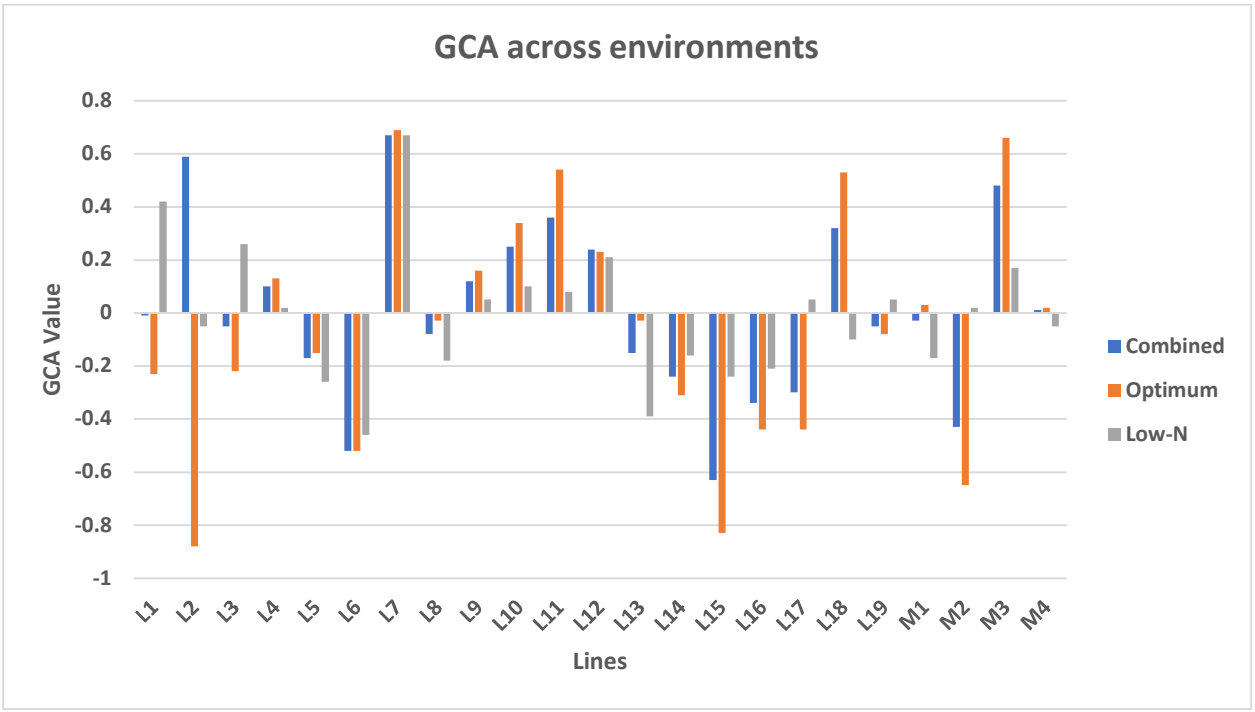

Figure 1. GCA effects for grain yield across the environments in maize inbred lines (L1-L14 designated as female parents while, Lines M1-M4 designated as male parents)

Table 6. General combining ability effects at optimal (OP) and low-N (LN) conditions for grain yield and other related traits

	DA		**DS**		**GY**		**EL**		**ED**		**KPR**		**RPE**		**TKW**	
	OP	LN	OP	LN	OP	LN	OP	LN	OP	LN	OP	LN	OP	LN	OP	LN
L1	-0.94	-3.38	-1.66	-2.58	-0.23	0.42	-0.1	-0.3	-2.8	-0.1	-0.4	-0.1	-0.9	-0.2	-47.8	-32.1
L2	0.38	0.13	0.24	-1.04	-0.88*	-0.05	-1.1	-2	-0.1	0.3	-0.8	0.2	1.1	0.3	-22.6	18.2
L3	0.74	-1.25	-0.14	-1.08	-0.22	0.26	-0.6	0.01	-1.2	0.1	0.7	0.3	-0.3	0.6	-25.9	20.2
L4	-0.9	-1.27	-0.93	-2.44	0.13	0.02	0.8	0.1	-1.7	-1.3	1.4	1.1	0.3	0.1	7.8	6.2
L5	0.68	0.28	1.51	0.32	-0.15	-0.26	-0.2	0.1	0.5	0.9	-1.7	-1.2	-0.2	0.2	39.2	34.1
L6	0.84	3.73*	1.18	3.34	-0.52	-0.46	0.5	-0.6	0.5	0.1	3.8*	2.1	1.3	1.1	-55.1*	-22.5
L7	-1.34	-2.4	-1.8	-2.44	0.69*	0.67*	-0.8	0.2	2.1	3.1	-2.6	-1.0	-0.4	-0.2	32.8	18.6
L8	-0.12	1.62	-1.11	0.67	-0.03	-0.18	0.6	0.2	-0.1	-0.3	2.7	2.1	1.1	1.2	-0.3	-.02
L9	-2.15	-0.52	-1.84	1.31	0.16	0.05	-0.1	-0.2	1.4	1.3	-1.8	-1.2	0.8	0.3	18.2	14.3
L10	-3.6*	-2.27	-2.75	-2.94	0.34	0.1	0.2	0.4	-2.4	-2.1	-0.3	-0.1	-1.4	-1.2	1.5	1.2
L11	0.02	1.15	0.12	0.98	0.54	0.08	0.1	0.01	2.7	2.3	-0.9	0.01	-0.1	0.1	20.3	16.2
L12	1.9	2.55	0.69	4.6*	0.23	0.21	0.2	0.1	1.3	1.2	-0.3	0.1	0.8	0.1	-10.9	-11.2
L13	1.66	2.37	1.52	2.3	-0.03	-0.39	0.7	0.3	2.0	2.1	0.1	0.6	0.9	0.9	3.0	2.1
L14	0.03	-0.37	0.33	0.08	-0.31	-0.16	-0.9	-0.5	-0.1	-0.3	-1.8	1.2	-0.9	-0.5	-2.6	2.0
L15	-0.54	2.52	-0.02	-0.84	-0.83*	-0.24	0.2	0.1	-1.1	1.4	0.4	0.3	-2.5*	-2	2.0	2
L16	2.73	0.05	3.14*	1.56	-0.44	-0.21	0.3	0.6	0.8	0.10	0.8	0.2	0.9	0.5	-22.8	-20.3
L17	-0.22	1.07	-0.13	2.37	-0.44	0.05	0.6	0.7	2.1	1.2	0.9	0.3	0.8	0.2	-6.8	3.5
L18	1.21	0.68	2.3	2.89	0.53	-0.1	0.9	0.7	1.9	1.6	0.3	0.1	0.8	0.5	2.9	3.9
L19	-0.62	-1.96	-1.24	-3.97	-0.08	0.05	-0.7	-0.3	5.5**	1.9	-0.4	0.2	-2.3*	-2.1	54.1*	42.3
L1	0.01	-0.14	0.15	-0.2	0.03	-0.17	0.0	0.01	-0.3	0.1	1.3	1.2	0.57	0.3	-20.1	-15.3
L2	0.22	-0.12	0.13	0.48	-0.65	0.02	0.7	0.6	-3.4	1.3	1.5	0.1	-0.60	0.3	-23.6	-12.3
L3	0.49	0.38	0.43	0.16	0.66	0.17	-0.4	-0.2	3.3	1.2	-1.4	0.6	0.05	0.02	3.2	3.0
L4	-0.78	-0.04	-0.83	-0.32	0.02	-0.05	-0.3	-0.1	0.5	0.6	-1.5	-0.3	-0.08	-0.1	37.7	23.9

DA = days to anthesis, DS = days to silking, GY= grain yield (t ha−1), EL= ear length, ED= ear diameter, KPR=number of kernels per row, RPE= number of rows per ear, TKW=thousand-kernel weight

Under low-N conditions, crosses L2 x L2, L2 x L15, L3 x L7, and L4 x L1 showed positive and significant ($P < 0.05$) SCA effects for GY, whereas crosses such as L2 x L15, and L4 x L18 recorded negative and significant effects for flowering. These results underscore the importance of selecting lines with favorable GCA and hybrids with strong SCA for developing high-yielding and resilient hybrids.

Table 7. Specific combining ability effects of selected significant crosses at combined locations

Crosses	DA	DS	GY	EL	ED	KPR	RPE	TKW
L1 X L1	1.36	2.02*	-0.28*	-0.16	-0.04	-0.08	0.87*	-9.03
L2X L1	-0.4	0.22	-0.11	-0.6	-0.59	-0.88	-0.88*	0.79
L4X L1	-1.15	-1.53	0.91*	1.05	0.49	2.55	-0.58	18.11
L3 X L4	1.22	0.08	-0.06	1.36*	0.57	1.39	-0.22	0.8
L4 X L4	0.56	1.38	-0.39	-0.86	-0.58	-2.93*	-0.24	38.03*
L1 X L5	1.09	1.22	0.36	0.02	-0.96	0.64	-0.19	12.32
L1 X L11	1.41	2.83**	-0.45	-0.57	0.66	-0.52	0.92*	-2.44
L4 X L13	0.33	-0.14	0.52	-0.39	-1.44	-1.31	1.27**	-13.26
L3 X L15	-0.57	-0.25	-0.93*	-0.83	-1	-4.80**	-0.68	3.94
L2 X L16	-0.68	-1.09	0.88*	0.41	-0.62	0.54	0.07	28.59
L3 X L16	0.76	1.32	-0.94*	-0.7	0.33	-1	0.42	-18.6
L4 X L16	1.38	1.23	0.66	0.46	0.82	1.88	0.06	-4.57
L2 X L17	0.3	0.44	0.43	0.17	1.71	2.44	0.14	-14.13
L4 X L17	-0.26	-0.13	-1.01**	0.5	1.01	1.15	0.39	26.77
L1 X L18	-3.70**	-2.81**	0.28	0.15	2.62*	0.8	0.19	-2.51
L2 X L19	0.16	-2.22*	-0.81	0.25	0.13	-2.19	0.02	34.77*
Table 7.2 Optimum N								
L1 X L1	2.66*	4.15**	-0.81	0.75	0.08	-0.81	1.35**	2.05
L2 X L1	-0.9	-0.01	-0.14	-0.79	-0.16	-0.14	-1.08*	-13.43
L1 X L4	-1.61	-1.73	0.41	3.16*	0.99	3.16*	0.39	15.68
L1 X L5	0.9	0.58	0.51*	-0.5	0.13	0.24	-0.27	-25.57
L3 X L6	2.06	2.69*	-1.26*	-1.19	-0.86	-1.65	-0.23	22.9
L3 X L9	-0.79	-1.03	1.27*	-1.31	-0.65	-0.55	-0.35	25.23

L2 X L11	-0.8	-1.67	0.24	-3.13*	-1.89	-2.23	-1.19*	-37.49
L2 X L13	0.91	0.99	-0.45	-1.13	-1.39*	-0.54	-0.12	-15.52
L3 X L13	-1.3	-0.97	-0.51	3.6*	1.66*	4.53**	-0.05	38.42
L2 X L16	-1.05	-1.44	1.33*	0.62	1.09	0.9	0.1	41.81
L3 X L16	1.91	2.88*	-1.5*	-0.65	-0.95	-0.94	0.64	-33.58
L1 X L18	-5.1	-3.67**	0.45	4.46**	-0.57	0.04	-0.18	-0.23
L2 X L18	1.15**	1.79	-0.23	-2.13	1.34*	1.3	0.37	58.57
L2 X L19	1.37	-1.81	-1.27*	1.41	0.56	-0.97	0.12	49.43
Table 7.3 Low-N								
L1 X L2	-1.36	-2.14	-0.49	-0.01	-3.21*	0.32	0.37	-7.95*
L1 X L4	-1.56	-1.84	0.08	-1.53	-3.09*	-1.35	0.21	-7.14*
L1 X L9	3.39*	1.47	-0.18	-0.33	-0.25	0.13	0.29	0.67
L2 X L2	-0.38	-0.97	0.68*	-0.87	0.7	0.04	0.4	2.62
L2 X L15	-4.28**	-4.17**	0.65*	-0.48	-1.57	-1.2	-1.18*	3.22
L3 X L6	0.52	-0.88	0.43	0.28	-6.22*	1.03	-1.48**	1.75
L3 X L7	-0.46	-1.2	0.61*	1.35	1.3	2.74	0.77	3.08
L3 X L 9	-1.33	0.05	0.1	0.56	-0.58	1.16	-0.06	2.83
L3 X L14	1.52	2.27	-0.15	-1.08	-1.37	1.78	0.27	-4.86
L3 X L15	-1.68	0.25	-0.87**	-2.26**	-2.04	-5.27**	-0.23	0.93
L4 X L1	-1.86	-0.52	0.75**	1.27	1.27	2.02	-0.09	1.04
L4 X L4	-0.46	-0.66	-0.09	-0.86	-0.22	-3.16	-0.25*	7.40*
L4 X L6	0.94	-0.4	-0.41	0.41	4.21*	0.57	1.41**	3.76
L4 X L7	-0.44	1.24	-1.02**	-2.39**	-3.40*	-4.40*	-1	-4.49
L4 X L8	-1.46	-1.38	0.56	1.83*	-0.87	4.19*	0.25	-0.72
L4 X L12	-0.29	-0.16	-0.12	-1.27	-1.16	-1.98	-0.75	-1.26
L4 X L15	7.64	3.64*	0.42	1.84*	1.04	4.44*	1.33*	-3.83
L4 X L18	-0.91	-3.01*	0.21	-0.88	-1.09	-2.27	-1.22**	-0.83

**=Significant at the 0.01 probability level, *=Significant at the 0.05 probability level, DA = days to anthesis (day), DS = days to silking (day), GY= grain yield (t ha^{-1}), EL= ear length (cm), ED= ear diameter (cm), KPR=number of kernels per row (number), RPE= number of rows per ear (number), TKW=thousand-kernel weight (g)

4. Discussion

The combining ability of maize inbred lines provides valuable insights for designing breeding strategies and predicting hybrid performance. The present findings revealed substantial genetic variation among genotypes under both low-N and optimal-N environments, providing opportunities to enhance grain yield (GY) and other agronomic traits through selection and

hybridization. Highly significant genotype x environment interactions observed for most traits confirm that genotypes respond differently to contrasting nitrogen conditions. Similar findings have been reported in tropical quality protein maize hybrids under stress (Wegary et al., 2014; Badu-Apraku et al., 2016; Bedassa et al., 2021). These interactions highlight the challenges and opportunities of breeding under low-input systems, emphasizing the importance of identifying inbred lines and hybrids that demonstrate both stability and resilience to low-N. Integrating ability analysis with heritability estimates provides a basis for selecting superior parents that can transmit favorable traits across environments. This can guide the development of maize varieties that are both high-yielding and well adapted to resource-limited production systems. The observed heterotic patterns also have practical implications, as lines with strong additive effects can be allocated to opposite heterotic groups to increase divergence and improve hybrid performance. Such information may contribute to refining heterotic groups and strengthening national maize breeding efforts in Ethiopia.

Significant GCA and SCA mean squares for GY under both optimal and low-N conditions indicate the involvement of both additive and non-additive gene actions. This suggests that genetic improvement can be achieved through direct selection for superior parents and by exploring hybrid vigor (Obeng et al., 2019; Amegbor et al., 2020). Across environments, GCA effects predominated for all the traits except GY, indicating additive control for flowering and kernel traits. These traits can therefore be improved through recurrent selection or the use of superior inbred lines in hybrid development (Kamara et al., 2024). In contrast, under low-N, SCA variance was higher for GY and EL, while under optimal conditions, GCA variance exceeded SCA variance for flowering and kernel traits. This pattern suggests that yield-related traits under stress rely strongly on heterosis (Okunlola et al., 2023). It further indicates that while earliness and kernel traits are more reliably inherited, GY and EL under stress depend largely on crossing to exploit heterosis. These findings also suggest that improvement of GY under low-N should not rely solely on direct selection. Instead, incorporating secondary traits associated with low-N adaptation may enhance selection progress, as previously proposed in studies on breeding for low-N environments (Banziger et al., 1997).

Overall, GY was strongly influenced by SCA under low-N, confirming the role of non-additive gene action and the importance of hybridization strategies. Similar dominance of non-

additive effects for GY was noted by Richard et al. (2020) and Nyasha and Charles (2020). The SCA results also highlight specific hybrid combinations that exhibit strong non-additive effects. These insights can guide the allocation of inbred lines into heterotic pools within Ethiopian breeding programs, ensuring that hybrids exploit maximum heterosis while maintaining stability under low-N conditions.

The identified inbred lines with favorable GCA effects have direct implications for breeding. Line L7 exhibited significant and positive GCA effects for GY under both optimal and low-N conditions. This indicates its potential as a donor of favorable alleles for hybrid development targeting nitrogen-stress environments. Similar findings were reported by Amegbor et al. (2020), who identified inbred lines with stable GCA effects across environments. Likewise, line L10 expressed significant negative GCA effects for DA, which is desirable for developing early maturing hybrids. Early maturing is increasingly important in the context of climate variability. Comparable results have been reported by Torela et al. (2017), Woldu et al. (2020), and Luz et al. (2024), who also observed negative GCA effects for DA in elite inbred lines. In Ethiopian breeding programs, such lines could play a pivotal role in strengthening the base of heterotic pool formation, particularly for the highland maize hybrid pipelines where intermediate maturing and stress resilience are important.

SCA effects, reflecting non-additive gene action, were crucial for yield-related traits. Crosses L2 x L16 and L4 x L1 showed significant positive SCA effects for grain yield, indicating their potential as promising hybrids. In contrast, L1 x L1, L3 x L15, L3 x L16, and L4 x L17 were less suitable for yield improvement. These results agree with previous findings that hybrid combinations may either enhance or reduce yield depending on the underlying gene action (Fortunate et al., 2022). Positive SCA effects across environments further indicate the potential of specific heterotic combinations in developing high-yielding hybrids adapted to low-N conditions. This highlights that hybrid performance under stress depends more on cross-specific effects than on general parental performance. Such observations agree with reports that SCA contributes more strongly than GCA to GY under contrasting nitrogen levels (Sedhom, 2022; Luz et al., 2024; Aboderin et al., 2024).

Heritability estimates were high to moderate for most traits in this study. This indicates that a substantial proportion of the observed phenotypic variation was genetically controlled. High heritability values suggest stronger additive genetic effects whereas moderate heritability reflects greater environmental influence and possible contributions of non-additive gene action. Similar patterns have been reported in tropical maize populations (Meseka et al., 2018; Nelimor et al., 2019).

From a breeding perspective, these differences have practical implications for selection strategies. Traits with high heritability can be improved through direct phenotypic selection and parental line development because their expression is more reliably transmitted across generations. In contrast, traits with moderate heritability, such as GY under low-N conditions, may respond less effectively to direct selection alone. For such traits, breeding programs may benefit from hybrid performance testing, marker-assisted selection, or genomic selection approaches. Previous studies also indicate that genomic prediction is generally more accurate for additive traits with higher heritability (Purcell et al., 2022; Wang et al., 2024). For traits with moderate heritability, combining marker-assisted pyramiding with genomic selection can help capture small-effect loci and genotype x environment interactions (Khatun et al., 2022; Zhou et al., 2022).

Overall, the findings reveal that additive effects predominate for flowering and kernel traits. This supports recurrent selection and parental line improvement. In contrast, grain yield under low-N is mainly governed by non-additive effects, highlighting the importance of heterosis breeding. Inbred lines such as L7 and L10 showed strong potential as parental resources. Single crosses L2 x L16 and L4 x L1 demonstrated promise for stability and potential release. The early-maturing hybrid L1 x L18 further has a breeding value for breeding programs targeting earliness. These findings highlight the complementary roles of additive and non-additive gene actions. They provide practical options for breeding resilient, high-yielding maize suited to nitrogen-limited environments. Although the study was conducted across three locations to capture environmental variability, the genetic background of the inbred lines was relatively restricted. This may limit the generalizability of the findings. In addition, potential genotype x management interactions were not assessed, suggesting the need for future studies that incorporate broader germplasm and diverse management practices.

5. Conclusion

The study revealed significant genetic variation among maize hybrids under both optimal and low-N conditions. Grain yield and related traits were influenced by both additive and non-additive effects. Moderate to high heritability estimates support the use of selection for traits under additive control, while heterosis breeding remains vital for improving yield under stress**.** Inbred lines such as L7 and L10, along with hybrids L2 x L16, L4 x L1, and L1 x L18, were identified as valuable genetic resources. Their integration into breeding pipelines can accelerate the development of resilient, high-yielding, and early-maturing varieties suited to nitrogen-limited environments and smallholder farming system in sub-Saharan Africa.

Authors contributions

Worknesh.T, Demissew. A, Tilahun. M, and Tileye. F contributed to the study conception and design. Worknesh.T, and Demissew. A prepared the material and conducted the field experiment. data management, formal data analysis, investigation and interpretation of the result was performed by Worknesh.T, Demissew. A, Tilahun. M, and Tileye. F. The manuscript was drafted by Worknesh.T. The experiment was supervised by Demissew. A, All the authors (W.T, D.A, T.M, and T.F) reviewed and commented on the first draft of the manuscript. The final manuscript is reviewed by W.T, D.A, T.M, and T.F. All the authors approved the submission of manuscript to Scientia Agriculturae Bohemia.

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Conflict of interest

The authors declare no conflict of interest.

Statement of data and materials availability

Data and materials will be available based on request from corresponding author.

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