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Research Paper

Performance of Testcrosses, Heterosis, and Combining Ability in Quality Protein Maize Inbred Lines under Moisture Stress and Non-Stress Environments in Ethiopia

Addisalem Mebratu
Department of Horticulture, Wolkite University, Wolkite, Ethiopia

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Abstract

The performance of newly developed, nutritionally enhanced, and stress-tolerant elite Quality Protein Maize (QPM) hybrids was evaluated under both moisture stress and non-stress conditions to assess their heterosis and combining ability. One hundred six hybrids were developed by crossing twenty-eight elite QPM inbred lines and four QPM testers following a line × tester mating design. The 106 F1 hybrids and four checks (standard and commercial hybrids) were evaluated in a 5×22 alpha-lattice design across four stress and non-stress environments in Ethiopia. Significant ($P \leq 0.05$) genetic variation was observed for most agronomic traits and grain yield. Across drought stress and non-stress conditions, inheritance of traits was governed by additive gene action, whereas under optimal moisture-growing conditions, additive and non-additive effects dominated inheritance of most traits. For grain yield, inbred line L16 showed the highest general combining ability (GCA). F1 QPM hybrids, L16 × T1, L16 × T3, L25 × T4, L10 × T4, and T12 × T1 resulted in grain yield higher than the commercial QPM and non-QPM hybrid checks, ranging from 20–42%, signifying high average parent (154–282%) and better-parent (120–249%) heterosis. Thus, this study identified important QPM lines for developing high-yielding, stress-tolerant QPM varieties in regions where malnutrition and recurrent drought prevail.

1. Introduction

Maize (Zea mays L.) is a major source of carbohydrates and plays a significant role for millions of people in Ethiopia (Asfaw et al., 2024; Alemu et al., 2024). Growing in various agro-ecological conditions, maize contributes about one-third of the calories obtained from cereals in Ethiopia, more than wheat (21%) and Teff (17%) (Shiferaw et al., 2011; Tadesse et al., 2018; FAOSTAT, 2022; Mebratu et al., 2024; Jambo et al., 2025). Despite the large production and consumption of common maize in Ethiopia, it is deficient in essential amino acids (lysine and tryptophan) (Mamatha et al., 2017; Chiuta and Mutengwa, 2020; Okunlola et al., 2023). The lack of these essential amino acids in the daily diets of millions whose diets are dominated by normal maize results in malnutrition, especially among lactating mothers, children, and pregnant women, who have limited alternatives to other protein sources (Priscila, 2021; Vissamsetti et al., 2023).

Quality Protein Maize (QPM) has been developed as an alternative to the normal maize through conventional maize breeding with improved agronomic traits, improved grain yield,

Author email: addisalem.mebratu@wku.edu.et

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and nutritional content (high lysine and tryptophan levels) and has the potential to reduce deficiency risks associated with conventional maize by about 21% (Kaur et al., 2020; Muleya et al., 2022; Hussan et al., 2024). Malnutrition in Ethiopia, driven by inadequate dietary protein for millions, remains a major problem (Jambo et al., 2025).

In Ethiopia, recurrent drought is among the most significant abiotic stresses affecting maize production (Kim and Lee, 2023; Deribe et al., 2025). The impact is high when it occurs during vulnerable stages of maize development, such as silking and grain filling, resulting in yield losses exceeding 50% (Maiti and Satya, 2014; Sah et al., 2020). Currently, drought stress is exacerbated by climate change, increasing its frequency and severity and leading to significant yield losses that affect the livelihoods of millions of small-scale farmers (Mebratu et al., 2024; Diriba et al., 2025). Moreover, maize production in Ethiopia is constrained by a lack of appropriate technologies, such as improved maize varieties tolerant to abiotic and biotic stresses, including drought (Engida et al., 2024). Such varieties are endorsed as a solution to combat the effects of recurrent drought and malnutrition for millions of livelihoods in which maize is the only stable food source (Jambo et al., 20250).

A major goal in maize breeding by the International Maize and Wheat Improvement Center (CIMMYT) in Eastern and Southern Africa is to develop maize varieties that are both stress-tolerant and nutritionally enriched to buffer the impacts of climate change and reduce the impacts of malnutrition by developing QPM maize varieties that are both stress-tolerant and with enhanced lysine and tryptophan content (Okunlola et al., 2023; Mebratu et al., 2024; Jambo et al., 2025). To develop multi-stress-tolerant, nationally enhanced maize varieties, CIMMYT has developed QPM inbred lines tolerant to abiotic and biotic stresses for Eastern and Southern Africa.

To exploit the potential of elite QPM inbred lines in hybrid combinations, heterotic performance, testcross performance, and combining ability (both general and specific) under drought-stress and non-stress conditions need to be evaluated. Thus, it is essential to test the combining ability of the elite QPM inbred lines under stress and non-stress conditions to identify superior parental lines and testcross hybrids for yield and agronomic and protein quality traits (Okunlola et al., 2023; Mebratu et al., 2024). Previous studies on QPM documented varied gene action under contrasting stress conditions, indicating that the gene action governing grain yield varies across environments (Owusu et al., 2017; Mebratu et al., 2024). Nonetheless, most studies studied a single stress condition at a time, providing incomplete information across varied growing conditions (Naveed et al., 2016). This knowledge gap constrains breeding efficiency and slows the adoption of drought-resilient QPM hybrids in Ethiopia and similar environments. Therefore, this study aimed to evaluate the performance of QPM single-cross hybrids under optimal and drought-stress conditions, assess heterosis, and estimate general and specific combining abilities of stress-tolerant inbred lines to support the development of high-yielding, drought-adapted QPM hybrids for diverse Ethiopian agro-ecologies.

2. Materials and Methods

2.1. Maize Germplasm

Twenty-eight medium- to late-maturing QPM inbred lines, identified for drought and low-nitrogen tolerance, were used as female parents. These inbreeds were crossed with four QPM testers representing two contrasting heterotic groups (two testers per group) using a line × tester mating design (Kempthorne, 1957). Detailed descriptions regarding the QPM inbred lines and testers used in this study can be found in a previous publication (Mebratu et al., 2019), as indicated in Table 1. The evaluation included commercial QPM (ZS261) and non-QPM (SC627) hybrids as universal checks, along with location-specific standards: BHQPY545 (QPM) and BH546 (non-QPM) at BARC, and MHQ138 (QPM) and MH140 (non-QPM) at MARC and Dhera.

2.2. Trial Sites Descriptions

Field trials were conducted across four environments in Ethiopia during the 2020–2021 season, comprising two well-watered and two drought-stress conditions. Optimum trials were run at BARC and MARC during the main season. A managed drought trial at MARC used supplemental irrigation, while a random drought stress trial at Dhera simulated typical farmer conditions (June–October 2021). These sites constitute mega-environments for maize cultivation (Hartkamp et al., 2000).

2.3. Experimental Design and Field Management

The study evaluated 110 hybrids (106 QPM and 4 commercial checks) and 32 parental lines (28 inbred lines and 4 testers). Hybrids were arranged in a 5 × 22 alpha lattice, and inbred lines in a 4 × 8 alpha lattice, each with two replications. Hybrids were hand-planted in 4 m × 0.75 m single rows at 53,333 plants ha^{-1}; inbred lines in two-row 4.5 m × 0.75 m plots. Fertilization followed recommended rates (92 kg N ha^{-1} in two splits, 69 kg P_2O_5 ha^{-1} at sowing). Standard management was applied, with managed drought at MARC (irrigation withheld two weeks before flowering) and random stress at Dhera.

2.4. Field Measurements

Measurements of growth, yield, and yield components were taken from each row, excluding border row plants. Days to anthesis (DA) and silking (DS) were recorded, and the anthesis–silking interval (ASI) was calculated as DS minus DA. Plant height (PH) and ear height (EH) were measured on ten randomly chosen plants per plot. Ears per plant (EPP) were calculated as the number of ears with at least one developed grain divided by harvested plants. Grain yield was standardized to 12.5% moisture. Additionally, five ears per plot were sampled to determine ear length (EL), rows per ear (RPE), and kernels per row (KPR).

2.5. Statistical Analyses

For each environment, analysis of variance (ANOVA) was conducted using PROC GLM in SAS (2011), while combined ANOVA across environments was based on block-adjusted lattice means using PROC MIXED. Effects of hybrids and environments were evaluated in the context of the hybrid × environment interaction. Standard checks were excluded from across-environment analyses but included in comparisons across management and locations. Line × tester analysis of 106 F_1 QPM hybrids separated the variation into components due to lines, testers, and their interactions. General combining ability (GCA) and specific combining ability (SCA) were calculated following Hallauer and Miranda (2010), with their contributions expressed as percentages of the total cross sum of squares (Kang, 1994). Mid-parent, better-parent, and standard heterosis were estimated for grain yield and other traits, with standard heterosis assessed relative to the QPM check ZS261 and the top-performing non-QPM check SC627.

3. Results

3.1. *Per se* Performance of Inbred Lines

Grain yield among parental lines was highly significant across all tested environments, with most agronomic traits also showing notable environment and parent × environment interactions (Table 1). Under optimal conditions, inbred grain yield ranged from 1.2 to 3.4 t ha^{-1} (mean 2.3), while under managed drought stress it ranged from 0.4 to 2.8 t ha^{-1} (mean 1.5), resulting in an overall mean of 1.9 t ha^{-1}. Plant height varied between 71.4 and 84.0 cm (mean 77.9), ear height from 73.3 to 94.9 cm (mean 80.1), and anthesis–silking interval (ASI) from −0.4 to 8.4 days (mean 2.2). Differences were also observed for ears per plant, rows per ear, and kernels per row, highlighting the genetic variability and differential environmental responses among the QPM inbred lines.

Table 1. *Mean performance of QPM inbred lines and testers for grain yield and major agronomic traits under optimal, drought-stress, and combined environments*

Parents	Grain yield (t ha^{-1})			AD	DS	ASI	PH	EH	EPP	RPE	KPR
	OPT	DRT	Across								
Inbred lines											
L1	2.2	2.0	2.1	76.4	79.0	2.6	148.1	65.3	0.8	15.5	18.5
L2	1.4	1.2	1.3	78.3	81.0	2.8	138.1	65.6	0.7	15.5	19.8
L3	3.4	2.8	3.1	71.4	73.8	2.4	144.9	68.2	1.6	11.5	22.8
L4	3.0	2.5	2.8	74.5	74.3	-0.3	130.4	62.2	1.0	13.5	23.8
L5	2.6	1.9	2.2	81.6	82.4	0.8	153.0	91.6	0.9	10.0	27.3
L6	2.1	0.7	1.4	78.1	80.1	2.0	152.2	63.2	0.9	14.5	13.8
L7	1.9	1.7	1.8	82.6	84.0	1.4	157.9	86.2	1.2	13.5	26.5
L8	2.5	1.4	1.9	80.8	81.5	0.8	156.7	79.9	1.1	13.5	19.5
L9	2.7	0.4	1.5	77.8	81.4	3.6	165.0	92.2	0.8	11.0	17.8
L10	2.3	1.6	1.9	75.6	78.6	3.0	163.0	88.8	0.9	11.5	19.3
L11	1.9	0.5	1.2	79.5	82.4	2.9	156.5	90.8	1.0	12.0	19.8
L12	2.3	1.6	2.0	76.9	81.1	4.3	169.5	89.6	1.0	12.5	19.3
L13	2.9	1.2	2.1	81.1	80.8	-0.4	149.4	94.9	0.9	10.0	23.8
L14	2.8	1.7	2.3	78.0	79.8	1.8	143.2	70.0	1.0	12.0	24.8
L15	3.0	1.5	2.2	72.4	80.8	8.4	147.2	67.5	0.8	13.0	22.8
L16	3.0	2.0	2.5	80.9	81.5	0.6	168.3	90.9	1.4	13.5	18.8
L17	1.4	1.5	1.5	80.1	81.8	1.6	139.1	72.5	1.3	12.5	19.0
L18	1.2	1.1	1.2	78.8	81.6	2.9	163.2	79.2	1.4	14.0	19.8
L19	2.3	1.3	1.8	76.8	81.1	4.4	147.4	68.0	0.6	13.0	21.3
L20	1.5	0.5	1.0	77.6	80.5	2.9	160.5	82.2	0.7	12.5	12.5
L21	2.1	1.3	1.7	78.0	80.1	2.1	153.7	79.9	1.1	12.0	19.0
L22	1.7	1.9	1.8	74.6	77.3	2.6	149.9	74.0	1.0	14.0	20.5
L23	1.6	1.3	1.4	75.4	77.0	1.6	150.2	63.2	1.7	12.0	20.8
L24	2.5	2.0	2.3	81.4	82.8	1.4	156.6	80.1	0.9	13.0	22.8
L25	1.3	1.7	1.5	78.5	78.5	0.0	142.3	60.1	1.2	14.0	23.3
L26	3.1	1.5	2.3	78.8	81.3	2.5	148.7	79.4	1.2	15.0	21.5
L27	2.6	1.5	2.1	77.6	81.4	3.8	163.6	90.5	1.4	12.5	24.3
L28	2.4	1.6	2.0	80.0	80.8	0.8	146.9	80.4	0.9	13.5	22.3
Testers											
T1	2.0	1.8	1.9	71.5	73.3	1.8	136.8	69.8	1.0	14.0	22.8
T2	3.4	1.4	2.4	81.5	83.1	1.6	150.4	76.9	1.1	13.5	25.3
T3	1.4	2.0	1.7	80.9	81.1	0.3	157.0	87.8	0.8	10.0	24.3
T4	1.8	0.8	1.3	77.1	80.5	3.4	146.8	86.1	1.0	12.5	18.0
Mean	2.3	1.5	1.9	77.9	80.1	2.2	151.8	78.0	1.1	12.8	21.1
Minimum	1.2	0.4	1.0	71.4	73.3	-0.4	130.4	60.1	0.6	10	12.5
Maximum	3.4	2.8	3.1	82.6	84.0	8.4	169.5	94.9	1.7	15.5	27.3
Environment (E)	**	**	**	**	**	**	**	**	**	ns	ns
Parent (P)	Ns	**	**	**	**	**	*	**	Ns	**	**
P x E	**	**	**	**	**	ns	ns	**	Ns	ns	ns
SE	0.4	0.3	0.2	1.2	1.4	1.3	7.6	5.3	0.2	0.9	2.4
CV (%)	24.5	25.2	25.2	3.2	3.4	7.8	10	13.6	29.1	9.6	16.4

* $P < 0.05$, ** $P < 0.01$. OPT, optimum management; DRT, managed drought; GY, grain yield (t ha^{-1}); AD, days to anthesis; DS, days to silking; ASI, anthesis-silking interval; PH, plant height (cm); EH, ear height (cm); EPP, ears per plant; RPE, rows per ear; KPR, kernels per row.

3.2. Analysis of Variance

Combined ANOVA under optimal conditions revealed that environment, genotype, hybrid, and their interactions significantly influenced most traits (see Appendix A). Across drought stress environments, genotypes, and hybrids significantly affected nearly all traits, although their effects on grain yield and the interactions for anthesis-silking interval (ASI) and rows per ear were not significant (see Appendix B). Across all environments, environment, genotype, and F_1 QPM hybrids, along with their interactions, had significant effects on all traits except for genotype × environment and hybrid × environment interactions for rows per ear (see Appendix D).

3.3. Performance of F_1 QPM Hybrids

Under optimal conditions, the top 25 F_1 QPM hybrids produced grain yields ranging from 6.0 to 9.25 t ha^{-1}, with an average of 6.0 t ha^{-1} (Table 2). The highest yields were achieved by H56 (L16 × T1, 9.25), H58 (L16 × T3, 8.92), H40 (L12 × T1, 8.22), H41 (L12 × T2, 8.12), and H57 (L16 × T2, 7.79 t ha^{-1}). Among these, 18% out yielded SC627, and 76% exceeded ZS261. Average anthesis and silking occurred at 71 and 72 days, respectively, with plant height averaging 228.3 cm, ear height 38.1 cm, 13 rows per ear, and 38 kernels per row. Under drought stress, mean grain yield dropped to 1.78 t ha^{-1} (range 1.03–3.03), with top performers H94, H22, H77, and H35 producing around 3 t ha^{-1}. Anthesis and silking averaged 74 days, with a 0.5-day ASI; plant height averaged 208 cm, ear height 122 cm, 13 rows per ear, and 37 kernels per row.

3.4. Combining Ability Analysis

In optimal environments, the general combining ability (GCA) of lines was highly significant for all evaluated traits, whereas tester GCA was significant for only some traits (see Appendix A). Specific combining ability (SCA) influenced most traits, except for days to anthesis, silking, and rows per ear, with GCA contributing 51–82% of the total hybrid variation (Table 2). Under managed drought stress, line GCA remained significant for most traits except grain yield, tester GCA affected several traits, and SCA was significant for most traits except grain yield, ASI, and plant height; GCA contributions ranged from 50–87%, highlighting the predominance of additive gene effects (see Appendix B). Both the GCA line and GCA tester were significant ($P \leq 0.05$) across environments for most traits, while the SCA was significant ($P \leq 0.05$) for all measured traits (see Appendix C). The GCA × E interactions were significant for most characters, with additive gene action contributing to 56–86.6%, underlining the preponderance of additive gene action.

3.5. Combining Ability Effects of Lines

Environmental conditions dictated the GCA effects of QPM inbred lines. Under optimal conditions, L16 (2.37 t ha^{-1}), L7 (0.94 t ha^{-1}), and L12 (1.22 t ha^{-1}) positively influenced grain yield, whereas L2 (−1.73), L11 (−1.34), and L28 (−1.74 t ha^{-1}) had negative effects. Across moisture stress conditions, a single inbred line, L10, exhibited a positive and significant effect, whereas lines L28 (−0.82) and L11 (−0.64) exhibited significant and negative effects. Interestingly, across stress and non-stress conditions, only L16 constantly sustained a significant and positive effect (1.22 t ha^{-1}), while lines L2, L11, and L28 showed significant and negative effects. Among testers, T4 showed a significant positive effect for grain yield (0.26 t ha^{-1}), and T3 increased ear height (3.56 cm) (Table 3).

Table 2. *Grain yield and primary agronomic traits for the 25 highest-yielding F_1 QPM hybrids and control varieties under stress and non-stress conditions*

		Grain yield (t ha^{-1})								
Hybrid	Cross	OPT	DRT	Across	AD	DS	PH	EPP	KPR	RPE
H56	L16 x T1	9.25	1.91	5.58	71.94	72.74	241.36	1.08	42.78	13.02
H58	L16 x T3	8.92	1.99	5.45	71.02	72.00	253.33	1.05	41.93	12.06
H94	L25 x T4	7.56	3.03	5.30	68.78	68.87	212.92	1.68	38.64	13.74
H35	L10 x T4	7.47	2.74	5.11	69.28	70.42	225.65	0.89	36.87	13.55
H40	L12 x T1	8.22	1.88	5.05	69.16	69.33	250.39	0.97	41.94	11.94
H66	L18 x T3	7.44	2.60	5.02	70.24	70.07	242.92	1.03	42.25	12.37
H59	L16 x T4	7.60	2.30	4.95	71.25	72.40	242.14	1.18	39.62	13.24
H70	L19 x T4	7.49	2.33	4.91	70.88	71.13	218.96	1.02	40.38	14.05
H47	L13 x T4	7.36	2.42	4.89	71.85	70.35	229.52	1.13	40.80	13.97
H10	L3 x T2	7.30	2.42	4.86	69.86	70.47	217.88	1.03	37.10	15.49
H22	L6 x T4	6.63	3.02	4.82	68.35	69.56	227.08	0.92	36.73	14.73
H80	L22 x T2	7.70	1.94	4.82	69.76	70.76	229.25	1.14	36.57	16.00
H26	L7 x T4	7.48	2.15	4.81	71.61	72.35	233.43	1.17	37.00	15.49
H90	L24 x T4	7.11	2.27	4.69	73.66	74.14	219.16	1.07	37.68	13.58
H93	L25 x T3	7.03	2.24	4.64	68.60	67.46	241.28	1.08	44.37	12.04
H18	L5 x T4	7.73	1.45	4.59	72.63	72.95	232.13	1.04	41.06	12.49
H41	L12 x T2	8.12	1.03	4.58	71.33	73.61	233.73	0.72	37.21	13.77
H85	L23 x T3	6.50	2.60	4.55	68.36	67.50	254.74	1.07	41.75	12.75
H11	L3 x T3	6.07	3.01	4.54	68.37	68.28	234.33	1.24	36.54	12.00
H42	L12 x T3	7.21	1.85	4.53	69.55	70.18	249.40	0.79	34.01	12.52
H57	L16 x T2	7.79	1.20	4.49	72.59	73.54	248.73	0.81	38.00	15.43
H71	L20 x T1	7.52	1.45	4.49	70.90	71.96	236.75	0.90	38.51	12.74
H77	L21 x T3	5.94	3.02	4.48	71.67	72.32	242.83	1.33	35.95	12.00
H45	L13 x T2	7.06	1.86	4.46	72.82	72.86	216.80	0.99	42.91	12.85
H68	L19 x T2	7.16	1.76	4.46	72.19	73.77	228.25	0.77	35.85	14.39
	Mean	6.00	1.78	3.89	71.30	71.70	228.29	0.97	38.11	13.43
	LSD $_{(0.05)}$	0.88	0.37	0.50	1.29	1.38	10.09	0.14	2.40	0.91
	NLOC	2	2	4	4	4	3	2	4	4
	Checks									
	SC627	6.29	1.77	4.03	66.28	66.94	245.08	0.95	40.54	14.99
	ZS261	4.38	2.11	3.24	65.35	65.24	219.38	0.87	38.76	13.97

OPT, optimum environment; DRT, managed drought; AD, days to anthesis; DS, days to silking; PH, plant height; EPP, ears per plant.

Table 3. *General combining ability (GCA) effects of 28 QPM inbred lines and four testers for grain yield and important agronomic traits across both optimal and stress conditions*

Parent	Grain yield			AD	DS	PH	EH	EL	KPR	RPE
	OPT	DRT	Across							
	t ha $^{-1}$			days		cm				
L1	-0.56	0.45	-0.06	-2.95**	-2.78**	-9.19**	-12.06**	0.32	-0.04	0.76**
L2	-1.73**	-0.44	-1.08**	0.5	1.43*	-15.81**	-10.87**	-1.74**	-5.11**	0.46
L3	0.28	0.76	0.52	-2.88**	-2.94**	-8.36**	-9.94**	-0.52	-1.33	0.17
L4	-1.72**	0.28	-0.72*	-1.41*	-2.71**	-3.87	-4.3	-0.26	-0.06	-0.17
L5	0.5	-0.38	0.06	2.04**	1.85**	4.65	15.25**	-0.27	3.42**	-1.22**
L6	0.16	0.41	0.29	-1.95**	-1.75**	3.28	-1.61	0.48	-1.12	1.14**
L7	0.94*	-0.2	0.37	2.00**	2.04**	12.90**	12.58**	-0.66	-0.19	0.83**
L8	0.25	0.48	0.36	-1.82**	-2.15**	0.24	-7.85**	0.24	1.3	0.15
L9	-0.87	-0.58	-0.72*	3.51**	3.21**	5.23	9.65**	-0.66	0.19	-0.25
L10	0.19	0.95*	0.57	-1.83**	-1.69**	3.28	-2.65	0.23	-2.12**	0.05
L11	-1.34**	-0.64	-1.00**	3.24**	2.55**	-0.35	9.16**	-0.74	-0.98	-0.85**
L12	1.22*	-0.08	0.57	-1.34*	-0.77	14.58**	15.49**	1.48**	-1.56	-0.58*
L13	-0.84	-0.07	-0.45	1.68**	0.83	-14.72**	-3.97	-0.67	0.68	-1.19**
L14	-0.48	-0.43	-0.45	2.51	1.95**	-8.00**	-0.31	-0.56	2.00*	-1.03**
L15	-0.37	0.18	-0.09	-1.51**	-0.98	-7.38*	-7.27**	0.18	0.58	-0.61*
L16	2.37**	0.08	1.22**	0.26	0.85	18.52**	7.57**	0.99*	2.49**	0.06
L17	0.2	-0.01	0.11	0.72	1.03	1.75	-1.96	0.77	1.92*	-0.52*
L18	0.58	0.33	0.45	0.58	1.01	10.06**	10.10**	1.31**	3.92**	-0.17
L19	0.67	0.18	0.43	-0.57	-0.27	3.35	1.74	0.97*	-0.47	0.61*
L20	-0.23	-0.41	-0.32	0.25	1.06	1.79	5.30	0.12	-2.22**	-0.50*
L21	0.39	0.46	0.42	0.77	1.22*	4.97	5.63	-1.35**	-1.53	-0.59*
L22	0.99*	0.01	0.50	-2.03**	-2.55**	3.48	-0.25	1.46**	0.01	1.28**
L23	0.2	0.44	0.32	-2.58**	-3.49**	10.54**	-7.63**	1.04*	3.43**	0.16
L24	-0.26	-0.12	-0.19	2.59**	2.97**	-5.58	-2.29	-0.15	-1.14	0.63*
L25	0.75	0.56	0.65	-1.75**	-2.52**	-2.94	-10.59**	0.26	2.79**	0.02
L26	0.00	-0.67	-0.33	-0.18	0.51	-5.5	-1.07	-0.54	-0.76	0.69**
L27	0.15	-0.47	-0.16	-0.09	0.26	-3.34	-1.18	-0.8	-0.15	0.38
L28	-1.74**	-0.82	-1.28**	2.50**	1.68**	-8.71**	-1.64	-0.79	-2.31**	-0.14
SE(gi)	0.47	0.47	0.35	0.56	0.58	3.01	2.86	0.45	0.83	0.25
T1	-0.15	-0.15	-0.15	0.04	-0.26**	0.25	3.33*	0.13	1.72**	-0.68**
T2	0.06	-0.32	-0.13	1.04*	1.94**	-5.29**	-3.27*	-0.11	-0.87**	1.17**
T3	-0.14	0.17	0.01	-0.60*	-1.26**	10.25**	3.56*	0.08	0.00	-0.90**
T4	0.24	0.29	0.26	-0.48*	-0.41	-5.78**	-3.63*	-0.10	-0.76*	0.41**
SE(gj)	0.21	0.2	0.13	0.24	0.29	1.15	1.47	0.19	0.31	0.07

$P \leq 0.05$; ** $P \leq 0.01$; OPT, Optimum management; DRT, drought stress; AD, days to anthesis; DS. days to silking; EH, ear height; EL, ear length; KPR, kernels per row; PH, plant height; RPE, number of rows per ear; SE(gi) = Standard error of GCA effects for inbred lines; SE(gj); Standard error of the GCA effects for testers

The specific combining ability analysis showed 19% of hybrids had significant positive effects on grain; these hybrids include H39, H47, H71, H45, and H56. Conversely, hybrids H12, H36, H44, and H104 showed negative SCA effects. Positive SCA for ear length was observed in H25, H27, H40, H45, H47, H60, H70, H93, and H103, and for kernels per row in H15, H45, H47, H60, H70, H93, and H103. Significant and negative specific combining abilities were recorded for DA and DS in hybrids H7, H30, H37, and H45, and for PH and EH. Two hybrids (H13 and H44) showed negative SCA effects (data not shown).

3.6. Heterosis for Yield and Agronomic Traits

Several QPM hybrids exhibited significant heterosis for GY and other parameters across environments. In optimum environments, mid-parent heterosis for grain yield ranged between 27.6% to 463.8% with a mean of 147.5%. Days to anthesis and silking resulted in moderate heterosis, while plant height and ear height showed the highest heterosis. Under managed drought, GY heterosis declined, with MPH from −70.6% to 299.9% (mean 26.2%) and BPH from −75.3% to 343.6% (mean 32.2%). Negative heterosis for flowering traits indicated delayed anthesis and silking, though plant and ear height maintained moderate positive values. Across all environments, mean MPH and BPH were 117.1% and 91.4%, respectively, demonstrating hybrid potential. Standard heterosis relative to checks ZS261 and SC627 followed a similar trend, higher under optimal conditions and reduced under drought stress (Figure 1).

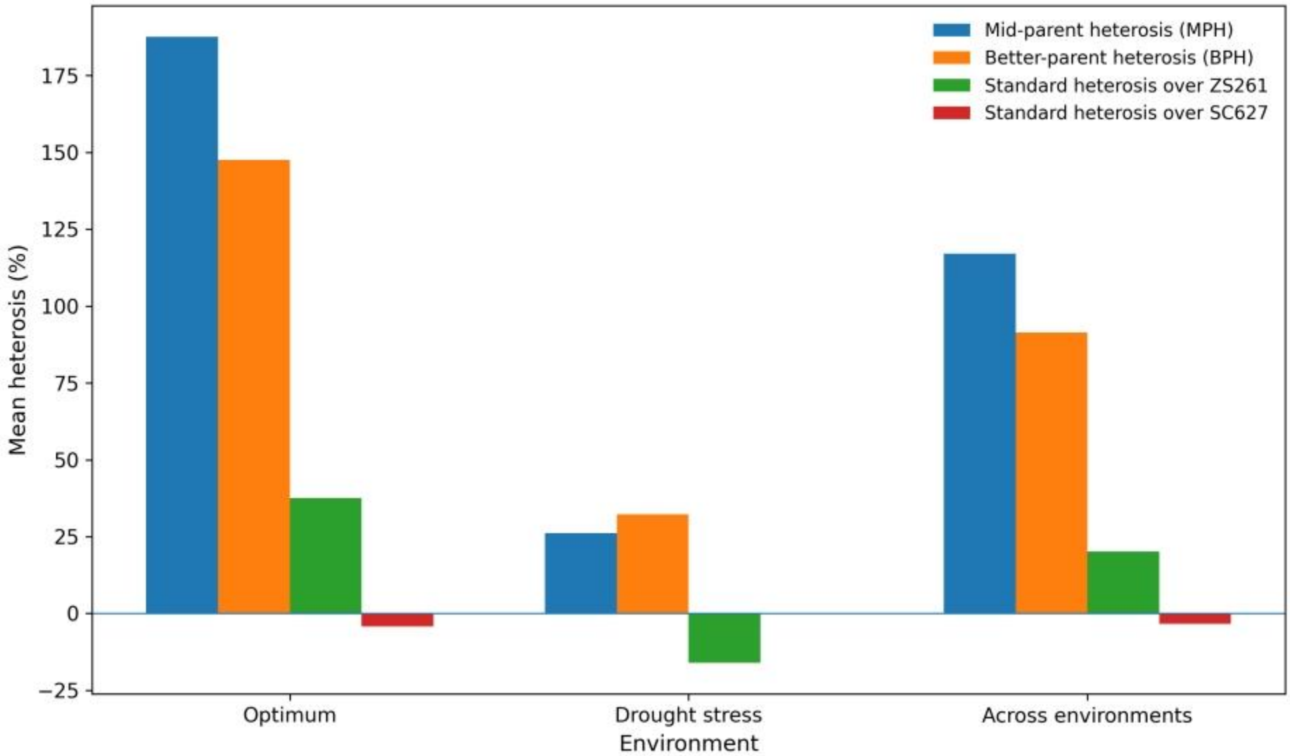

Figure 1. *Mean mid-parent, better-parent, and standard heterosis for grain yield of maize hybrids under optimum management, managed drought stress, and across environments.*

4. Discussion

Significant differences among QPM inbred lines and F_1 hybrids for grain yield and key agronomic traits across optimal, managed drought-stress, and combined environments (see Appendix A, B, C) indicate the presence of substantial exploitable genetic variability in the evaluated QPM materials. The wide yield ranges observed among parental lines under optimal (1.2–3.4 t ha^{-1}) and drought stress conditions (0.4–2.8 t ha^{-1}) (Table 1) reflect differential genetic responses to environmental conditions, providing a strong basis for effective selection. Comparable levels of variability have been reported in QPM and normal maize evaluated under contrasting environments (Wegary et al., 2011; Njeri et al., 2017; Mebratu et al., 2019; Chiuta and Mutengwa, 2020).

The significant Genotype × Environment interactions detected for GY and other parameters under drought stress across environments and across all environments (Tables 4 and 5) underscore the strong effect of environment on the performance of F1 QPM hybrids. In contrast, the stability of other parameters measured, such as ASI and RPE across environments, suggests limited environmental sensitivity. The marked reduction in mean hybrid grain yield from optimal (6.0 t/ha) to moisture stress environments (1.78 t ha^{-1}) (Table 2) confirms the effectiveness of the managed drought stress in discriminating genotypes for stress tolerance, consistent with established maize drought-screening protocols (Bolanos and Edmeades, 1996)

Several experimental F_1 QPM hybrids outperformed both the QPM (ZS261) and non-

QPM (SC627) commercial checks across optimal environments (Table 2). Notably, hybrids such as H56, H58, and H40 achieved grain yields above 8 t ha^{-1}, with 18% and 76% of hybrids exceeding SC627 and ZS261, respectively. These results demonstrate that yield competitiveness can be achieved in QPM hybrids without compromising nutritional quality, corroborating previous findings (Gudeta et al., 2017; Chiuta and Mutengwa, 2020). Under managed drought stress, although overall grain yield declined, hybrids including H94, H22, H77, and H35 maintained relatively higher yields (nearly 3 t ha^{-1}) (Table 2), indicating superior drought tolerance. Maintaining short anthesis–silking intervals under stress further suggests enhanced reproductive resilience, a key adaptive trait under water-limited conditions.

The combining ability analysis revealed significant (GCA) effects for most traits in all environments, with GCA accounting for 50–87% of the total hybrid variation (Tables 3–5). This predominance of additive genetic effects indicates that recurrent selection and population improvement approaches would be effective for improving GY and other parameters in QPM improvement programs. Inbred line L16 consistently exhibited significant and positive GCA effects for GY in all environments (Table 3), explaining the superior performance of F1 QPM hybrids derived from this line (e.g., H56 and H58). In contrast, lines with negative GCA effects (e.g., L2, L11, and L28) produced relatively poorer-performing hybrids, confirming the predictive value of GCA for hybrid performance (Wegary et al., 2014).

Results from many F1 QPM hybrids suggest that there are many non-additive gene action effects in determining the performance of hybrid F1 plants. In maize hybrids that show significant positive SCA effects for grain yield (i.e., H39, H47, H45, and H56), it appears the F1 hybrids outperformed their expectation based on the combined average performance of their parents (i.e., smaller GCA than expected). The positive grain yield SCA effects produced by these hybrids suggest that there must have been some level of additive and/or epistatic dominance being expressed in the interaction of the parental alleles. Similar conclusions have been made about maize hybrids produced from genetically diverse sources. Studies documenting the additivity of hybrid performance relative to the GCA of their parents have shown that SCA acts as an additional contributor or aid for enhancing yields and other traits of hybrid maize, especially for those hybrids having some degree of genetic diversity (Hallauer et al., 2010; Njeri et al., 2017; Chiuta and Mutengwa, 2020). Therefore, both additive and non-additive effects should continue to be intentionally exploited if the highest level of heterosis is to be exported for marketable QPM hybrids.

Better-parent heterosis (BPH) and mid-parent heterosis (MPH) for grain yield (GY) at optimal growth conditions also demonstrate strong heterotic responses across the tested parent lines (Figure 1). Hybrids exhibited reduced levels of heterosis under drought stress but still contained several hybrids that maintained a positive heterotic response, indicating greater ability to buffer from stress than the inbred parents (Dai et al., 2024). This observation corresponds with previous studies showing that heterosis in maize decreased under stress but remained significant (Makumbi et al., 2011). Additionally, the strong correlations among hybrid performance (Table 2), combining ability estimates, and Heterosis estimates demonstrate that hybrid performance is determined by both additive and non-additive gene effects, with predominantly additive effects across all environments.

5. Conclusion

This study revealed considerable variation in yield and agronomic traits among newly developed stress-tolerant QPM hybrids under contrasting environments. Several F_1 QPM hybrids outperformed both QPM and non-QPM commercial checks, highlighting their potential as high-yielding, stress-resilient cultivars. Line L16 showed strong general combining ability, while crosses L13 × T4, L11 × T4, L13 × T2, and L20 × T1 exhibited superior specific combining ability across environments. Additive gene effects predominated, with prominent standard, better-parent, and high-parent heterosis. Promising F1 QPM single-cross hybrids should be advanced for multi-location testing and considered for release to enhance maize productivity and nutritional quality in target regions.

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Appendix A. *Mean squares from the combined ANOVA for grain yield and agronomic performance of evaluated hybrids under optimal management*

Sources of Variation	df	GY ($t\ ha^{-1}$)	AD (days)	DS (days)	EL (cm)	RPE (#)	KPR (#)
Environment (E)	1	89.91**	199.56**	185.59**	97.92**	2.95	351.23**
Genotype (G)	107	3.46**	8.81**	9.70**	4.03**	3.38**	19.92**
G x E	107	1.02**	3.78*	3.57**	1.21**	0.97	5.57
F_1 hybrids (H)	105	3.54**	7.73**	8.49**	4.05**	3.48**	20.06**
GCA_{Line}	27	6.82**	18.68**	20.86**	9.85**	4.79**	38.33**
GCA_{Tester}	3	2.08	22.5	42.4	3.91	56.25**	103.30**
SCA	75	2.42**	3.2	2.68	1.96**	0.89	10.16**
H x E	105	1.00**	3.92*	3.5*	0.9716*	0.97	5.664*
GCA_{Line} x E	27	1.86**	6.08**	6.09**	0.98	1.06	7.45**
GCA_{Tester} x E	3	3.20**	8.09	8.91*	0.83	1.23	1.74
SCA x E	75	0.61*	2.68	2.34	0.95*	0.93	5.08
Pooled error (G)	134	0.4	2.57	2.33	0.71	0.83	4.15
Pooled error (H)	126	0.4	2.57	2.31	0.67	0.82	3.8
% SS GCA		51.19	70.48	77.42	65.34	81.65	63.84
% SS SCA		48.81	29.52	22.58	34.66	18.35	36.16
Mean		6.00	68.97	69.23	18.62	13.47	38.91
Minimum		1.79	63.41	63.32	14.81	10.5	29.92
Maximum		9.25	73.55	73.09	22.43	17	47.24
SE (m)		0.45	1.13	1.08	0.59	0.65	1.44
CV (%)		10.54	2.32	2.2	4.52	6.77	5.24

$P < 0.05$, $*P < 0.01$. Abbreviations: GY, grain yield; DA, days to anthesis; DS, days to silking; EL, ear length; RPE, rows per ear; KPR, kernels per row.

Appendix B. *Combined ANOVA mean squares for grain yield and agronomic traits across managed drought and random stress conditions*

Sources of Variation	df	GY (t ha^{-1})	AD (days)	DS (days)	ASI (days)	PH (cm)	EH (cm)	RPE (#)	KPR (#)
Environment (E)	1	134.86**	13455.87**	10370.96**	194.77**	54857.30**	31583.35**	4.14**	270.66**
Genotype (G)	107	0.7	15.31**	19.90**	3.86**	350.29**	229.52**	3.32**	24.05**
G x E	107	0.59**	2.31**	3.40**	1.43	1.50*	102.91*	1.11	10.68*
F_1 hybrids (H)	105	0.71	14.68**	19.21**	3.84**	340.73**	235.04**	3.16**	24.85**
GCA_{Line}	27	1.64	43.89**	44.48**	3.74**	500.33**	524.73**	3.61**	40.71**
GCA_{Tester}	3	4.51	53.01*	169.89**	71.75*	2494.78**	874.41	48.47**	63.19
SCA	75	0.24	2.63**	4.08**	1.16	197.11	107.84	1.18	17.60***
H x E	105	0.61**	2.08**	2.77**	1.41	142.73*	102.13*	0.9	10.38
GCA_{Line} x E	27	1.51**	4.03**	4.26**	1.37	69.75	94.1	1.04	11
GCA_{Tester} x E	3	2.94**	2.55**	57**	5.05**	158.4	176.15	0.87	20.65
SCA x E	75	0.20**	1.36**	2.09*	1.28	169.50*	102.88*	0.85	9.77
Pooled error (G)	134	0.07	0.84	0.96	1.22	97.07	72.95	0.86	7.74
Pooled error (H)	126	0.07	0.79	1.39	1.18	101.34	71.44	0.85	7.73
% SS GCA		76.63	87.21	84.82	78.45	58.68	68.04	73.22	49.39
% SS SCA		23.37	12.79	15.18	21.55	41.32	32.77	26.78	50.61
Mean		1.78	73.64	74.17	0.51	207.59	122.06	13.38	37.3
Minimum		0.47	67.18	67.16	-2.54	162.82	181.91	10.47	27.74
Maximum		3.03	80.67	83.63	3.72	235.98	147.69	17.05	49.41
SE (m)		0.19	0.65	0.69	0.78	6.97	6.04	0.66	1.97
CV (%)		14.85	1.25	1.32	7.26	4.75	7	6.93	7.46

$P \leq 0.05$, *$P \leq 0.01$. GCA, general combining ability; SCA, specific combining ability; SS, sum of squares; GY, grain yield; PH, plant height; DA, days to anthesis; DS, days to silking; ASI, anthesis-silking interval; EH, ear height; RPE, rows per ear; KPR, kernels per row.

Appendix C. *Mean squares from the combined analysis of variance for grain yield and measured agronomic traits across testing environments*

Sources of variation	df	GY ($t\ ha^{-1}$)	AD (days)	DS (days)	KPR (#)	RPE (#)	df	PH (cm)	EH (cm)	EL (cm)
Environment (E)	3	729.17**	5350.88**	4410.90**	297.55**	2.51**	2	168829.73**	56452.64**	1179.98**
Genotypes (G)	107	2.68**	21.27**	25.72**	34.38**	5.72**	109	529.89**	312.78**	3.54**
G x E	321	1.03**	2.98**	3.61**	8.61**	0.92	218	124.73**	90.98*	1.44**
F_1 hybrids (H)	105	2.80**	19.46**	23.79**	35.46**	5.78**	105	518.13**	320.12**	3.43**
GCA_{Line}	27	5.59**	56.98**	58.92**	63.28**	7.44**	27	853.10**	737.05**	8.25**
GCA_{Tester}	3	4.76	60.17**	190.22**	147.09**	104.32**	3	4536.27**	1471.33**	0.94
SCA	75	1.71**	4.33**	4.48**	20.98**	1.24*	75	236.82**	123.97*	1.80**
Hybrids x E	315	1.04**	2.92**	3.37**	8.56**	0.91	210	124.83**	92.03*	1.33**
E x GCA_{Line}	81	2.08**	5.23**	5.59**	11.40**	2.48**	54	112.5	102.04*	2.51**
E x GCA_{Tester}	9	2.66**	8.66**	12.21**	13.92**	0.83	6	147.47	241.18**	4.01**
SCA x E	225	0.58**	1.84	2.24	7.21*	0.87	150	128.09**	80.08	0.83**
Pooled error (G)	268	0.25	1.71	1.97	5.94	0.85	201	78.59	68.12	0.61
Pooled error (H)	252	0.24	1.68	1.85	5.53	0.84	189	80.96	68.24	0.59
% SS GCA		56.21	84.11	86.55	57.74	84.64		67.35	72.34	62.62
% SS SCA		43.79	15.89	13.45	42.26	15.36		32.65	27.66	37.38
Mean		3.89	71.3	71.7	38.11	13.43		228.29	133.16	16.77
Minimum		1.2	65.35	65.24	29.48	10.74		182.22	111.4	13.12
Maximum		5.58	76.68	77.98	46.06	16.03		257.12	164.06	19.55
SE (m)		0.25	0.65	0.7	1.22	0.46		5.12	4.77	0.45
CV (%)		12.97	1.83	1.96	6.4	6.85		3.88	6.2	4.65

$P \leq 0.05$, *$P \leq 0.01$; GCA, general combining ability; SCA, specific combining ability; SS, sum of squares; GY, grain yield; PH, plant height; ASI, anthesis-silking interval; DA, days to anthesis; DS, days to silking; EH, ear height; KPR, kernels per row; RPE, rows per ear.