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Combining ability for grain yield and other agronomic traits of early tropical maize lines under optimal, drought, and suboptimal soil nitrogen conditions

Abdoulazize Banhoro[1], Rasmata Nana[1], Yoseph Beyene[2], Isaiah Aleri[2], Andrew Chavangi[2], Aboubacar Sory[1], Marc Heijde[3,4]

[1]Biosciences Laboratory, Doctoral School of Science and Technology, Joseph KI-ZERBO University, 03 BP 7021, Ouagadougou 03, Burkina Faso.
[2]International Maize and Wheat Improvement Center (CIMMYT), P.O. Box 1041-00621, Nairobi, Kenya.
[3]International Plant Biotechnology Outreach, VIB, Technologiepark 71, 9052 Ghent, Belgium.
[4]Department of Plant Biotechnology and Bioinformatics, Ghent University, Technologiepark 71, 9052 Ghent, Belgium.

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ABSTRACT

Maize (*Zea mays* L.) is crucial for food security and industrial use in Sub-Saharan Africa. However, its production is limited by drought and low soil nitrogen. Therefore, developing stress-tolerant maize hybrids is essential for enhancing productivity in the region. Effective selection of these hybrids depends on understanding the mode of inheritance of new maize lines under stress conditions. The objectives of this study were thus to assess the general combining ability (GCA) and specific combining ability (SCA) effects of new maize lines under optimal, drought, and suboptimal soil nitrogen conditions. A total of 320 testcrosses, 32 lines, and 10 testers were evaluated under these conditions. Significant differences ($P \leq 0.05$) were found between lines, testers, and line-by-tester interactions for most traits. Seven lines (L2, L6, L10, L18, L20, L25, and L31) and four testers (T2, T5, T9, and T10) had positive GCA effects for yield across the three growing conditions, highlighting favorable additive genetic effects under stress conditions. In addition, specific crosses including L1 × T2 and L5 × T3 (optimal conditions) and L9 × T9 and L32 × T6 (suboptimal soil nitrogen) showed positive SCA effects for yield. These lines and testers with positive GCA and SCA represent valuable genetic resources for the development of high-yielding, drought and suboptimal soil nitrogen-tolerant maize varieties.

1. INTRODUCTION

Maize (*Zea mays* L.) is one of the most important food crops in the world, playing a crucial role in food security and agricultural economies, especially in sub-Saharan Africa [1]. In Burkina Faso, maize is the main cereal crop, with an annual production of approximately 2 million tons [2]. It is essential for the country's food security, with a growing demand due to population growth and the growth of the poultry and industrial sectors [3]. However, maize production faces numerous abiotic stresses such as drought and suboptimal soil nitrogen, which reduce yield and grain quality [4,5]. Indeed, both drought and suboptimal soil nitrogen reduce maize photosynthetic rates, cause ear abortion, and limit assimilate translocation, affecting grain filling and leading to yield loss [1,6]. In addition, climate change exacerbates these abiotic constraints by decreasing the availability of water and soil nutrients [7]. These climatic and edaphic challenges emphasize the need to develop resilient and high-yielding maize varieties adapted to stressful environmental conditions.

A common strategy for developing high-yielding and stress-tolerant varieties is to exploit heterosis, or hybrid vigour [8], which is a process where hybrids resulting from crosses between two parental lines show superior performance [9]. However, not all parental lines exhibit exploitable heterosis when hybridized. Therefore, analysing the combining ability of parental lines is crucial to determine the performance of hybrids [10]. Several authors used combining ability to create superior hybrids with high grain yields [11], strong tolerance to biotic [12] and abiotic stresses [13]. Different methods, including diallel design [1], "line by tester" design [14], and North Carolina design [15], have been used to estimate the combining ability of new maize lines. The "line by tester" method is commonly used because it provides information on general combining ability (GCA) and specific combining ability (SCA) effects of lines and testers. However, very few large-scale studies have been carried out on new parental lines using the "line by tester" method. Therefore, this study aims to estimate GCA and SCA of new maize lines developed at CIMMYT, under optimal, drought, and suboptimal soil nitrogen conditions, using a large-scale line by tester analysis.

**Corresponding Author:*
Abdoulazize Banhoro,
Biosciences Laboratory, Doctoral School of Science and Technology, Joseph KI-ZERBO University, 03 BP 7021, Ouagadougou 03, Burkina Faso.
E-mail: abdoulazizebanhoro@gmail.com

Table 1: Characteristics of the experimental sites.

Site	Elevation (masl)	Rainfall (mm)	Soil type	Longitude	Latitude	Year 2021	Year 2022
Kiboko	975	545–629	Sandy clay	37°75’ E	2°15’ S	OP	OP, DS, and LN
Kitale	1900	1,000–1,499	Clay loam	35°0’E	1.0°N	-	OP
Kirinyaga	1,464	800–1,200	Clay loam	37°20’E	0°30’S	-	OP
Embu	1510	1,200–1,500	Clay loam	37°42’E	0°449’S	OP	-
Kakamega	1585	1995	Sandy loam	34°45’E	0°16’N	OP	-

OP: Optimal moisture and nitrogen fertilization condition, DS: Drought stress condition, LN: Low nitrogen condition.

2. MATERIAL AND METHODS

2.1. Experimental Sites

The trials were conducted at five research stations in Kenya in 2021 and 2022: Kiboko, Embu, Kirinyaga, Kitale, and Kakamega [Table 1]. The Kiboko station, located at an altitude of 975 m with rainfall ranging from 545 to 629 mm and a sandy-clay soil, is situated at coordinates 37°75‘E, 2°15’S [Table 1]. The Kiboko station hosted trials under optimal moisture and optimal soil nitrogen, suboptimal soil in 2021 and 2022, as well as trials under drought stress (DS) and suboptimal soil nitrogen (LN) conditions in 2022. The Kitale station is located at 35.0°E, 1.0°N at an altitude of 1,900 m, with rainfall ranging from 1,000 to 1,499 mm and a clay-loam soil type [Table 1]. The Kirinyaga station is located at an altitude of 1,464 m at coordinates 37°20‘E, 0°30’S, with rainfall ranging from 800 to 1,200 mm and a clay-loam soil. Trials under optimal moisture and soil nitrogen fertilization (OP) were carried out at the Kitale and Kirinyaga stations in 2022. The Embu station is located at an altitude of 1,510 m, with a rainfall of 1,200 to 1,500 mm and a clay-loam soil, at coordinates 37°42‘E, 0°449’S. Finally, the Kakamega station, located at an altitude of 1585 m with a rainfall of 1995 mm and sandy-loam soil, is situated at coordinates 34°45‘E, 0°16’N [Table 1]. Trials under optimal moisture and nitrogen fertilization (OP) were carried out at Embu and Kakamega in 2021 and 2022.

2.2. Plant Material

Thirty-two tropical maize lines developed at CIMMYT were used in this study [Table 1].

Among these lines, 14 were from the CIMMYT-Zimbabwe maize breeding program, and 18 were from the CIMMYT-Kenya program. These 32 lines were crossed to 10 testers to develop single-cross hybrids [Table 2]. These lines and testers have been used in hybrid development in CIMMYT maize breeding programs [7,16].

2.3. Experimental Design

In 2021, the test-cross hybrids were evaluated under optimal conditions using a 4 × 83 alpha lattice design with two replications. In 2022, the testcross hybrids were evaluated under optimal, drought, and suboptimal soil nitrogen using a 4 × 83 alpha lattice design with two replications for the stress trials. For optimal conditions, a sparse testing was used to evaluate the 320 test-crosses over five sites, with 220 test-crosses per site using a 10 × 23 alpha lattice design.

2.4. Field Managements

In all trials, each entry was sown in a 5 m long single row plot, with a spacing of 0.75 m between rows and 0.25 m between hills corresponding to a density of 53,333 plants/ha. In the 2022 trials, water deficit was induced by stopping irrigation 2 weeks before flowering until harvest. Suboptimal nitrogen levels were achieved at the site by continuous maize planting without the application of nitrogen fertilizer. Under suboptimal nitrogen, 50 kg P_2O_5/ha was applied, whereas an additional 192 kg N/ha was applied under optimal and DS conditions. The optimal condition is characterized by an adequate supply of water through regular irrigation or in areas with high rainfall, and a recommended nitrogen application used for optimal maize growth.

2.5. Data Collection

Data were collected for the following parameters:

- Plant height (PH): This corresponds to the size of the plant from the base to the last node before the panicle. Measurements were taken in centimeters, after anthesis, using a measuring tape on a randomly selected sample of 10 plants per plot;
- Ear height (EH): This corresponds to the measurement in centimeters of the insertion height of the ear from the base of the plant to the insertion node of the main ear. Measurements were also taken on a sample of 10 plants per useful plot, using the measuring rod, chosen at random;
- Days to 50% anthesis (DA): This was assessed on half the plants in the plot by counting the number of days between sowing and pollen shed;
- Days to 50% silking (DS): This was assessed by counting the number of days between sowing and stigma emission on half the plants in the plot.
- Anthesis-silking interval (ASI): This is the number of days between male and female flowering. It is calculated using the following formula $ASI = DS - DA$
- Plant aspect (PA): Rated on a scale of 1–5 according to plant and EH, uniformity, disease, and insect damage, and lodging: 1: Excellent. Healthy plants, optimal height, well-positioned ears, perfect uniformity, no disease or insect damage, no lodging; 2: Very good. Slight variations in height or uniformity, some minor disease or insect damage, but overall healthy, slight lodging possible; 3: Fair. Variable height and uniformity, visible signs of disease or insect damage, some poorly positioned ears, moderate lodging; 4: Poor. Marked height and uniformity problems, significant disease and insect damage, several poorly positioned ears, pronounced lodging; 5: Very poor, plants in poor condition, very poor height and uniformity, severe disease and insect damage, severe lodging compromising harvest.
- Ear aspect (EA): This was assessed on a scale of 1–5 according to ear size, filling, uniformity, disease, and insect damage. 1: Excellent, large ears, well filled, uniform, no signs of disease or insect damage; 2: Very good, good size ears, slightly irregular, with some minor imperfections, but overall sound; 3: Fair, ears of variable size, uneven filling, some signs of disease or insect damage, but acceptable; 4: Poor, small and poorly filled ears,

Table 2: Plant material used.

N°	Code	Pedigree	Type	Source
1	L1	CZL1470	Lines	CIMMYT-Zimbabwe
2	L2	CZL15089		CIMMYT-Zimbabwe
3	L3	CZL15109		CIMMYT-Zimbabwe
4	L4	CZL15110		CIMMYT-Zimbabwe
5	L5	CZL15111		CIMMYT-Zimbabwe
6	L6	CZL15206		CIMMYT-Zimbabwe
7	L7	CZL15231		CIMMYT-Zimbabwe
8	L8	CZL15237		CIMMYT-Zimbabwe
9	L9	CZL16101		CIMMYT-Zimbabwe
10	L10	CZL16151		CIMMYT-Zimbabwe
11	L11	CZL17003		CIMMYT-Zimbabwe
12	L12	CZL17015		CIMMYT-Zimbabwe
13	L13	CZL17016		CIMMYT-Zimbabwe
14	L14	CZL17033		CIMMYT-Zimbabwe
15	L15	EB098-76		CIMMYT-Kenya
16	L16	EBL17595		CIMMYT-Kenya
17	L17	EBL17596		CIMMYT-Kenya
18	L18	EBL17599		CIMMYT-Kenya
19	L19	EBL17602		CIMMYT-Kenya
20	L20	EBL17608		CIMMYT-Kenya
21	L21	EBL192108		CIMMYT-Kenya
22	L22	EBL192110		CIMMYT-Kenya
23	L23	EBL192112		CIMMYT-Kenya
24	L24	EBL192127		CIMMYT-Kenya
25	L25	EBL192163		CIMMYT-Kenya
26	L26	EBL192166		CIMMYT-Kenya
27	L27	EBL192167		CIMMYT-Kenya
28	L28	EBL192168		CIMMYT-Kenya
29	L29	EBL192169		CIMMYT-Kenya
30	L30	EBL192170		CIMMYT-Kenya
31	L31	EBL192184		CIMMYT-Kenya
32	L32	EBL192185		CIMMYT-Kenya
33	T1	CKDHL120918/ CML494	Testers	CIMMYT-Kenya
34	T2	CKLMARSI0037/ CKLTI0138		CIMMYT-Kenya
35	T3	CKLMARSI0037/ CML543		CIMMYT-Kenya
36	T4	CKLTI0138/ CKLMARSI0022		CIMMYT-Kenya
37	T5	CKLTI0138/ CML550		CIMMYT-Kenya
38	T6	CKLTI0227/ CKDHL120918		CIMMYT-Kenya
39	T7	CML322/CML543		CIMMYT-Kenya
40	T8	CML543/CML566		CIMMYT-Kenya
41	T9	CML566/CML395		CIMMYT-Kenya
42	T10	CML566/CML569		CIMMYT-Kenya

with visible disease or insect damage, reduced quality; 5: Very poor, very small ears, poorly filled, with significant undesirable characteristics, seriously affecting their quality.

- Ear per plant (EP): This corresponds to the number of ears with at least one fully developed grain divided by the number of plants harvested.
- Grain yield (GY): This is the production potential of the variety based on the weight of the ear, the grains harvested, and the relative humidity of the grains after drying. This yield is calculated using the following formula: $GY = RW \times \left(\frac{GWs}{EWs}\right) \times \left(\frac{100 - H}{87{,}5}\right) \times \frac{10}{S}$.

With: RW: Raw weight in kilograms of all the ears harvested per elementary plot; GWs: Grain weight in kilograms of the ears in the sample; EWs: Weight in kilograms of the ears in the sample. H: Relative humidity of grain at harvest S: Plot area in square meters (m^2); GY: Grain yield in t/ha.

2.6. Data Analysis

The "Line by Tester" procedure was used to estimate GCA, SCA, and variance components for all parameters studied using AGD-R software [17]. The analysis was carried out using the Kempthorne [18] method for multi-environment data from trials conducted using the alpha lattice experimental design. The sums of squares of the genotypic and genotype-by-environment variances were partitioned into variations due to the lines, the testers (GCA), the line-by-tester interaction (SCA), and their interactions with the environments. The following statistical model was used: Yijk = μ + Li + Tj + LTij + LEie + TEje + LTEije + Ee + REPk(Ee) + BLK(REPk(Ee)) + ϵijke; Where: Y_{ijk} = Mean trait value observed on a cross i × j in k^{th} replication, μ = Grand mean, L_i = GCA effect of the i^{th} line, T_j = GCA effect of the j^{th} tester, LT_{ij} = SCA effect of the cross i x j, LE_{ie} = Effect of the i^{th} line in the e^{th} environment, TE_{je} = Effect of the j^{th} tester in the eth environment, LTE_{ije} = Effect of the cross i × j in e^{th} environment, Ee = Effect of the eth environment, REP_k (E_e) = Effect of k^{th} replication nested within eth environment, BLK $(REP_k$ $(E_e))$ = Random effect of block nested in replicate k nested in environment e, ϵ_{ijke} = Error associated with each observation or experimental error. The proportion of additive and dominance variance components was computed using

$$\text{Baker's ratio: } \frac{GCA}{SCA} = \frac{2\sigma 2\ GCA}{2\ \sigma 2\ GCA +\ \sigma 2\ SCA}$$ [19].

3. RESULTS AND DISCUSSION

3.1. Effects of Genotypes and Environments on Measured Parameters

The analysis of variance revealed significant variations between lines, testers, and line by tester interaction for most of the parameters measured under optimal, drought, and suboptimal soil nitrogen conditions [Table 3]. These results show significant genetic diversity among the lines and testers tested, highlighting the potential to identify superior parental lines with strong combining ability for the development of stress-tolerant and high-yielding hybrid maize varieties. Similar results have been reported by several authors [20,21]. In addition, the significant variation in line-by-tester interactions indicates that the variability in measured parameters is primarily due to gene combinations in test-crosses. These interactions reveal unique combined effects on yield and plant morpho-physiological traits, underscoring the importance

Table 3*:* ANOVA for the parameters studied under three management conditions.

Optimal									
Source	**DF**	**GY**	**DA**	**DS**	**ASI**	**EH**	**PH**	**EP**	**EA**
Site (S)	7	224.31***	19483.12***	19204.03***	318.62***	10388.85***	12038.30***	1.07***	15.57***
Rep (S)	8	20.58***	18.62***	26.64***	13.17***	672.61***	1167.99***	0.07***	6.95***
G.	311	5.64***	20.92***	22.40***	2.96***	505.46***	702.86***	0.02***	0.54***
L.	31	28.47***	113.52***	113.59***	8.38***	2972.41***	3585.59***	0.05***	2.18***
T.	9	37.05***	204.93***	213.57***	16.50***	3207.96***	2981.76***	0.12***	2.14***
L × T	271	1.99***	4.21***	5.61***	1.88**	133.47***	297.42***	0.02***	0.30***
S × G	1684	1.67***	3.36***	3.90***	1.61*	83.27***	147.07**	0.01	0.27***
S × L	217	3.54***	6.16***	6.36***	2.26***	157.40***	281.34***	0.02***	0.49***
S × T	63	5.92***	10.20***	12.37***	2.60***	88.9	193.58*	0.02*	0.51***
S × L × T	1404	1.19	2.63	3.14	1.50	71.34	123.81	0.01	0.22
Error	1401	1.19	1401	3.13	1.50	66.50	121.34	0.01	1398
Drought									
Source	**DF**	**GY**	**DA**	**DS**	**ASI**	**EH**	**PH**	**EP**	**EA**
Rep	1	87.71***	23.76***	1.23	47.42***	360.94**	2458.17***	2.30***	11.67***
G.	311	0.52*	3.37***	5.78***	2.51**	121.30***	163.67***	0.03	0.24
L.	31	1.47***	15.22***	22.08***	7.57***	563.61***	535.68***	0.07***	0.76***
T.	9	0.85*	17.19***	36.29***	8.72***	505.90***	203.46**	0.08***	0.37
L × T	271	0.39*	1.56	2.89	1.72	57.93***	119.80***	0.02	0.18
Error	167	0.40	1.44	2.57	1.75	29.94	66.54	0.02	0.21
Suboptimal soil nitrogen									
Source	**DF**	**GY**	**DA**	**ASI**	**DS**	**EH**	**PH**	**EP**	**EA**
Rep	1	0.16	15.89***	28.86***	86.70***	15.10	75.23	0.02*	0.06**
G.	311	0.64***	3.25***	2.76***	6.87***	92.33***	196.13***	0.03	0.15*
L.	31	1.72***	16.49***	9.06***	25.22***	547.18***	752.21***	0.07***	0.30***
T.	9	1.33**	22.01***	10.47***	53.50***	169.40***	556.00***	0.12***	0.22
L × T	271	0.50*	1.11	1.79	3.22*	37.74**	120.57	0.02	0.13
Error	167	0.39	0.99	1.75	2.54	26.52	99.34	0.02	0.12

Rep: replication, G.: Genotypes, DF: Degree of freedom, GY: Grain yield, DA: Days to anthesis, ASI: Interval between anthesis and silking, DS: Days to silking, PH: Plant height, EH: Ear height, EP: Ear per plant, EA: Ear aspect, MS: Mean square, ANOVA: Analysis of variance, *Significance at $P<0.05$; **Significance at $P<0.01$; ***Significance at $P<0.001$

of selecting appropriate testers for evaluating new germplasm, as reported by Chandel *et al.* [22]. Moreover, the ANOVA results also showed that experimental site conditions significantly affected the measured traits, confirming the need for multi-environment testing to accurately select stress-tolerant varieties [23]. These findings enhance understanding of factors influencing crop performance under stress and support the development of stress-tolerant maize varieties for diverse agroecological zones, as noted in previous studies [7].

3.2. GCA

3.2.1. GCA under optimal conditions

Under optimal conditions, lines L1, L2, L4, L5, L6, L9, and L10 as well as testers T8, T9, and T10, showed positive and significant GCA for grain yield (GY), plant height (PH), ear height (EH), days to anthesis (DA), and days to silking (DS) [Table 4], indicating their potential as good general combiners. Conversely, lines L7, L8, L11, L13, L14, L15, and L32, as well as testers T1, T4, and T6, showed negative GCA, indicating their status as poor general combiners under optimal conditions. These GCA values for lines and testers indicate their potential role in hybrid development, reflecting additive gene effects passed on to the offspring [10,24]. The positive GCA observed for grain yield (GY) in this study suggests that these lines and testers enhance yield potential. Similarly, positive GCA values for PH and EH may reflect desirable plant architecture and ear positioning, supporting overall plant performance. A positive GCA for male and female flowering days indicates a genetic tendency toward delayed flowering, which can lead to late maturity and prolonged grain filling. Many previous studies have also reported positive GCA for maize yield and other traits under optimal conditions, highlighting the predominance of additive genetic effects [21,25].

3.2.2. GCA under drought and low N conditions

Under drought conditions, lines L1, L2, L3, L4, L5, L14, L15, L18, L20, and L25, together with testers T2, T3, T5, T6, and T7 showed a positive GCA for grain yield (GY) [Table 5], indicating their potential for drought tolerance. These lines and testers are promising germplasm to breed for drought tolerance, highlighting the presence of effective physiological mechanisms. These mechanisms could include traits such as deep root systems and efficient photosynthetic processes that promote optimal water uptake to maintain productivity during drought periods [6]. Similar observations have been reported by several authors [7,26]. Conversely, some lines (L19, L22, L23, L24, L26, L27,

Table 4: General combining ability (GCA) of lines and testers under optimal conditions.

Line	GY	DA	DS	ASI	EH	PH	EA	PA	EP
L1	0.51*	1.22***	1.39***	0.16	1.82	3.86	−0.03	−0.05	0.02*
L2	0.74***	1.04***	0.69*	−0.25	15.39***	13.93***	0.06	0.05	0.00
L3	0.17	0.65*	0.72*	0.06	−1.95	−2.4	−0.05	−0.01	−0.03*
L4	0.69***	0.57*	0.75*	0.14	3.88*	8.32***	−0.01	0.00	0.00
L5	0.55***	0.92***	0.95***	0.03	4.65*	5.35*	0.07	0.01	−0.01
L6	0.5*	1.04***	0.96***	−0.02	−1.69	4.99	−0.15*	−0.09	0.01
L7	−0.72***	1.03***	0.93***	−0.03	−10.09***	−16.6***	0.13*	−0.03	−0.01
L8	−0.38*	1.2***	0.85*	−0.24	1.51	−6.27*	0.13*	0.06	0.01
L9	0.57***	0.64*	0.03	−0.44***	4.03*	4.15	−0.2***	−0.06	0.00
L10	0.76***	0.11	−0.04	−0.13	9.3***	8.08***	−0.13*	−0.08	0.00
L11	−0.22	−0.39	−0.64*	−0.21	−6.47***	−1.45	−0.09	−0.02	0.00
L12	0.24	1.77***	1.86***	0.08	3.31	−0.28	−0.01	0.02	0.02
L13	−1.04***	−3.32***	−2.93***	0.18	−13.48***	−13.3***	0.05	−0.02	−0.01
L14	−0.45*	−0.11	−0.3	−0.13	0.97	5.59*	−0.09	−0.01	0.01
L15	−0.54*	−2.01***	−1.98***	−0.01	−2.12	2.00	0.03	−0.07	0.00
L16	−0.02	−0.29	−0.27	0.04	−1.50	−1.12	−0.14*	0.00	−0.01
L17	−0.09	−0.31	−0.28	0.04	1.11	−0.57	−0.11	0.00	0.00
L18	0.35	0.17	0.33	0.14	4.28*	7.7***	−0.11	−0.03	0.00
L19	0.07	0.98***	0.79*	−0.12	4.84*	4.46	−0.09	0.02	−0.01
L20	−0.11	−0.37	−0.67*	−0.23	4.09*	−5.55*	−0.07	0.01	0.01
L21	−0.39*	−1.05***	−0.78*	0.22	−6.35***	−0.39	0.09	0.04	0.00
L22	−0.15	−0.47	−0.34	0.09	0.91	5.55*	0.1	0.03	−0.01
L23	−0.29	−0.73*	−0.52	0.12	−4.21*	0.58	0.07	0.03	0.01
L24	−0.24	0.48	0.57*	0.06	−3.59*	−3.55	−0.06	0.03	−0.01
L25	0.16	−0.49	−0.73*	−0.17	−0.35	0.73	0.11	0.06	0.03*
L26	−0.22	−0.78*	−0.83*	−0.05	3.29	−0.76	0.13*	0.05	0.01
L27	0.06	−0.39	−0.37	0.01	2.41	−0.58	−0.02	0.04	0.02*
L28	0.00	−0.49	−0.55	−0.07	3.18	−0.23	−0.04	0.00	0.00
L29	0.33	0.19	0.22	0.01	5.46*	2.51	0.04	0.07	0.00
L30	−0.3	−1.12	−1.28***	−0.14	−0.85	−5.68*	0.12*	0.03	−0.01
L31	−0.15	−0.04	0.43	0.36***	−9.17***	−7.23*	0.14*	−0.01	−0.02
L32	−0.4*	0.36	1.03***	0.49***	−12.62***	−11.86***	0.13*	−0.04	−0.01
Tester									
T1	−0.37*	0.12	−0.01	−0.13	−3.42***	−3.45*	0.01	0.04	0.01
T2	−0.19	−0.5*	−0.68*	−0.14	−3.26*	−1.63	0.06	0.00	0.01
T3	0.13	−0.13	0.28	0.37***	−0.89	−1.13	−0.01	0.00	−0.02*
T4	−0.27*	−0.16	−0.2	−0.04	−3.53***	−2.58	0.11***	0.02	0.00
T5	−0.04	−1.11***	−1.2***	−0.09	−0.87	0.62	−0.03	−0.01	0.03***
T6	−0.38*	−0.97***	−0.88***	0.05	−2.6*	−1.75	0.05	0.05	0.00
T7	0.19	0.44*	0.54*	0.11	0.04*	−2.72	−0.06	0.00	−0.01
T8	0.36*	0.94***	0.65*	−0.23***	5.91***	5.77***	−0.06	−0.04	0.00
T9	0.29*	0.7***	0.80***	0.09	4.33***	5.04***	−0.04	−0.03	−0.02*
T10	0.29*	0.68***	0.7*	0.02	4.3***	1.83	−0.04	−0.04	−0.01

GY: Grain yield, DA: Days to anthesis, ASI: Anthesis silking interval, DS: Days to silking, PH: Plant height, EH: Ear height, EP: Ear per plant, EA: Ear aspect. *Significance at $P<0.05$; **Significance at $P<0.01$; ***Significance at $P<0.001$. The underlines mean positive and significance GCA for Grain Yield

L31, and L32) and testers (T1, T4, T8, T9, and T10) showed negative GCA for GY, suggesting their limited usefulness to breed for drought tolerance.

Under suboptimal soil nitrogen conditions, lines such as L1, L2, L6, L8, L9, L10, L12, L18, L20, L25, and L31, together with testers T5 and T2, showed positive GCA for GY [Table 6]. These lines and

Table 5: General combining ability (GCA) of lines and testers under drought conditions.

Line	GY	DA	DS	ASI	EH	PH	EA	EP
L1	0.14	1.45***	1.02*	−0.45	0.61	0.69	−0.03	0.04
L2	0.19	0.27	−0.65	−0.64*	9.18***	7.46*	0.15	0.00
L3	0.25	0.11	−0.38	−0.35	−4.27	−5.09*	−0.08	−0.01
L4	0.31*	−0.11	0.09	0.30	0.65	2.10	−0.16	0.01
L5	0.25	0.80*	0.74	−0.03	1.38	−1.98	0.03	−0.02
L6	0.00	1.01***	1.05*	0.05	1.63	6.75*	0.12	−0.01
L7	−0.03	1.74***	1.42*	−0.07	−0.55	−9.68***	0.03	−0.05
L8	0.02	1.07***	0.51	−0.44	−1.38	−6.85*	0.21*	−0.02
L9	0.08	0.82*	0.46	−0.43	2.03	0.12	−0.05	0.00
L10	0.02	0.24	0.27	0.06	8.00***	4.81*	−0.15*	−0.04
L11	0.07	−0.03	−0.55	−0.51	−5.16*	−1.67	−0.20*	0.04
L12	−0.07	1.43***	2.32***	0.80*	8.12***	−1.45	0.10	0.02
L13	−0.09	−2.74***	−2.31***	0.24	−14.31***	11.42***	−0.02	0.01
L14	0.14	−0.34	−1.18*	−0.84*	0.76	4.02	−0.35***	0.05
L15	0.11	−1.59***	−1.72***	−0.25	−2.97	0.33	0.06	0.07*
L16	0.05	−0.34	−0.36	0.01	−2.03	0.12	−0.28*	0.04
L17	0.05	0.74*	−0.54	0.20	0.24	−0.33	−0.10	0.02
L18	0.29*	−0.16	−0.48	−0.31	1.44	5.03*	−0.10	0.03
L19	−0.18	0.66*	1.31***	0.61*	5.46*	3.34	0.05	−0.06*
L20	0.34*	−0.21	−0.71	−0.49	8.9***	2.34	−0.4***	0.06
L21	−0.02	−1.48***	−1.09*	0.37	−7.59***	1.14	0.11	−0.01
L22	−0.15	−0.43	−0.26	0.10	1.05	1.93	0.09	0.00
L23	−0.28	−0.79*	0.02	0.57*	−1.93	−0.11	0.14	−0.05
L24	−0.23	0.62	1.34***	0.72*	−7.1***	−6.78*	0.13	−0.01
L25	0.30*	0.21	−0.57	−0.65*	−0.38	4.94*	−0.01	0.07*
L26	−0.26	−0.55	−0.92*	−0.34	3.24	3.27	0.12	−0.06
L27	−0.19	−0.03	−0.23	−0.18	2.89	3.77	0.08	0.00
L28	−0.05	−0.23	−0.07	0.13	3.27	0.99	0.01	−0.03
L29	0.01	−0.12	−0.06	−0.03	4.16*	6.88*	0.09	−0.01
L30	0.00	−0.16	−0.77	−0.48	2.98	−1.10	−0.01	0.05
L31	−0.41*	−0.08	0.80	0.80*	−7.66***	−3.22	0.17	−0.03
L32	−0.65***	−0.30	1.50***	1.52***	−10.70***	−10.34***	0.26*	−0.10***
Tester								
T1	−0.02	0.17	0.19	0.04	−1.46	−1.03	−0.03	0.01
T2	0.04	−0.68*	−0.57	0.06	−1.94	−0.31	0.03	0.01
T3	0.09	0.17	0.98*	0.63*	1.15	0.79	−0.02	0.03
T4	−0.01	−0.28	−0.86*	−0.41*	−5.02***	−1.01	0.05	0.01
T5	0.04	−0.86***	−1.3***	−0.35	−2.76*	−1.11	−0.05	0.04
T6	0.02	−0.45*	−0.71*	−0.14	0.14	0.49	−0.02	0.01
T7	0.08	0.71*	1.04*	0.20	1.64	−0.86	−0.02	0.00
T8	−0.04	0.72*	0.47	−0.26	4.46*	1.69	−0.02	−0.02
T9	−0.09	0.15	0.15	0.00	0.55	1.58	0.02	−0.05*
T10	−0.11	0.34	0.62*	0.24	3.23*	−0.23	0.06	−0.04

GY: Grain yield, DA: Days to anthesis, ASI: Interval between anthesis and silking, DS: Days to silking, PH: Plant height, EH: Ear height, EP: Ear per plant, EA: Ear aspect, *Significance at $P<0.05$; **Significance at $P<0.01$; ***Significance at $P<0.001$. The underlines mean positive and significance GCA for Grain Yield

testers had tolerance to suboptimal soil nitrogen [25]. In addition, the positive GCA for PH in lines L2, L6, L18, L20, L22, L25, and L31 indicates the ability to maintain optimal PH under suboptimal soil nitrogen application. Suboptimal soil nitrogen has a direct effect on PH due to the essential role of nitrogen in growth [27]. Optimal PH under suboptimal soil nitrogen conditions indicates efficient nitrogen

Table 6: General combining ability (GCA) of lines and testers under suboptimal soil nitrogen conditions.

Line	GY	DA	DS	ASI	EH	PH	EA	EP
L1	0.36*	1.06***	0.47	−0.45	−2.30	3.32	−0.14*	0.02
L2	0.42*	0.15	−0.66	−0.77*	8.29***	11.58***	−0.02	0.05
L3	−0.11	0.00	0.41	0.40	−2.35	−3.35	0.01	0.01
L4	0.00	−0.19	0.40	0.52	−0.85	1.11	0.03	−0.04
L5	−0.04	0.62*	0.86*	0.23	−0.75	−1.76	0.03	−0.04
L6	0.27	1.79***	1.07*	−0.54	1.12	6.64*	−0.08	0.02
L7	−0.01	0.33	0.18	−0.06	−7.51***	−9***	−0.01	0.01
L8	0.16	0.10	−0.70	−0.65*	0.86	−4.34	0.07	0.01
L9	0.16	0.71*	−0.59	−1.18***	2.21	4.73	0.03	0.03
L10	−0.08	0.84***	0.88*	0.09	8.95***	6.56*	0.04	−0.01
L11	0.09	0.23	0.37	0.05	−1.93	4.00	−0.05	0.04
L12	0.05	1.21***	1.27*	0.17	5.44***	0.89	−0.02	0.04
L13	−0.09	−4.3***	−3.76***	0.04	−13.21***	−9.62*	0.03	−0.02
L14	0.05	−0.51	−1.44***	−0.86***	5.42***	9.02***	−0.14*	0.04
L15	0.05	−1.67***	−1.84***	−0.09	−2.75	5.40	−0.01	0.05
L16	0.05	0.75*	−0.92*	−0.26	−0.56	−2.35	−0.11	0.02
L17	0.07	−0.70*	−0.83*	−0.16	2.77	−0.03	−0.11	0.03
L18	0.02	0.02	−0.18	−0.21	4.08*	5.71*	0.03	0.04
L19	−0.07	1.37***	1.28*	−0.01	4.35*	2.02	−0.08	−0.02
L20	0.47***	0.74*	−1.44***	−0.78*	11.55***	3.45	−0.14*	0.01
L21	−0.26	−0.42	0.78	1.12***	−6.5***	−6.47*	0.00	0.02
L22	−0.19	−0.18	0.24	0.33	1.56	5.19*	0.03	0.00
L23	−0.30	−0.10	0.5	0.56*	1.47	2.12	0.06	0.00
L24	−0.12	0.40	0.42	−0.05	−2.93	−4.41	0.06	−0.02
L25	0.19	0.60*	−0.33	−0.7*	2.6	2.11	0.04	0.00
L26	−0.36*	0.02	0.57	0.48	−1.94	−7.22*	0.09	−0.04
L27	−0.16	0.38	0.60	0.27	−0.38	−4.35	0.11	−0.01
L28	0.02	−0.87*	−0.41	0.36	1.45	1.40	0.01	−0.01
L29	0.16	−0.01	0.32	0.30	2.10	0.38	0.06	−0.05
L30	0.15	−0.51	−0.57	−0.02	−0.83	−3.75	0.03	0.03
L31	−0.6***	0.60*	1.86***	1.21***	−9.3***	10.44***	0.15*	−0.14***
L32	−0.36*	0.51	1.19*	0.68*	−10.15***	8.54***	0.03	0.08*
Tester								
T1	−0.02	0.41*	0.22	−0.17	−1.12	−0.56	−0.02	0.04
T2	0.11	−0.7*	−1.10***	−0.36*	−0.67	2.2	−0.01	0.04
T3	−0.05	0.41	1.19***	0.72***	0.58	−1.33	0.03	−0.02
T4	−0.11	0.26	0.29	0.04	−2.58*	−2.76	0.04	−0.06*
T5	0.22*	−1.41***	−2.03***	0.54*	−1.55	−1.27	−0.05	0.06*
T6	0.05	−0.14*	−0.31	−0.17	0.50	2.71	0.00	−0.01
T7	0.00	−0.09	0.21	0.23	−0.46	−3.81	−0.01	0.01
T8	−0.03	0.67*	0.75*	0.01	1.99*	4.49*	0.00	−0.01
T9	−0.06	0.08	0.18	0.14	2.29*	2.05	0.01	−0.04*
T10	−0.10	0.50*	0.61*	0.09	1.03	−1.72	0.00	0.00

GY: Grain yield, DA: Days to anthesis, ASI: Interval between anthesis and silking, DS: Days to silking, PH: Plant height, EH: Ear height, EP: Ear per plant, EA: Ear aspect; *Significance at $P<0.05$; **Significance at $P<0.01$; ***Significance at $P<0.001$. The underlines mean positive and significance GCA for Grain Yield

uptake and use, which is essential for maintaining productivity in nitrogen-limited environments. Similar results have been reported by many authors when assessing the combining ability of new maize lines under low soil nitrogen [25,28]. Conversely, lines (L13, L14, L15, L21, and L32) showed negative GCA for GY under low soil nitrogen, suggesting that they are not well adapted to nitrogen deficiency. On the other hand, the identification of specific inbred lines (L2, L6, L10, L18, L20, L25, and L31) and testers (T2, T5, T9, and T10) with consistently positive GCA under the three growing conditions has important implications for breeding programs [10,29]. These lines and testers may possess genetic traits associated with efficient photosynthesis, adaptive root systems, and nitrogen use efficiency, making them valuable germplasm for the development of resilient and high-performing maize varieties.

3.3. SCA and Variance Components

The heat map showed several combinations with high positive SCA effects for grain yield (GY) in each condition [Figure 1], indicating high yield potential [30]. These combinations include L1 × T2, L24 × T2, L5 × T3, L30 × T8, L22 × T10, and L10 × T10 under optimal conditions; L9 × T9, L5 × T7, L6 × T5, L32 × T6, L29 × T4, and L20 × T10 under suboptimal soil nitrogen conditions; and L2 × T5, L4 × T7, L5 × T8, and L1 × T2 under drought conditions. These crosses showed favorable

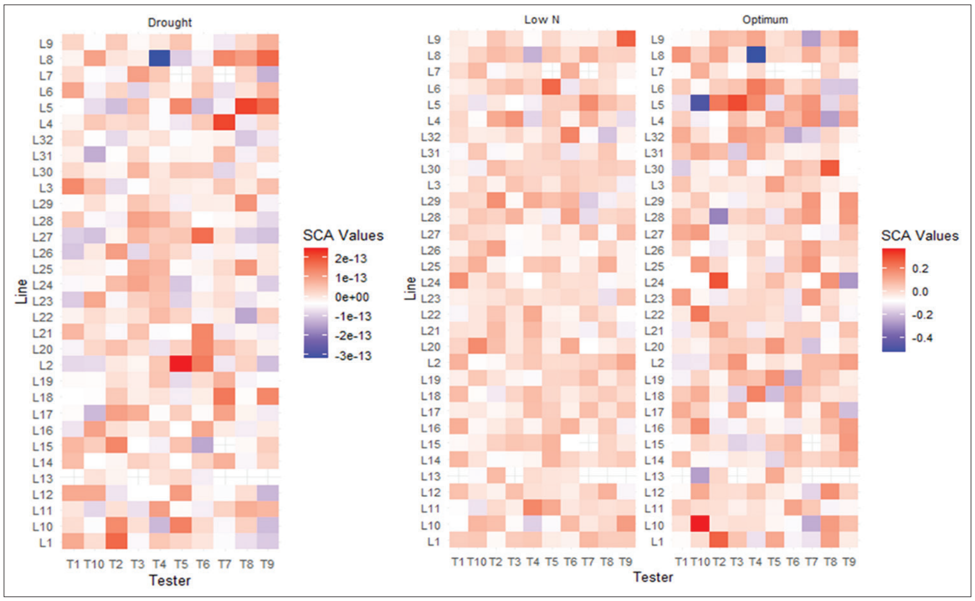

Figure 1: Specific combining ability estimates of line-by-tester combinations for grain yield under optimal, drought, and low N management conditions.

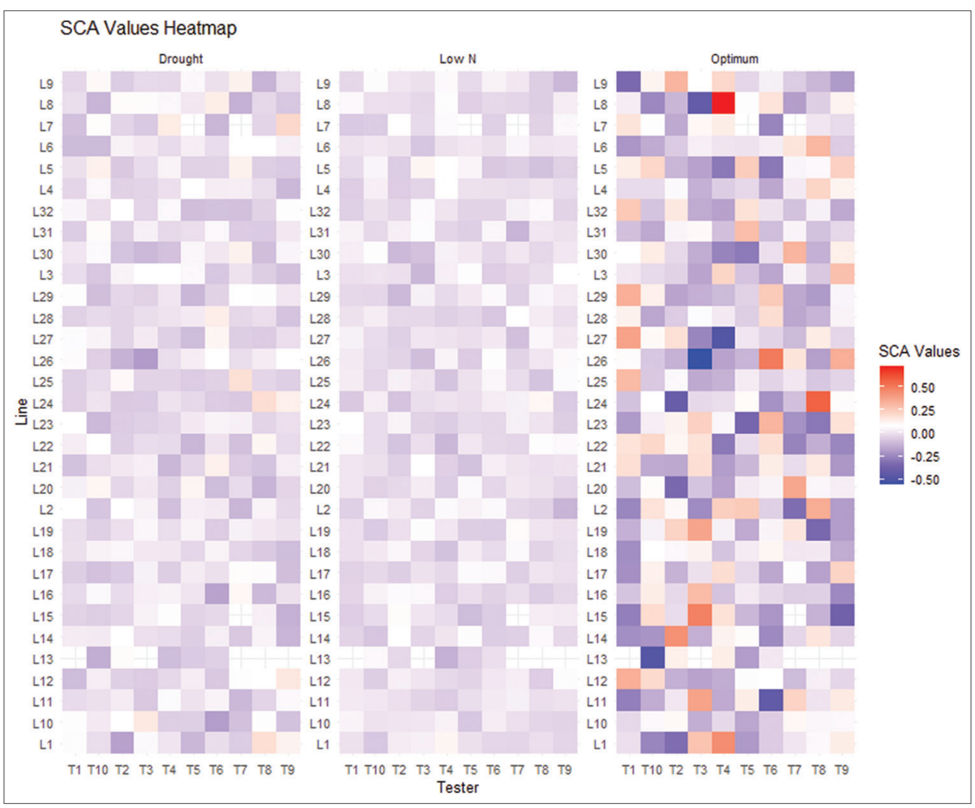

Figure 2: Specific combining ability estimates of line-by-tester combinations for days to anthesis under optimal, drought, and suboptimal soil nitrogen conditions.

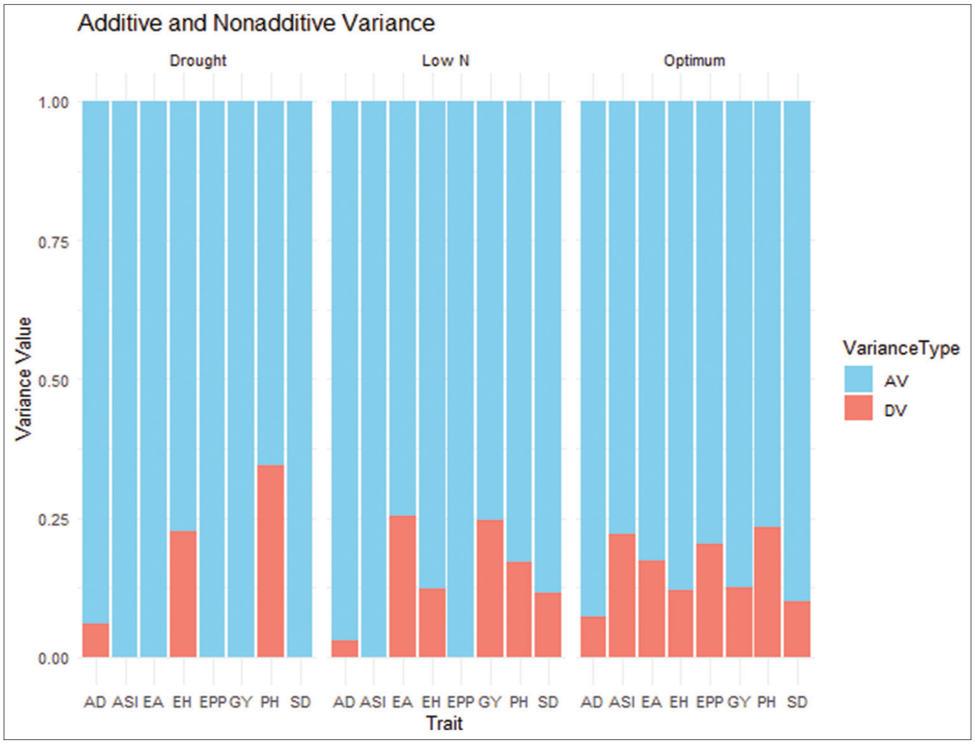

Figure 3: Proportion of additive (lower bar) and non-additive (upper bar) genetic variance for study parameters.

alleles interacting synergistically to increase GY in some environments. Indeed, SCA measures the non-additive gene effects, such as dominance and epistasis, that result from the interaction between parental genes in test-crosses [10,15]. SCA is important for selecting hybrids that show hybrid vigor [31]. The SCA effects can vary depending on environmental conditions and the traits of interest [30,32]. However, SCA effects for grain yield were relatively low under drought compared to optimal and low soil nitrogen conditions, suggesting that additive gene action is more important for yield (GY) under DS [7,19].

The heat map reveals that, under drought and low soil nitrogen, most line-by-tester crosses had negative SCA effects for days to anthesis (DA) [Figure 2]. This result indicates that additive gene action is more significant than non-additive effects for flowering under drought and low soil nitrogen. In addition, the proportion of GCA and SCA variance [Figure 3] confirms high additive variance and low non-additive variance for DA and DS across all growing conditions, suggesting these traits are controlled by multiple genes. Similarly, PH showed the highest non-additive variance under drought, decreasing under optimal and suboptimal soil nitrogen conditions. EA and EH also exhibited high additive variance consistently, with increased non-additive variance under low soil nitrogen and optimal conditions. Ertiro *et al.* [7] reported similar results when evaluating the combining ability of drought-tolerant maize inbred lines under optimal, drought, and low soil nitrogen conditions in Kenya. These findings highlight that traits are controlled by complex genetic interactions, emphasizing the importance of breeding strategies that consider specific genetic architectures and their responses to different environmental conditions.

4. CONCLUSION

The current study has been carried out to assess the combining ability of lines and testers developed at CIMMYT under optimal, drought, and low soil nitrogen conditions. The analysis of variance showed significant differences among lines, testers, and line-by-tester interactions for most measured parameters across all three environmental conditions. The best lines and testers with positive GCA effects across stressful and optimal growing conditions have the potential to develop productive hybrids. Furthermore, the SCA effects for grain yield were relatively low under drought conditions compared to optimal and low soil nitrogen conditions, suggesting that the general performance of the parents is more critical for grain yield under DS. However, strong and positive SCA effects for grain yield were observed in specific combinations, such as L1 × T2 and L5 × T3 under optimal conditions, and L9 × T9 and L32 × T6 under suboptimal soil nitrogen conditions. In addition, there is a variation in the GCA and SCA variance ratios for flowering and plant morphology parameters. This underscores the complexity of maize trait expression and the need for targeted breeding strategies to address environmental challenges. Lines and testers with consistently positive combining ability represent valuable genetic resources for developing maize varieties that are resilient to pedoclimatic stresses.

5. AUTHORS' CONTRIBUTIONS

All authors made substantial contributions to conception and design, acquisition of data, or analysis and interpretation of data; took part in drafting the article or revising it critically for important intellectual content; agreed to submit to the current journal; gave final approval of the version to be published; and agreed to be accountable for all aspects of the work. All the authors are eligible to be authors as per the International Committee of Medical Journal Editors (ICMJE) requirements/guidelines.

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7. CONFLICTS OF INTEREST

The authors report no financial or any other conflicts of interest in this work.

8. ETHICAL APPROVALS

This study did not involve any human participants or animals; therefore, ethical approval was not required. Field experiments were conducted according to national guidelines and institutional regulations governing agricultural research and biosafety.

9. DATA AVAILABILITY

The datasets generated and/or analyzed during the current study are available from the corresponding author upon reasonable request.

10. PUBLISHER'S NOTE

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11. USE OF ARTIFICIAL INTELLIGENCE (AI)-ASSISTED TECHNOLOGY

The authors declares that they have not used artificial intelligence (AI)-tools for writing and editing of the manuscript, and no images were manipulated using AI.

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