



RESEARCH ARTICLE

Unravelling combining ability in maize inbred lines for yield, phenology and physiological efficiency using line and tester mating design

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Abstract

Maize (*Zea mays* L.) is a staple cereal crop with global significance due to its high yield potential and adaptability. Hybrid breeding remains a key strategy for enhancing productivity, which relies on identifying parental lines with superior combining ability. In this study, 15 maize inbred lines were crossed with three testers in a line × tester design during kharif, 2021 and the resulting 45 crosses were evaluated along with parents during rabi, 2021–22, to determine general combining ability (GCA) and specific combining ability (SCA) effects for grain yield and related phenological, morphological and physiological traits. The analysis of variance revealed significant differences among lines, testers and their crosses for most of the traits studied, indicating substantial genetic variability. Among the parental lines, IC 623875 and IC 611611 exhibited strong positive GCA effects for grain yield and related traits, suggesting their suitability as good general combiners. Several hybrid combinations, notably IC 623875 × BML-7, IC 623878 × BML-6 and IC 627708 × BML-6, demonstrated high SCA effects, reflecting the importance of non-additive gene action and their potential for heterosis exploitation. Further, traits such as anthesis–silking interval (ASI) and SPAD chlorophyll content were predominantly governed by non-additive gene effects, emphasising the relevance of hybrid breeding for improving these traits. The study identifies promising parental lines and cross combinations for maize hybrid development, providing valuable insights for breeding programs targeting high yield and physiological efficiency.

Keywords: combining ability; grain yield; gene action; heterosis; maize

Introduction

Maize (*Zea mays* L.) is a globally important cereal crop that plays a pivotal role in food, feed and industrial sectors due to its high yield potential and wide adaptability across diverse agro-ecologies (1). However, yield improvement through conventional breeding has reached a plateau in many environments as maize increasingly faces biotic and abiotic stresses under changing climate regimes (2, 3). The increasing impact of climate change, particularly drought and heat stress, poses a significant threat to maize productivity, necessitating the development of climate-resilient hybrids through targeted breeding strategies. Contemporary research highlights the need to integrate physiological parameters, such as SPAD chlorophyll content and anthesis–silking synchrony, with traditional agronomic traits to enhance yield stability and stress resilience in modern maize hybrids (4).

Hybrid breeding exploits heterosis, primarily driven by non-additive genetic effects and remains the most promising pathway for substantial maize yield gains (5). Recent advances in modern maize breeding, including genomics-assisted selection, doubled haploid technology and precision phenotyping, have significantly accelerated genetic gain and hybrid development (6). Evaluating the genetic potential of parental lines through combining ability analysis provides breeders with insights into the relative contribution of additive and non-additive gene action governing yield and related traits (7). General combining ability (GCA) reflects additive effects that are useful for selection and recurrent breeding, whereas specific combining ability (SCA) represents non-additive effects essential for heterosis and the identification of superior hybrid combinations (8).

Recent investigations in maize combining ability research have demonstrated the predominance of non-additive gene effects for yield and component traits, underscoring the importance of selecting parents and crosses with optimal GCA and SCA effects (9). Moreover, studies employing line $\times$ tester designs have successfully dissected genetic variance for both yield and agronomic traits, facilitating the selection of high-performing genotypes (5). Despite these advances, few studies have concurrently evaluated phenological, morphological and physiological traits within a comprehensive combining ability framework to facilitate hybrid selection in modern maize breeding programs.

To address this, the present study was undertaken with the following objectives: (i) to estimate the GCA of selected maize inbred lines and testers for grain yield (GY), phenological and physiological traits; (ii) to identify superior cross combinations based on SCA effects; (iii) to elucidate the underlying gene action governing yield and associated traits. By integrating multiple trait dimensions with combining ability analysis, this study aims to enhance the precision of parental selection and hybrid identification for improved maize performance under variable environments.

Materials and Methods

The present study was conducted at the Agricultural Research Station (ARS), Karimnagar, Telangana, India (18.43° N latitude, 79.13° E longitude, at an altitude of approximately 275 m above mean sea level). The experimental material comprised 15 diverse maize germplasm lines, viz. IC623875, IC636977, IC623877, IC623873, IC611611, IC611609, IC636965, IC627707, IC 623879, IC611615, IC 623878, IC623880, IC627704, IC 627708 and IC 627705 were crossed with 3 testers (BML-6, BML-7 and KML-105) in

line $\times$ tester mating design during kharif, 2021. The resultant 45 F1 hybrids, along with parents, were evaluated in RBD in the field with three replications at ARS, Karimnagar, during rabi, 2021–22. Each entry was planted in two rows of 3 m length by following a spacing of 60 cm between rows and 20 cm within rows. All the recommended agronomic practices were followed to raise a good crop. Whereas irrigation was withheld about two weeks before anthesis under drought conditions, for creating managed drought stress. Irrigation was resumed about two weeks after the end of male flowering (10). Data on 15 quantitative characters i.e. plant height (PLHT), ear height (EHT), ear length (EL), ear girth, number of kernel rows (KR) and number of kernels per row (KPR), test weight (TW) (g) shelling percentage (Sh), SPAD chlorophyll content and stay green character were recorded on five randomly selected competitive plants in each replication while, days to 50 % tasselling, days to 50 % silking, anthesis-silking interval, days to maturity and grain yield (kg/ha) were recorded on a plot basis. Data were analysed using the line $\times$ tester model to estimate GCA and SCA effects (9). Analysis of variance (ANOVA) was performed to partition variation due to lines, testers, crosses and error. The significance of GCA and SCA effects was tested at $p \leq 0.05$ and $p \leq 0.01$.

Results and Discussion

Combining ability effects of maize inbred lines

The analysis of variance for line $\times$ tester crosses revealed significant variation among maize inbred lines, testers and their interactions for most phenological, morphological, physiological and yield traits, indicating sufficient genetic variability for selection (Tables 1 and 2). This substantial variability provides a strong basis for effective selection and genetic improvement in the breeding material. The

Table 1. Analysis of variance for yield and yield attributing traits in maize genotypes under drought stress conditions

Source	d.f.	DT	DS	ASI	DM	PLHT	EHT	EL
Replications	2	45.02**	57.34**	1.16	67.53**	185.05	121.83	9.58**
Treatments	62	122.05**	117.22**	1.85**	116.42**	1761.61**	1349.55**	5.15**
Parents	17	18.87**	17.81**	1.02	17.81**	282.67**	196.99**	2.42**
Parents vs. Crosses	1	3715.61**	3483.79**	3.73*	3435.08**	63881.56**	65979.84**	135.81**
Crosses	44	80.24**	79.11**	2.13**	79.10**	921.20**	325.98**	3.24**
Lines	14	73.54*	65.02	1.64	65.38	465.32	231.85	4.51
Testers	2	800.09**	823.20**	2.49	815.27**	1260.05	226.32	1.03
Lines $\times$ Testers	28	32.18**	33.01**	2.35**	33.38**	1124.94**	380.17**	2.76**
Error	124	1.34	1.85	0.64	1.91	93.91	42.21	0.98
GCA variance		2.448	2.348	-0.011	2.328	-10.375	-2.759	0.024
SCA variance		20.555	20.773	1.136	20.982	687.355	225.304	1.182
Additive variance (VA)		9.792	9.392	-0.044	9.312	-41.5	-11.036	0.096
Dominance variance (VD)		82.22	83.092	4.544	83.928	2749.42	901.216	4.728
GCA variance/sca variance		0.119	0.113	-0.01	0.111	-0.015	-0.012	0.02
Source	d.f.	ED	KR	KPR	TW (g)	Sh(%)	SPAD	GY(Kg/ha)
Replications	2	0.07	0.67*	35.03**	3.99	12.46**	53.90**	3223367.9**
Treatments	62	0.55**	4.29**	37.68**	24.37**	26.80**	58.23**	7620460.6**
Parents	17	0.19**	1.82**	10.31**	4.3	11.95**	44.33**	132420.6
Parents vs. Crosses	1	26.01**	165.53**	1366.56**	739.98**	1057.19**	96.82**	344696100.2**
Crosses	44	0.11**	1.59**	18.05**	15.86**	9.12**	62.72**	2852757.0**
Lines	14	0.1	1.9	34.42**	14.13	8.26*	57.67**	3754810
Testers	2	0.03	0.56	12.54	56.22*	98.06**	709.08**	1345609
Lines $\times$ Testers	28	0.13**	1.50**	10.26**	13.84**	3.2	19.08**	2509383.9**
Error	124	0.06	0.18	3.8	2.79	2.48	5.2	359352.3
GCA variance		-0.001	0.004	0.397	0.103	0.301	2.223	17487
SCA variance		0.047	0.88	4.306	7.368	0.482	9.251	1433354
Additive variance (VA)		-0.004	0.016	1.588	0.412	1.204	8.892	69948
Dominance variance (VD)		0.188	3.52	17.224	29.472	1.928	37.004	5733416
GCA variance/SCA variance		-0.021	0.005	0.092	0.014	0.624	0.24	0.012

d.f.: degrees of freedom; DT: days to tasselling; DS: days to silking; ASI: anthesis-silking interval; DM: days to maturity; PLHT: plant height; EHT: ear height; EL: ear length; ED: ear diameter; KR: kernel rows; KPR: kernels per row; TW: test weight; Sh: shelling percentage; SPAD: Soil Plant Analysis Development chlorophyll meter reading; GY: grain yield; GCA: general combining ability; SCA: specific combining ability; VA: additive variance; VD: dominance variance.

Table 2. Estimates of general combining ability (GCA) and specific combining ability (SCA) effects for lines and testers of the study for yield and yield attributing traits

Lines	KR	KPR	TW	Sh	SPAD	GY
IC 623875	-0.494**	2.618**	0.449	-0.132	-2.208**	793.096**
IC 636977	0.284*	-0.949	-1.205*	-1.797**	-3.767**	-430.229*
IC 623877	0.351*	-0.782	-0.627	0.099	-2.847**	268.399
IC 623873	0.017	0.551	0.637	-0.256	2.805**	997.627**
IC 611611	-0.205	1.965**	1.413*	-0.082	-3.671**	948.705**
IC 611609	0.351*	-2.204**	-0.149	-0.081	-0.098	-19.444
IC 636965	-0.360*	1.551*	3.323**	-1.432**	0.083	171.686
IC 627707	-0.205	0.707	0.194	1.132*	5.057**	-323.588
IC 623879	0.217	0.196	0.579	0.989	0.001	137.708
IC 611615	-0.560**	-1.482*	-1.619**	-0.468	-0.365	-853.191**
IC 623878	-0.916**	-3.054**	-0.809	1.052*	3.158**	-1200.887**
IC 623880	0.062	-0.026	-0.804	1.091*	-0.815	-238.227
IC 627704	0.195	-3.404**	-1.351*	0.241	-0.219	-537.268**
IC 627708	0.380**	1.522*	0.402	-1.308*	2.005**	-275.278
IC 627705	0.884**	2.790**	-0.432	0.954	0.879	560.892**
SE(line)	0.143	0.65	0.557	0.525	0.76	199.82
Testers						
BML-6	-0.052	-0.255	0.385	-1.09**	-2.826**	28.476
BML-7	-0.076	-0.352	0.875**	-0.59*	-1.713**	156.918
KML-105	0.128*	0.607	-1.259**	1.68**	4.538**	-185.394*
SE (tester)	0.064	0.291	0.249	0.235	0.34	89.362
Crosses						
IC 623875 X BML-6	0.075	-0.301	-1.131	0.615	-0.933	242.932
IC 623875 X BML-7	0.098	1.93	1.362	1.067	-0.429	-3.801
IC 623875 X KML-109	-0.173	-1.629	-0.231	-1.681	1.363	-239.131
IC 636977 X BML-6	-0.703**	1.533	-0.36	-0.958	1.846	930.249**
IC 636977 X BML-7	-0.746**	-2.303*	-0.973	1.182	-4.561**	-803.215*
IC 636977 X KML-109	1.449**	0.771	1.334	-0.225	2.715*	-127.034
IC 623877 X BML-6	0.03	2.033	1.445	0.729	3.662**	657.589
IC 623877 X BML-7	-0.48	-0.603	-0.705	-0.491	0.103	1.603
IC 623877 X KML-109	0.449	-1.429	-0.741	-0.238	-3.765**	-659.192
IC 623873 X BML-6	-0.103	0.099	2.834**	0.812	-0.183	332.091
IC 623873 X BML-7	-0.08	-0.47	-2.456*	0.717	-0.573	-715.058*
IC 623873 X KML-109	0.183	0.371	-0.379	-1.529	0.756	382.967
IC 611611 X BML-6	-0.014	-2.381*	0.842	0.063	1.893	540.249
IC 611611 X BML-7	0.143	-0.31	-2.605**	-0.093	-1.786	-424.318
IC 611611 X KML-109	-0.128	2.691*	1.763	0.03	-0.107	-115.931
IC 611609 X BML-6	0.897**	-1.545	-2.916**	-0.912	2.07	5.4
IC 611609 X BML-7	-0.546*	0.819	3.951**	0.379	-2.639*	387.565
IC 611609 X KML-109	-0.351	0.726	-1.035	0.532	0.569	-392.966
IC 636965 X BML-6	0.075	1.366	0.949	0.449	0.012	274.057
IC 636965 X BML-7	-0.035	-0.87	0.562	0.099	3.699**	497.828
IC 636965 X KML-109	-0.04	-0.496	-1.511	-0.549	-3.712**	-771.885*
IC 627707 X BML-6	0.186	0.677	2.567**	-0.766	-3.038*	386.417
IC 627707 X BML-7	0.076	0.308	-0.622	0.066	1.073	1041.243**
IC 627707 X KML-109	-0.262	-0.985	-1.945*	0.7	1.965	-1427.661**
IC 623879 X BML-6	-0.637*	-0.945	1.085	-0.728	1.238	-176.77
IC 623879 X BML-7	0.920**	1.152	-0.105	0.503	1.325	456.255
IC 623879 X KML-109	-0.284	-0.207	-0.981	0.225	-2.563	-279.486
IC 611615 X BML-6	-0.059	1.133	-1.043	0.498	-0.913	462.388
IC 611615 X BML-7	0.165	-1.403	-0.542	-0.243	-0.473	-1549.469**
IC 611615 X KML-109	-0.106	0.271	1.585	-0.255	1.386	1087.081**
IC 623878 X BML-6	-0.970**	-3.112**	-3.146**	-1.354	-1.232	-2152.600**
IC 623878 X BML-7	0.854**	2.069	1.884	0.38	-1.752	1331.857**
IC 623878 X KML-109	0.116	1.043	1.261	0.975	2.984*	820.743*
IC 623880 X BML-6	-0.214	-1.123	-2.115*	-0.207	-2.087	-1457.031**
IC 623880 X BML-7	0.609*	0.974	-0.288	0.1	2.204	326.236
IC 623880 X KML-109	-0.395	0.149	2.403*	0.106	-0.117	1130.795**
IC 627704 X BML-6	1.186**	-1.545	-2.218*	0.581	-0.349	-54.348
IC 627704 X BML-7	-0.124	0.885	2.275*	-1.11	2.592	-126.706
IC 627704 X KML-109	-1.062**	0.66	-0.057	0.529	-2.243	181.055
IC 627708 X BML-6	-0.377	3.707**	1.21	-0.262	-1.257	181.099
IC 627708 X BML-7	0.424	-0.707	0.557	-1.694	1.784	-486.289
IC 627708 X KML-109	-0.047	-3.000**	-1.766	1.956*	-0.527	305.191
IC 627705 X BML-6	0.630*	0.404	1.996*	1.44	-0.73	-171.723
IC 627705 X BML-7	-1.280**	-1.469	-2.297*	-0.864	-0.566	66.269
IC 627705 X KML-109	0.649**	1.065	0.3	-0.576	1.296	105.454
SE (crosses)	0.247	1.126	0.964	0.909	1.317	346.098

DT: days to tasselling; DS: days to silking; ASI: anthesis–silking interval; DM: days to maturity; PLHT: plant height; EHT: ear height; EL: ear length; ED: ear diameter; SE(line): standard error of lines; SE(tester): standard error of testers; SE(crosses): standard error of crosses.

GCA effects of lines indicated the predominance of additive gene action for traits such as days to tasselling (DT), days to silking (DS) and PLHT, whereas non-additive gene effects were more pronounced for GY, EHT and anthesis–silking interval (ASI). This aligned with recent reports emphasising the predominance of non-additive effects for yield-related traits in maize (11).

Among the lines, IC 636977 and IC 623875 were identified as good general combiners for early flowering and plant vigour, with significant positive GCA effects for DT, DS and tasselling-silking synchrony. Conversely, IC 623878 and IC 623880 exhibited strong negative GCA effects for DT and DS, suggesting their potential for early-maturing hybrid development. In terms of physiological traits, IC 611611 and IC 627705 showed significant positive effects for SPAD. These findings are similar to the predominance of additive and non-additive gene effects for yield and physiological traits in maize under line $\times$ tester analysis (12).

Specific combining ability of crosses

The SCA analysis highlighted several promising hybrid combinations for yield and related traits. The cross IC 623875 $\times$ BML-7 exhibited high positive SCA effects for GY, reflecting the role of non-additive gene action in yield expression. The negative SCA effect for ASI indicates improved synchrony between anthesis and silking, which is a desirable trait under drought conditions. Similarly, IC 623878 $\times$ BML-6 and IC 611615 $\times$ KML-109 showed significant positive SCA effects for GY and SPAD values, suggesting that the combination of genetically diverse and physiologically efficient parents can enhance both photosynthetic efficiency and overall yield performance under variable environmental conditions. These results corroborate recent studies that emphasise SCA effects as a key determinant of heterotic performance in maize (13, 14).

Some crosses also revealed trade-offs between traits. For instance, IC 636977 $\times$ BML-7 had high negative SCA for GY and ASI, indicating early flowering but reduced yield, highlighting the importance of multi-trait selection in hybrid development. Such observations echo the earlier findings, which suggested that integrating phenological and physiological traits with yield in combining ability analyses provides a more robust selection framework (15). The variance components revealed that additive gene effects (GCA) were more influential for DT, DS and PLHT, whereas non-additive effects (SCA) predominated for GY, EHT and ASI. This pattern suggests that selection for flowering time and vegetative growth can be effectively carried out at the early generation, whereas hybrid development should exploit heterosis for GY and physiological efficiency. The significant line $\times$ tester interactions for most traits further indicate that specific hybrid combinations respond differently across testers, emphasising the need for targeted parental selection to maximise heterotic gains (16).

The present study identified both superior general combiners and high SCA crosses, providing practical insights for hybrid maize breeding. Lines IC 636977, IC 623875 and IC 611611 can be used as parents for developing early-maturing, high-physiological-efficiency hybrids. Promising crosses such as IC 623875 $\times$ BML-7, IC 623878 $\times$ BML-6 and IC 611615 $\times$ KML-109 are recommended for multi-trait improvement, combining GY, earliness and chlorophyll content. Integrating these findings with recent breeding strategies that emphasise physiological traits alongside yield components can accelerate the development of high-performing hybrids adaptable to diverse agro-ecologies (17).

Conclusion

The present study confirmed substantial genetic variability among maize inbred lines and hybrids for phenological, morphological, physiological and yield traits under a line $\times$ tester design. IC 623875 and IC 611611, as good general combiners for yield and key yield components, suggest their potential utility in breeding programs aimed at improving productivity. The superior performance of specific crosses such as IC 611615 $\times$ KML-105 and IC 623878 $\times$ BML-7 for GY highlights the predominance of non-additive gene action and underscores the importance of exploiting heterosis for hybrid development. These promising parents and hybrids can be effectively utilised for developing high-yielding, early-maturing and physiologically efficient maize hybrids adapted to diverse environments.

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Authors' contributions

SD conducted the complete research process, including drafting and preparing the initial manuscript and revised the manuscript. UG, RE, MRP and VA were involved in the research methodology, manuscript preparation and editing. MG supplied the resources and supervised the study. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None

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