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Assessment of genetic architecture, combining ability, and heterotic potential for yield and agronomic traits in Maize (*Zea mays* L.)

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Abstract

Maize (*Zea mays* L.) is a critical cereal crop globally, requiring continuous genetic improvement to meet rising demands and combat environmental stresses. To assess genetic architecture, combining ability, and heterotic potential, thirty-four diverse maize genotypes were evaluated in a Randomized Block Design (RBD). Based on mean performance, variability parameters, path analysis, and Mahalanobis D^2 divergence, twelve diverse lines and five testers were selected to generate sixty F_1 hybrids via a Line $\times$ Tester mating design. Analysis of variance among hybrids revealed highly significant differences ($p < 0.01$) across all evaluated traits, demonstrating substantial genetic variability. Genetic parameter estimates indicated that yield and structural traits such as seed yield per plant, biological yield, and cob length exhibited high broad-sense heritability coupled with moderate genetic advance as a percentage of mean. Multiple linear regression and path analyses identified 1000-seed weight and cob length as primary direct drivers of seed yield. Combining ability variances demonstrated the simultaneous presence of both additive and non-additive gene actions; however, the ratio of additive to non-additive variance ($\sigma_A^2/\sigma_D^2 < 1.0$) established that non-additive gene action (dominance and epistasis) overwhelmingly predominated across all traits. Elite general combiners included BMI-45 and LM-14 among lines, and DMH 1301 and DKC7044 among testers. Specific combining ability (SCA) analysis identified outstanding cross combinations, such as HKI-163 $\times$ DKC7044 and K25 $\times$ DMH 1301, which exhibited substantial seed yield spikes driven by non-additive gene interactions. Furthermore, heterosis evaluation revealed significant mid-parent and better-parent heterosis, alongside a desirable "Early-Maturity Breakthrough" (average mid-parent heterosis of -38.17% for days to 50% flowering). These findings confirm that the germplasm is ideally suited for hybrid maize development, and the identified superior crosses should be advanced to multi-location trials for commercial exploitation.

Keywords: Maize, line $\times$ tester, combining ability, heterosis, gene action, genetic divergence

Introduction

Maize (*Zea mays* L.) is one of the world's most important cereal crops because of its high production volume, broad adaptability, and diverse uses in food, feed, fodder, and industry [1, 2, 3]. Its importance in global food systems continues to rise, with demand driven by expanding agri-food, livestock, and industrial sectors, while climate change and increasing biotic and abiotic stresses intensify the need for sustained genetic improvement [1, 4, 5, 3]. Accordingly, modern maize breeding is directed toward the development of high-yielding, stable, and stress-resilient hybrids that can perform reliably across diverse production environments [4, 5, 6].

The genetic improvement of maize depends fundamentally on identifying parental lines that combine agronomic superiority with sufficient genetic divergence and favorable combining ability [7, 8, 9, 6]. Assessment of genetic diversity is a prerequisite in hybrid breeding because crosses among divergent inbreds tend to produce more heterotic and agronomically useful combinations than crosses among closely related lines [8, 9, 10]. In this context, multivariate approaches such as Mahalanobis D^2 analysis are widely used to classify germplasm into distinct clusters, estimate inter-cluster divergence, and identify promising parents for hybridization [8, 9]. Studies in maize consistently show substantial variation among inbred lines and indicate that crosses involving parents from more divergent clusters often provide greater scope for heterosis and broader segregating variability [8, 9, 10].

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Combining Ability

A clear understanding of the genetic architecture of yield and related traits is central to successful hybrid breeding, and combining ability analysis remains one of the most informative tools for this purpose [11, 6]. General combining ability (GCA) refers to the average performance of a parent across hybrid combinations and mainly reflects additive genetic effects, whereas specific combining ability (SCA) represents the deviation of a particular cross from expectation and is associated with non-additive effects such as dominance and epistasis [7, 11, 12]. Because additive effects are more readily fixed through selection, parents with strong GCA are especially valuable for the development of superior inbreds and hybrids [7, 11, 13].

The line $\times$ tester design is widely used in maize because it permits efficient evaluation of many parental combinations while partitioning variation into GCA and SCA components [11, 6]. Empirical studies show that both additive and non-additive gene actions contribute to grain yield and related traits, although their relative importance varies with germplasm and environment [7, 11, 13, 6]. Several maize studies, especially those based on inbred-line crosses, report a predominance of GCA effects, indicating an important role for additive gene action in hybrid performance [7, 11, 6].

Heterosis and Divergence

The commercial success of hybrid maize is rooted in heterosis, whereby F_1 progenies outperform one or both parents, particularly for grain yield [14, 12]. In maize, heterosis is strongly exploited in breeding because genetically distinct, homozygous parental lines can generate highly productive heterozygous hybrids [6, 11]. Recent studies report substantial heterotic responses in maize, with mid-parent heterosis for grain yield reaching 33.7% to 76.3% in one study and better-parent heterosis reaching 111.91% in another germplasm set [15, 10].

Evidence also shows that heterosis is not determined by divergence alone, but by its interaction with combining ability and the underlying genetic constitution of the parents [9, 6, 12]. For example, genetic distance was positively associated with F_1 mean performance and SCA for grain yield in one recent maize study, yet it was not significantly associated with mid-parent or better-parent heterosis for most traits [7]. Complementary quantitative genetic analyses likewise show that additive models alone do not adequately explain hybrid performance, with dominance contributing strongly to heterosis and epistasis contributing importantly to grain-yield performance [12].

Despite substantial progress, an important gap remains in integrating genetic variability, divergence, combining ability, and heterosis within the same localized breeding populations [7, 11, 6]. Many studies emphasize one component at a time, such as divergence analysis, combining ability, or heterosis estimation, whereas breeders need frameworks that directly connect parental divergence profiles with hybrid performance across environments [8, 11, 15]. This integrated approach is especially important under climate variability, where the goal is not only high yield but also stability, resilience, and efficient parent selection for future hybrid development [4, 5, 6].

Maize breeding improvement depends on combining genetically diverse parental lines, robust divergence analysis, reliable estimates of GCA and SCA, and careful exploitation of heterosis to identify superior hybrids. A redrafted introduction built on these elements is well supported across the supplied literature, including lower-ranked studies on fodder use, QPM divergence, and recent systematic evidence on combining ability in maize [3, 10, 6].

Therefore, the present investigation was undertaken to bridge these gaps through a systematic evaluation of diverse maize genotypes. The specific objectives of this study were:

1. To assess the extent of genetic variability, heritability, and trait associations among thirty-four diverse maize genotypes;
2. To determine genetic divergence using Mahalanobis D^2 statistics to select elite lines and testers;
3. To estimate general and specific combining abilities and identify the predominant nature of gene action governing yield and yield-attributing traits via a Line $\times$ Tester mating design; and
4. To quantify the magnitude of mid-parent and better-parent heterosis across sixty experimental hybrids to identify superior commercial candidates.

Materials and Methods

The present investigation was carried out to evaluate genetic variability, divergence, combining ability, and heterosis in maize (*Zea mays* L.). The experimental work was conducted using standard field and biometrical procedures.

Experimental Site and Crop Management

The field experiments were conducted during the Kharif season at the Research Farm, Department of Genetics and Plant Breeding, AKS University, Satna (M.P.). The experimental site is characterized by agro-climatic conditions representative of the region, featuring uniform soil fertility and topography. Standard agronomic practices—including thorough land preparation, recommended seed rates, precise spacing, optimal fertilizer application (nitrogen, phosphorus, and potassium), timely irrigation, and necessary plant protection measures—were followed uniformly to ensure healthy crop establishment and optimal expression of genetic potential.

Experimental Design and Evaluation Phase I (Genotypic Assessment)

A diverse set of thirty-four maize genotypes—comprising inbred lines, open-pollinated varieties, and commercial hybrids—was evaluated in a Randomized Block Design (RBD) with three replications. Each genotype was planted in separate plots maintaining a recommended spacing of 60 cm $\times$ 20 cm via manual dibbling.

Observations were recorded on five randomly selected, competitive plants from each replication (totaling fifteen plants per genotype) across eleven quantitative traits:

1. **Days to 50% flowering (DF):** Number of days from sowing until approximately 50% of plants shed pollen.
2. **Days to maturity (DM):** Number of days from sowing to physiological maturity (black layer formation).
3. **Plant height (cm) (PH):** Height measured from ground level to the base of the tassel.
4. **Number of tillers per plant:** Total count of productive and non-productive tillers.
5. **Number of cobs per plant:** Count of well-developed, harvestable cobs per plant.
6. **Number of kernels per cob (Ker):** Manual count of total kernels on a representative shelled cob.
7. **Cob length (cm) (CL):** Measurement from the base to the tip of harvested cobs.
8. **1000-seed weight (g) (TSW):** Weight of a random sample of 1000 dried kernels adjusted to 12–14% moisture.
9. **Biological yield per plant (g) (BY):** Total above-ground dry matter per plant at harvest.
10. **Seed yield per plant (g) (SY):** Cleaned grain weight per

plant adjusted to standard moisture.

11. Harvest index (%) (HI): Ratio of seed yield to biological yield expressed as a percentage.

Experimental Design and Evaluation Phase II (Line × Tester Hybridization)

Based on per se performance, variability parameters, correlation coefficients, path analysis, and Mahalanobis D^2 divergence values from Phase I, twelve genetically diverse genotypes were selected as female lines, and five high-yielding, divergent genotypes were selected as male testers.

Following Kempthorne's (1957) Line × Tester mating design, the selected lines and testers were crossed in a crossing block using staggered sowing to synchronize flowering, generating a total of sixty F_1 hybrid combinations. Controlled hand pollination and emasculation procedures were rigorously maintained, with tassels and silks protected using butter paper bags.

The resulting sixty F_1 hybrids, along with their seventeen parents and standard checks, were evaluated in a Randomized Complete Block Design (RCBD) with three replications under uniform field conditions. Observations for the same eleven quantitative traits were recorded following identical sampling procedures.

Biometrical and Statistical Analyses

Data recorded across evaluations were subjected to comprehensive biometrical analyses:

- **Analysis of Variance (ANOVA):** Partitioning of total variation for RBD and Line × Tester designs was performed following Panse and Sukhatme (1967) and Kempthorne (1957).
- **Genetic Parameters:** Genotypic and phenotypic coefficients of variation (GCV and PCV) were estimated following Burton and De Vane (1953). Broad-sense heritability (h^2) and genetic advance (GA as% of mean) were calculated according to Hanson *et al.* (1956) and Johnson *et al.* (1955).
- **Character Association:** Phenotypic correlation coefficients and path coefficient analyses (partitioning direct and indirect effects) were computed using Al-Jibouri *et al.* (1958) and Dewey and Lu (1959) methods.
- **Genetic Divergence:** Mahalanobis D^2 statistics and Tocher's clustering method were utilized to evaluate

multivariate genetic divergence among genotypes (Mahalanobis, 1936).

- **Combining Ability:** General Combining Ability (GCA) of parents and Specific Combining Ability (SCA) of F_1 hybrids were estimated using the Line × Tester model to deduce additive and non-additive gene action ratios (σ_A^2/σ_D^2).
- **Heterosis:** Mid-parent heterosis (MPH%) and better-parent heterosis (BPH%) over standard checks were calculated to quantify hybrid vigor.

Results and Discussion

1. Genetic Variability and Quantitative Parameters

Analysis of variance (ANOVA) revealed highly significant differences ($p < 0.001$) among the thirty-four maize genotypes for nearly all evaluated developmental, morphological, and yield-attributing traits, indicating substantial genetic diversity within the experimental material. The number of cobs per plant showed non-significant variation, while the number of tillers exhibited absolute zero variance across all samples.

Genotypic (σ_g^2) and phenotypic (σ_p^2) variance estimates demonstrated that phenotypic coefficients of variation (PCV) were consistently slightly higher than genotypic coefficients of variation (GCV) across all traits, reflecting a minimal degree of environmental influence.

- **High Heritability and Moderate Genetic Advance:** Traits such as seed yield per plant, biological yield per plant, cob length, number of kernels per cob, and plant height exhibited exceptionally high broad-sense heritability ($h^2 > 92\%$) coupled with moderate genetic advance as a percentage of mean (GAM between 12% and 20%). This close alignment between GCV and PCV confirms that these traits are predominantly governed by additive gene action, making direct phenotypic selection highly effective for isolating high-yielding genotypes.
- **High Heritability and Low Genetic Advance:** Phenological traits (days to 50% flowering and days to maturity) alongside 1000-seed weight and harvest index displayed high heritability but low GAM ($< 10\%$), indicating that these tightly regulated physiological traits are primarily influenced by non-additive gene interactions and are better exploited via heterosis breeding.

Table 1: Genetic Variability Parameters for Quantitative Traits in Maize

Trait	Grand Mean	Genotypic Variance (σ_g^2)	Phenotypic Variance (σ_p^2)	GCV (%)	PCV (%)	Broad-Sense Heritability (H_2) (%)	Genetic Advance (GA)	GAM (%)
Days to 50% Flowering (DF)	94.82	20.61	21.52	4.79	4.89	95.75	9.15	9.65
Days to Maturity (DM)	133.5	35.28	36.21	4.45	4.51	97.42	12.08	9.05
Plant Height (PH)	228.65	196.57	205.15	6.13	6.26	95.82	28.27	12.36
Number of Tillers/Plant	1.22	0	0.179	0	34.54	0	0	0
Number of Kernels/Cob (Ker)	372.84	559.33	587.9	6.34	6.5	95.14	47.52	12.75
Cob Length (CL)	17.21	1.3	1.37	6.64	6.81	94.91	2.29	13.32
1000 Seed Weight (TSW)	313.47	201.12	209.46	4.52	4.62	96.01	28.63	9.13
Biological Yield/Plant (BY)	282.92	396.98	427.3	7.04	7.31	92.9	39.56	13.98
Seed Yield/Plant (SY)	121.5	146.37	155.19	9.96	10.25	94.32	24.2	19.92
Harvest Index (HI)	42.86	1.6	1.7	2.96	3.04	94.55	2.54	5.92

2. Character Association and Path Coefficient Analysis

Correlation analysis demonstrated that growth, maturity, and yield traits shared overwhelmingly strong positive phenotypic relationships ($r = 0.93$ to 0.99 , $p < 0.01$), with the exception of the number of cobs per plant, which showed a non-significant, near-neutral correlation with other metrics.

- **Yield Drivers:** Seed yield per plant was almost perfectly correlated with 1000-seed weight ($r = 0.995$), biological

yield ($r = 0.994$), cob length ($r = 0.988$), and kernel count ($r = 0.984$).

- **Path Coefficient Partitioning:** Path analysis revealed that 1000-seed weight exerted the highest positive direct effect on seed yield (0.8438), confirming its role as a true causal determinant. Conversely, traits like cob length and kernel count—despite high total correlations—exercised their influence largely indirectly through 1000-seed weight and

phenological duration. The low residual effect ($R = 0.0818$) confirmed that the evaluated agronomic parameters accounted

for 99.33% of the total phenotypic variation in seed yield.

Table 2: Phenotypic Correlation Matrix Among Quantitative Traits in Maize

Trait	DF	DM	PH	Cobs	Ker	CL	TSW	BY	SY	HI
DF	1	0.993	0.987	-0.047	0.953	0.963	0.965	0.966	0.97	0.934
DM	0.993	1	0.994	-0.062	0.959	0.967	0.976	0.969	0.976	0.941
PH	0.987	0.994	1	-0.061	0.963	0.971	0.981	0.975	0.981	0.945
Cobs	-0.047	-0.062	-0.061	1	-0.052	-0.052	-0.067	-0.051	-0.057	-0.06
Ker	0.953	0.959	0.963	-0.052	1	0.997	0.985	0.981	0.984	0.949
CL	0.963	0.967	0.971	-0.052	0.997	1	0.988	0.984	0.988	0.953
TSW	0.965	0.976	0.981	-0.067	0.985	0.988	1	0.991	0.995	0.958
BY	0.966	0.969	0.975	-0.051	0.981	0.984	0.991	1	0.994	0.935
SY	0.97	0.976	0.981	-0.057	0.984	0.988	0.995	0.994	1	0.968
HI	0.934	0.941	0.945	-0.06	0.949	0.953	0.958	0.935	0.968	1

Table 3: Phenotypic Direct (Diagonal) and Indirect (Off-Diagonal) Path Effects on Seed Yield per Plant

Trait	DF	DM	PH	Cobs	Ker	CL	TSW	Total Correlation with SY (r)
DF	0.3367	-0.3239	0.07	-0.0002	0.0964	-0.0234	0.8143	0.9698**
DM	0.3345	-0.3261	0.0704	-0.0002	0.097	-0.0235	0.8235	0.9756**
PH	0.3325	-0.3242	0.0709	-0.0002	0.0975	-0.0236	0.8282	0.9810**
Cobs	-0.0158	0.0202	-0.0044	0.0035	-0.0053	0.0013	-0.0565	-0.057
Ker	0.3209	-0.3126	0.0683	-0.0002	0.1012	-0.0242	0.8311	0.9844**
CL	0.3243	-0.3155	0.0688	-0.0002	0.1008	-0.0243	0.834	0.9880**
TSW	0.3249	-0.3182	0.0695	-0.0002	0.0996	-0.024	0.8438	0.9955**

Bold diagonal values represent direct path effects; off-diagonal values reflect indirect effects. Residual Effect $R = 0.0818$

3. Mahalanobis D^2 Genetic Divergence and Clustering

Multivariate Mahalanobis D^2 analysis classified the thirty-four genotypes into six distinct clusters, revealing substantial genetic divergence independent of geographical origin.

- Divergence Extremes:** The maximum inter-cluster distance was recorded between Cluster I and Cluster V ($D^2 = 2060.72$), exemplified by divergent pairs such as HARITA_VMH 180 and Pop-167 ($D^2 = 2518.62$).

- Breeding Strategy:** Crosses between genotypes from widely separated clusters (such as Cluster I and Cluster V) were established as optimal mating blocks to maximize heterozygosity, allelic complementation, and heterotic response in subsequent hybrid generations. In contrast, Cluster VI exhibited low intra-cluster distance ($D^2 = 104.96$), indicating a narrow genetic base that should be avoided in crossing blocks.

Table 4: Cluster Distribution and

Cluster No.	Number of Genotypes	Genotypes Included
I	2	DMH 1301, HARITA_VMH 180
II	8	DKC 9099, DKC 9144, DKC7044, HARITA_VMH 150, P-3396, P-3404, P-3522, PAC 751
III	8	BML-7, K25, KARANTI, LAXMI108, LAXMI333, LM-14, POP-61, V-351
IV	4	BL-6, CML-161, CML-165, CML-224
V	2	HKI-163, Pop-167
VI	10	BMI-45, CML-163, CML-411, CML-465, CML-468, CML-471, DHOLI M10, HKI-1105, HKI-323-B, HKLC-78

Table 5: Average Inter- and Intra-Cluster D^2 Values

Cluster	Cluster I	Cluster II	Cluster III	Cluster IV	Cluster V	Cluster VI
Cluster I	22.42	192.91	1917.37	1479.97	2060.72	1218.22
Cluster II	—	64.03	1099.42	820.8	1175.82	555.88
Cluster III	—	—	84.07	275.33	519.2	277.68
Cluster IV	—	—	—	123.95	782.09	297.98
Cluster V	—	—	—	—	167.17	338.51
Cluster VI	—	—	—	—	—	104.96

Bold values along the diagonal represent intra-cluster distances, while off-diagonal values represent inter-cluster distances

4. Combining Ability and Gene Action (Line $\times$ Tester Analysis)

The Line $\times$ Tester ANOVA for the sixty F_1 hybrids showed highly significant mean squares ($p < 0.01$) for crosses, lines, testers, and line $\times$ tester interactions across all evaluated traits, validating the presence of both additive and non-additive genetic variances.

- General Combining Ability (GCA):** Parents exhibiting significant positive GCA effects were identified as elite

additive donors. Line BMI-45 proved to be an exceptional general combiner for earliness, dwarfism, and biological yield, while LM-14 and POP-61 excelled as universal donors for direct seed yield. Among testers, DMH 1301 and DKC7044 contributed robust additive alleles for grain weight and productivity.

- Specific Combining Ability (SCA) and Gene Action:** Significant SCA effects indicated prominent non-additive

"lock-and-key" interactions. Outstanding specific crosses included HKI-163 × DKC7044 and CML-163 × DKC 9144 for absolute seed yield. Crucially, the ratio of additive to non-additive variance (σ_A^2/σ_D^2) was drastically less than 1.0 for

every evaluated trait, confirming that non-additive gene action (dominance and epistasis) overwhelmingly governs yield expression in this population. Consequently, commercial exploitation must rely exclusively on hybrid development rather than line fixation.

Table 6: Line × Tester ANOVA Mean Squares and Variance Ratio Estimates

Source of Variation	df	DF	DM	PH	Cobs	Ker	CL	TSW	BY	SY	HI (%)
Replications	2	0.05	0.02	0.84	0.03	0.19	0.03	2.65	1.97	14.16	1.55
Crosses	59	41.19**	63.15**	1306.74**	0.34**	13810.0**	18.82**	4942.25**	13076.8**	4992.47**	794.75**
Lines	11	59.97**	69.64**	1194.86**	0.70**	9763.5**	18.43**	5089.27**	15903.2**	3804.44**	676.98**
Testers	4	26.75**	18.04**	1092.33**	0.10**	22799.3**	22.50**	5145.48**	5644.4**	5395.13**	855.21**
Line × Tester	44	37.81**	65.62**	1354.20**	0.27**	14004.4**	18.58**	4887.02**	13045.8**	5252.87**	818.70**
Error	118	0.07	0.13	5.27	0.02	38.2	0.07	6.04	18.9	8.93	1.16

indicates statistical significance at $p < 0.01$

Table 7: Line × Tester Variance Ratio Estimates

Trait	σ_{GCA2} (Average)	σ_{SCA2}	Ratio (σ_{A2}/σ_{D2})	Predominant Gene Action
Days to 50% Flowering	0.74	12.58	0.117	Non-Additive (Dominance)
Days to Maturity	0.13	21.83	0.012	Non-Additive (Dominance)
Plant Height	0	449.64	0	Non-Additive (Dominance)
Kernels/Cob	122.15	4655.41	0.052	Non-Additive (Dominance)
Cob Length	0.05	6.17	0.018	Non-Additive (Dominance)
1000 Seed Weight	10.33	1626.99	0.013	Non-Additive (Dominance)
Biological Yield/Plant	95.25	4342.31	0.044	Non-Additive (Dominance)
Seed Yield/Plant	1.98	1747.98	0.002	Non-Additive (Dominance)

Table 8: General Combining Ability (GCA) Estimation for Promising Crosses

Line	DF	DM	PH	Cobs	Ker	CL	TSW	BY	SY	HI
BMI-45	-1.63**	-3.07**	-20.04**	-0.43**	18.59**	-1.39**	6.71**	51.99**	3.92**	-6.22**
CML-161	0.71**	-0.24*	12.45**	-0.07*	-2.29	-1.63**	11.61**	32.00**	-21.83**	-10.01**
CML-163	-2.17**	-1.64**	0.32	0.22**	-57.19**	-0.56**	-16.72**	-11.97**	-9.85**	-2.91**
CML-165	-1.80**	-0.86**	-4.19**	0.25**	13.73**	0.73**	25.39**	21.89**	-14.15**	-8.32**
CML-224	3.62**	2.68**	7.10**	-0.21**	-14.94**	2.13**	-23.71**	-70.80**	4.92**	13.17**
CML-465	1.10**	0.14	3.67**	-0.18**	-25.80**	-0.44**	-22.18**	-13.74**	16.08**	6.40**
CML-468	-2.77**	-2.42**	7.32**	0.25**	-3.44*	-0.63**	14.16**	-5.56**	-16.71**	-3.93**
HKI-163	1.98**	2.54**	7.58**	0.01	5.32**	1.34**	9.54**	-8.68**	-8.59**	1.05**
HKI-323-B	1.25**	3.81**	1.33*	0.25**	31.88**	-0.29**	9.11**	-37.18**	-10.82**	0.11
K25	1.47**	1.28**	-2.72**	-0.11**	6.79**	-0.03	16.82**	18.80**	10.31**	1.43**
LM-14	0.04	-0.93**	-2.16**	0.02	-8.50**	-0.23**	-0.45	11.89**	28.38**	6.08**
POP-61	-1.79**	-1.30**	-10.64**	0.03	35.86**	1.01**	-30.28**	11.36**	18.34**	3.17**

Tester	DF	DM	PH	Cobs	Ker	CL	TSW	BY	SY	HI
DKC 9144	0.35**	-0.32**	-2.96**	-0.09**	9.10**	-0.17**	-6.87**	16.33**	-18.25**	-8.08**
DKC7044	0.96**	1.24**	3.07**	0.02	-24.69**	0.94**	-0.38	-1.98**	11.84**	4.30**
DMH 1301	-1.36**	-0.53**	7.71**	0	-17.08**	-0.63**	16.26**	-11.33**	4.39**	3.12**
HARITA_VMH 180	0.25**	-0.13*	-1.35**	0.03	38.87**	-0.84**	-14.98**	9.06**	8.25**	1.17**
PAC 751	-0.20**	-0.26**	-6.48**	0.03	-6.20**	0.70**	5.97**	-12.08**	-6.23**	-0.51**

Table 9: Specific Combining Ability (SCA) Estimation for promising Crosses

Cross (Line × Tester)	DF	DM	PH	Ker	CL	TSW	BY	SY
HKI-163 × DKC7044	3.42**	0.82**	-3.27*	-15.80**	0.36*	-45.91**	-64.19**	62.69**
CML-163 × DKC 9144	5.02**	7.33**	-6.49**	117.28**	-0.97**	-15.50**	0.32	56.29**
K25 × DMH 1301	2.48**	3.55**	-0.76	90.37**	3.89**	-62.42**	-106.13**	55.37**
BMI-45 × HARITA_VMH 180	4.80**	5.05**	-12.86**	-121.59**	0	70.33**	56.24**	50.23**
HKI-163 × DMH 1301	2.30**	6.11**	-0.23	-6.99	0.64**	6.42**	-49.10**	48.42**
CML-161 × HARITA_VMH 180	-0.27	1.47**	17.41**	-80.04**	0.53**	11.96**	-29.57**	45.56**
CML-165 × PAC 751	1.02**	-3.29**	-20.20**	-19.58**	1.35**	4.39**	43.12**	45.49**
CML-465 × HARITA_VMH 180	-2.85**	-5.19**	-30.33**	78.38**	5.09**	20.83**	-74.88**	43.43**
CML-224 × PAC 751	1.72**	3.56**	9.69**	-85.08**	1.22**	-31.74**	-10.78**	43.19**
CML-224 × DKC7044	-3.00**	-6.18**	-9.21**	15.95**	0.34*	52.27**	-35.58**	42.85**

5. Heterosis and Hybrid Vigor

Evaluation of the sixty F_1 hybrids revealed substantial mid-parent heterosis (MPH) and better-parent heterosis (BPH) across

quantitative parameters.

- **Yield Vigor:** Seed yield per plant exhibited a grand mean MPH of 34.23% and an average BPH of 22.57%. The elite

hybrid K25 ×DMH 1301 achieved a remarkable seed yield of 241.63g/plant, corresponding to a 92.64%increase over its mid-parent value, driven by exceptional harvest index partitioning. HKI-163 ×DKC7044 recorded the highest better-parent heterosis (72.02% BPH), demonstrating true over-dominance.

- **Early-Maturity Breakthrough:** A highly desirable negative heterosis was observed for phenological traits, with grand mean MPH reaching −38.17%for days to 50% flowering and −19.82%for days to maturity. Cross CML-163 ×HARITA_VMH 180 matured in just 99.69days, providing an effective mechanism for escaping terminal stress and fitting intense cropping rotations.

Table 10: Top Heterotic Hybrids for Seed Yield with MPH and BPH Percentages

Rank	Cross Combination	Seed Yield (g/plant)	Mid-Parent Heterosis (MPH%)	Better-Parent Heterosis (BPH%)	Primary Core Driver
1	K25 × DMH 1301	241.63	92.64%	69.13%	Hyper-partitioning / Harvest Index (+112.83% MPH)
2	POP-61 × DMH 1301	231.33	89.98%	61.34%	Biomass Accumulation (+64.36% MPH)
3	POP-61 × PAC 751	223.36	89.02%	64.64%	Sink Frame / Cob Length (+43.50% MPH)
4	HKI-163 × DKC7044	237.51	87.80%	72.02%	True Heterobeltiosis Over Elite Tester
5	LM-14 × DMH 1301	234.35	86.73%	61.27%	Balanced Reproductive Acceleration

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