



RESEARCH ARTICLE

Genetic architecture of yield and adaptive traits in maize under rainfed conditions using diallel analysis

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Abstract

Hybrid development under rainfed environments requires precise identification of superior parental combinations governed by non-additive gene action. The present study was conducted at the Maize Breeding Research Sub-Station (SKUAST-Jammu), Poonch, during the kharif seasons of 2023 and 2024 under rainfed subtropical conditions to evaluate combining ability and cross-direction effects in maize. Eight diverse inbred lines were crossed in a full diallel design, generating 56 F₁ hybrids that were evaluated along with parents in a randomized block design. Analysis of variance (ANOVA) revealed highly significant differences among genotypes for all 14 phenological, morphological, cob and yield-related traits studied. Full diallel analysis following Griffing's Method I (fixed model) showed significant general combining ability (GCA) and specific combining ability (SCA) effects, with SCA variance exceeding GCA variance for grain yield per plant (Mean square (MS) = 21119.35) and kernels per cob (MS = 88387.18), indicating predominance of non-additive gene action. A total of four parental lines (CML-141, DMR-649, PMS-116 and IB-3012) exhibited significant positive GCA effects for grain yield and major yield components. A total of three cross combinations, namely CML-141 × DMR-649, PMS-116 × CML-150 and IB-3012 × CML-150, expressed significant positive SCA effects for grain yield, while several crosses showed desirable negative SCA effects for flowering and maturity traits, indicating earliness. Reciprocal effects were significant in only a few combinations, suggesting limited maternal influence. The results demonstrate the effectiveness of SCA-based selection for identifying superior hybrids and provide a practical genetic framework for developing high-yielding and adaptable maize hybrids suited to rainfed agro-ecologies of the north-western Himalayan region.

Keywords: combining ability; heterosis; hybrid breeding; non-additive gene action; rainfed environment

Introduction

Maize (*Zea mays* L.) is one of the most important cereal crops globally, serving as a major source of food, feed and industrial raw material. Its wide adaptability and high yield potential make it a key component of food security systems across both developed and developing countries (1). In India, maize is cultivated under diverse agro-climatic conditions, including irrigated plains, rainfed and hilly regions. In the north-western Himalayan region, including Jammu and Kashmir, maize is predominantly grown under rainfed conditions where productivity is constrained by erratic rainfall, short growing seasons, temperature fluctuations and poor soil fertility. Enhancing productivity under such conditions requires the development of hybrids combining high yield potential with stability and adaptability. Hybrid breeding has been the most successful approach for yield improvement in maize due to the exploitation of heterosis (1, 2). However, successful hybrid development depends on the identification of suitable parental combinations capable of producing superior hybrids across important agronomic traits. In this context, combining ability analysis provides a reliable framework for evaluating parental lines and their cross combinations.

Diallel mating designs are widely used to estimate general combining ability (GCA) and specific combining ability (SCA) effects. The GCA reflects the average performance of a parent and is mainly associated with additive gene action, whereas SCA measures the performance of specific cross combinations and is largely attributed to non-additive gene effects such as dominance and epistasis (3, 4). Estimation of SCA is particularly important in maize hybrid breeding because superior hybrid performance often arises from favourable interactions between specific parental lines (5). Despite several reports on combining ability in maize, information on the genetic architecture of yield and adaptive traits under rainfed subtropical conditions of Jammu and Kashmir remains limited. There is an inadequate understanding of the relative contribution of additive and non-additive gene action and the extent of cross-direction effects under these agro-ecological conditions. Therefore, a systematic diallel analysis is necessary to quantify combining ability effects and to identify superior parental combinations suited to rainfed environments.

Phenological traits such as days to tasselling, silking and maturity are critical determinants of hybrid adaptability under rainfed and stress-prone environments. Earliness enables hybrids to escape terminal drought and temperature stress, which is

particularly relevant in Jammu and Kashmir (6). Morphological traits, including plant height, ear height and stem girth influence plant architecture and lodging resistance (7). Grain yield in maize is governed by yield-attributing traits such as kernel rows per cob, kernels per row, kernels per cob, cob girth, cob length, test weight, shelling percentage and grain yield per plant. Favourable SCA effects for these traits indicate improved sink capacity and superior hybrid performance (8, 9). In addition, reciprocal differences may influence hybrid expression due to maternal or cytoplasmic effects (10, 11).

It was hypothesised that significant variation exists among parental inbred lines and their cross combinations for yield and adaptive traits under rainfed subtropical conditions and that non-additive gene action would predominate in governing grain yield and associated traits. It was further hypothesised that reciprocal effects would be limited and cross-directional effects would influence only specific trait combinations.

Based on these considerations, the objectives of the present investigation were to estimate general and specific combining ability effects for phenological, morphological, cob and yield-related traits in maize under rainfed conditions, to determine the relative importance of additive and non-additive gene action and to identify superior parental lines and cross combinations for hybrid development suited to the rainfed agro-ecology of Jammu and Kashmir.

Materials and Methods

Experimental site

The field experiment was conducted during kharif 2023 and 2024 at the Maize Breeding Research Sub-Station (SKUAST-Jammu), located at latitude 33.77° N and longitude 74.1° E. The site represents rainfed subtropical agro-ecological conditions, characterised by hot summers, monsoon-dependent rainfall and sandy loam soils of moderate fertility. During the cropping seasons, the region received an average seasonal rainfall of approximately 1951.5 mm, predominantly during the monsoon months, with mean maximum and minimum temperatures ranging between 31.7 °C and 14.3 °C, respectively. The rainfall distribution was erratic, typical of rainfed subtropical conditions, thereby providing a suitable environment for evaluating hybrid performance under moisture-limited situations.

Experimental material

A total of eight maize (*Z. mays*) inbred lines were selected from a set of 64 genetically diverse inbreds maintained at the Maize Breeding Research Sub-Station (SKUAST-Jammu) based on their morphological performance and agronomic suitability. These inbred lines, representing diverse genetic backgrounds, were used as parents in the diallel crossing programme. The list and identifiers of the selected parental lines are provided in Table 1.

Crossing programme and experimental design

A full diallel mating design was implemented using eight maize

Table 1. Selected maize inbred lines representing diverse genetic backgrounds used in the study

Sl. No	Parent inbred	Origin	Source
1	CML- 141	CIMMYT	MBRSS
2	IB-141	Local	MBRSS
3	DMR-649	IIMR	MBRSS
4	PMS-116	MBRSS	MBRSS
5	CML-150	CIMMYT	MBRSS
6	CML-447	CIMMYT	MBRSS
7	IB-3012	Local	MBRSS
8	PMS-100	MBRSS	MBRSS

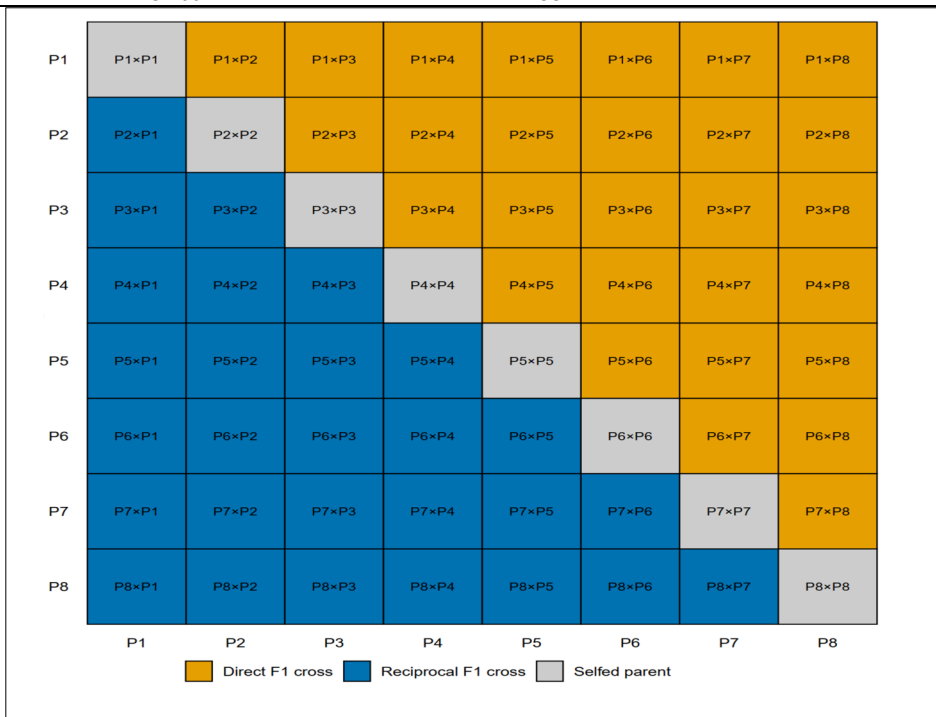


Fig. 1. Schematic representation of the full diallel mating design involving eight maize inbred lines. Diagonal cells represent selfed parental lines, cells above the diagonal indicate direct F_1 crosses and cells below the diagonal denote reciprocal crosses, consistent with Griffing's Method I fixed-effects model.

inbred lines, following Griffing's diallel analysis including parents, F₁ hybrids and reciprocal crosses (Method I) under a fixed-effects model (4). All possible inter-se combinations among the parental lines were generated, resulting in 56 F₁ hybrids, comprising 28 direct crosses and their corresponding 28 reciprocals (Fig. 1). The parental inbred lines were maintained through self-pollination and evaluated alongside the hybrids. Accordingly, the experimental material consisted of 64 genetic entries (56 hybrids and 8 parental inbred lines), which constituted the basis for subsequent analyses of general combining ability, specific combining ability and reciprocal effects using the fixed model diallel framework (4, 12, 5).

Field evaluation and layout

The experimental material comprising parental inbred lines and F₁ hybrids was evaluated in the field using a randomized block design (RBD) with three replications. Each entry was grown in plots consisting of four rows, with a row-to-row spacing of 60 cm and plant-to-plant spacing of 25 cm. All agronomic and crop management practices were followed as per the recommended package of practices for maize. A basal dose of 90 kg N, 45 kg P₂O₅ and 20 kg K₂O per hectare was applied; nitrogen was applied in two splits, with half at sowing and the remaining half at the knee-height stage. Standard plant protection measures were adopted to manage insect pests and diseases as and when required. Irrigation was not provided, as the crop grew entirely under rainfed conditions.

Observations recorded

Observations were recorded on phenological, morphological, cob and yield-related traits following standard procedures used in maize breeding experiments. For each trait, measurements were taken on 5 randomly selected competitive plants per plot and the mean value per plot was used for statistical analysis.

Phenological traits

Days to 50 per cent tasselling: Recorded as the number of days from sowing to the date when approximately half of the plants in a plot exhibited complete tassel emergence and pollen shedding.

Days to 50 per cent silking: Recorded as the number of days from sowing to the date when approximately half of the plants in a plot showed visible silk emergence from the ear shoot.

Days to maturity: Recorded as the number of days from sowing to physiological maturity, indicated by black layer formation in kernels or when most plants in a plot had reached full maturity.

Morphological traits

Plant height (cm): Measured from the soil surface to the base of the tassel on 5 representative plants at physiological maturity using a measuring scale. Values were recorded in cm and averaged.

Ear height (cm): Measured from the soil surface to the node bearing the uppermost primary ear on the same sampled plants.

Stem girth (cm): Measured at approximately 5 cm above ground level using a measuring tape.

Cob traits

Kernel rows per cob: Kernel rows per cob were counted after harvest from representative cobs of 5 randomly selected plants in each plot. The number of complete kernel rows around the mid-portion of each cob was recorded and the average value was expressed as kernel rows per cob.

Kernels per row: Kernels per row were recorded after harvest by counting the number of kernels in a single representative row from cobs of 5 randomly selected plants in each plot. The mean value was expressed as kernels per row.

Kernels per cob: Kernels per cob were determined after harvest from representative cobs of 5 randomly selected plants in each plot using an automated seed counter (SSI-1028 SC, Super Scientific Industries). The average value was recorded as kernels per cob.

Cob girth (cm): Cob girth was measured at the middle portion of the cob after removal of the husk using a measuring tape and expressed in cm.

Cob length (cm): Cob length was measured from the base to the tip of the cob after removal of the husk using a measuring scale and expressed in cm.

Yield and yield-attributing traits

Test weight (g): Test weight was recorded as the weight of 1000 randomly selected dried kernels. The grains were first counted using an automated seed counter and then weighed on a digital balance. The weight was expressed in g.

Shelling percentage (%) is calculated using the formula:

$$\text{Shelling percentage} = \left(\frac{\text{Weight of kernels after shelling}}{\text{Weight of unshelled cobs}} \right) \times 100$$

Grain yield per plant (g): Grain from each sampled plant was harvested at maturity, shelled, dried to approximately 13 % moisture and weighed. Grain yield per plant was calculated as:

Grain yield per plant =

$$\frac{\text{Total grain weight from sampled plants}}{\text{Number of sampled plants}}$$

All yield values were expressed on a dry weight basis to ensure uniformity across replications.

Statistical analysis

The data recorded for all traits were subjected to analysis of variance (ANOVA) under an RBD to test the significance of genotypic differences. The linear model for ANOVA was:

$$Y_{ij} = \mu + g_i + r_j + e_{ij}$$

Where,

Y_{ij} = observation of the i^{th} genotype in the j^{th} replication,

μ = overall mean,

g_i = effect of the i^{th} genotype,

r_j = effect of the j^{th} replication,

e_{ij} = experimental error associated with Y_{ij} .

Diallel analysis was conducted following Griffing's method (Method I, Model I), considering parents, F₁ hybrids and reciprocal crosses under a fixed-effects model (4). The fixed-effects model was considered appropriate because the selected inbred lines represent a specific set of breeding materials of interest rather than a random sample from a larger population. Therefore, inference was restricted to the parental lines and cross combinations included in the study. The statistical model used for diallel analysis was:

$$Y_{ij} = \mu + g_i + g_j + S_{ij} + r_{ij} + e_{ij}$$

Where,

Y_{ij} = mean performance of the cross between i^{th} and j^{th} parents,
 μ = general mean,
 g_i, g_j = GCA effects of parents i and j ,
 s_{ij} = SCA effect,
 r_{ij} = reciprocal effect
 e_{ij} = experimental error.

The GCA effect for the i^{th} parent was estimated as:

$$g_i = \frac{1}{n+2} \left[\sum (X_{ij} + X_{ji}) - \frac{2}{n} T \right]$$

Where,

X_{ij} = mean of cross between i and j ,
 T = total of all crosses,
 n = number of parents.

The SCA effect for a cross between i and j was estimated as:

$$S_{ij} = X_{ij} - \mu - g_i - g_j$$

In the present analysis, reciprocal effects were pooled with SCA effects to represent total non-additive variance, consistent with Griffing's Method I (Model I). However, reciprocal differences were also interpreted separately at the trait level to assess cross-direction effects and reciprocal effects were estimated as:

$$R_{ij} = \frac{(X_{ij} - X_{ji})}{2}$$

The significance of GCA, SCA and reciprocal effects was tested using appropriate mean square ratios against the error mean square. Statistical inferences were drawn at the 5% and 1% probability levels. Before conducting the analysis, the residuals were examined to ensure that the assumptions of normality and homogeneity of variance were satisfied. The distribution of errors was assessed using diagnostic plots along with the Shapiro-Wilk test and homogeneity of variance was evaluated across replications prior to final interpretation of the results. All analyses were performed using R statistical software (version 4.4.1; R Core Team, Vienna, Austria).

Results and Discussion

Analysis of genetic variability and combining ability for key phenological, morphological and yield-related traits in maize hybrids

Analysis of variance clearly indicated the presence of substantial genetic variability among the parental lines and their hybrids for all the traits studied (Table 2). The significant variation observed for days to 50% tasseling (18.51), days to 50% silking (23.28) and days to maturity (28.87) reflects the diversity in flowering behaviour and crop duration among the genotypes. Such variability is particularly important under rainfed subtropical conditions, where synchronisation of flowering and maturity with rainfall distribution directly influences productivity.

Marked variation was also recorded for morphological traits, including plant height (2203.22) and ear height (1137.82), indicating differences in plant architecture among the genotypes. Variability in these traits is critical, as plant stature and ear placement influence assimilate partitioning, standability and ultimately grain yield. Yield-contributing traits such as kernels per cob (8299.10) and grain yield per plant (2049.23) also exhibited significant differences, suggesting that the genetic material used in

the present study possesses adequate variability for effective hybrid improvement.

The significant general combining ability mean squares for all traits indicate the presence of additive genetic variance among the parental lines. Notably, relatively high GCA mean square values were observed for grain yield per plant (14327.58) and kernels per cob (35021.39), suggesting that additive gene effects contributed meaningfully to the expression of these traits. Additive genetic effects are of primary importance in breeding programmes, as they can be accumulated and fixed through selection (4, 13, 14). The presence of appreciable additive variance for yield-related traits, therefore, provides scope for developing superior breeding populations.

At the same time, specific combining ability mean squares were also highly significant across traits. The SCA mean square for grain yield per plant (21119.35) was greater than the corresponding GCA mean square (14327.58), indicating that non-additive gene action played a prominent role in determining yield under the tested conditions. A similar trend was observed for kernels per cob, where the SCA mean square (88387.18) substantially exceeded the GCA mean square (35021.39). This pattern suggests that dominance and possible epistatic interactions were instrumental in enhancing hybrid performance. Earlier investigations in maize have also reported the predominance of non-additive gene action for grain yield, particularly under stress-prone environments (2, 15).

Although reciprocal effects were pooled with SCA, their relatively smaller magnitude indicates that maternal influences were limited and that nuclear gene interactions largely governed trait expression. From a breeding standpoint, this suggests that emphasis on identifying superior direct crosses remains a reliable strategy for hybrid development (15).

General combining ability effects for phenological, morphological and yield-related traits

The GCA effects showed marked differences among maize inbred lines for phenological, morphological and yield-related traits (Fig. 2), indicating variation in the ability of parents to contribute favourable traits across hybrid combinations. Such differences in GCA among parental lines have been widely documented in maize and are considered essential for the identification of promising parents in hybrid breeding programmes (16–18).

For phenological traits, negative GCA effects were desirable as they indicate earliness. In this regard, CML-141 (G1) and CML-150 (G26) exhibited favourable GCA effects for days to 50% tasseling and maturity. The ability of these lines to transmit genes for early flowering and maturity is particularly valuable under rainfed conditions, where delayed maturity may expose the crop to terminal moisture stress (6). The presence of additive control for these traits implies that early maturity can be effectively incorporated into breeding programmes (19).

In terms of morphological traits, CML-141 (G1), DMR-649 (G15) and PMS-116 (G24) exhibited favourable GCA effects for plant height, whereas DMR-649 (G15), CML-447 (G28) and IB-3012 (G35) showed desirable GCA effects for ear height. Balanced plant and ear height are important for maintaining structural stability while optimising photosynthetic efficiency. Significant GCA effects for stem girth, particularly in PMS-116 (G24) and PMS-100 (G49), further indicate additive genetic control for traits associated with lodging

Table 2. Mean squares from analysis of variance for genotypes, general combining ability (GCA) and specific combining ability (SCA) across phenological, morphological, cob and yield-related traits in maize hybrids

Source of variation	Degrees of freedom	Days to 50% tasseling	Days to 50% silking	Days to maturity	Plant height (cm)	Ear height (cm)	Stem girth (cm)	Kernel rows per cob	Kernels per row	Kernels per cob	Cob girth (cm)	Cob length (cm)	Test weight (g)	Shelling percentage (%)	Grain yield per plant (g)
Replication	2	0.34	4.97	0.49	11.36	1.294	0.004	1.609	98.121	635.76	1.2529	9.637	4881.37	16.60	1358.84
Genotype	63	18.51**	23.28**	28.87**	2203.22**	1137.82**	3.35**	9.55**	151.76**	8299.10**	8.55**	24.87**	7517.7**	104.12**	2049.23**
GCA	7	16.155**	71.87**	574.22**	1704.93**	380.27**	6.557**	14.654**	77.452**	35021.39**	10.025**	28.553**	4242.67**	77.07**	14327.58**
SCA	56	19.34**	17.01**	38.89**	88.80**	1223.03**	2.98**	11.578**	154.553**	88387.18**	8.377**	18.818**	12169.02**	107.48**	21119.35**
Error	126	4.43	1.99	0.71	11.50	6.87	0.03	0.604	9.224	2625.43	0.3376	0.852	799.39	40.43	543.35

*Significant at $p < 0.05$ * Significant at $p < 0.01$ ** SCA denotes pooled non-additive variance, obtained by combining SCA and reciprocal effects.

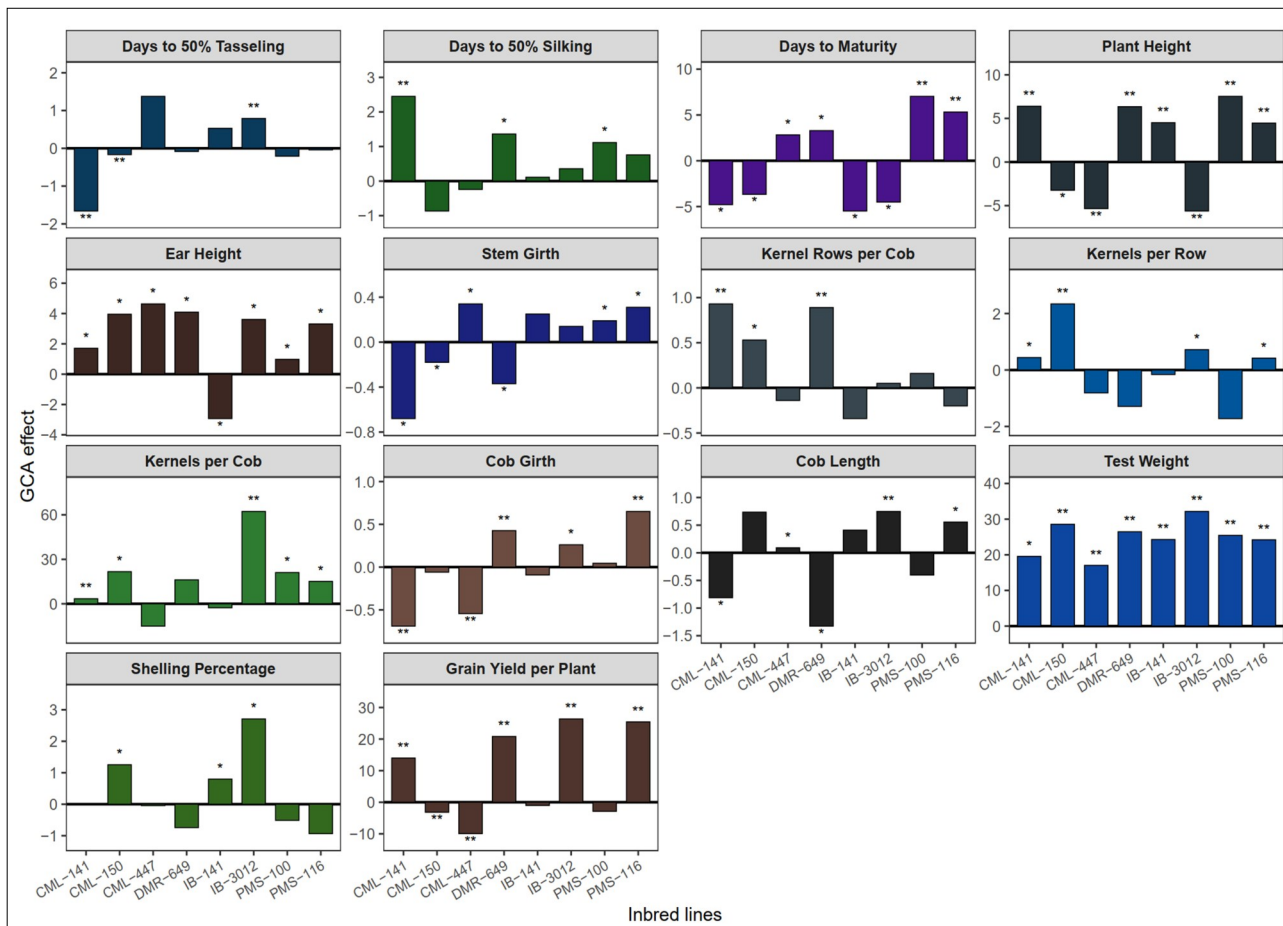


Fig. 2. General combining ability (GCA) effects of parental inbred lines for phenological, morphological, yield-attributing and yield traits. Bars indicate GCA effects, while asterisks denote significance at $p < 0.05$ and $p < 0.01$.

resistance (20, 21).

With respect to yield components, CML-150 (G26) and IB-3012 (G35) emerged as good general combiners for kernels per row and kernels per cob, while DMR-649 (G15) and PMS-116 (G24) showed favourable GCA effects for kernel rows per cob. Since kernel number contributes directly to sink size, the presence of additive variance for these traits is advantageous for sustained yield improvement (22, 23).

Grain yield per plant exhibited significant positive GCA effects in CML-141 (G1), DMR-649 (G15), PMS-116 (G24) and IB-3012 (G35), indicating their consistent contribution to yield across hybrid combinations. These inbred lines also showed favourable GCA effects for one or more yield-contributing traits, suggesting that their superior performance for grain yield was supported by improved component traits. The identification of such parents with stable and desirable GCA effects for grain yield is of prime importance in maize hybrid breeding. Earlier studies have similarly reported that inbred lines with high GCA for grain yield and associated traits are reliable candidates for use as parents in hybrid development programmes (24, 25). Overall, no single inbred line was superior for all traits, emphasising the necessity of trait-specific parental selection. However, parents exhibiting favourable GCA effects for grain yield along with key yield components may be considered promising donors for future hybridisation and maize improvement efforts.

Trait-wise expression of specific combining ability effects in direct crosses

The estimates of SCA effects for direct crosses showed substantial variation across phenological, morphological, cob-related and yield traits, indicating the importance of specific parental

interactions in determining hybrid performance. The heat map visualisation (Fig. 3) provides an integrated overview of the magnitude and direction of SCA effects across trait groups, facilitating identification of superior cross combinations. For traits related to earliness, negative and significant SCA effects were considered desirable, whereas for yield and its components, positive SCA effects were preferred.

For flowering traits, crosses such as CML-141 \times DMR-649 and DMR-649 \times CML-150 exhibited desirable SCA effects for earliness. The manifestation of favourable SCA effects for days to tasseling and maturity suggests that hybrid combinations can achieve flowering synchronisation beyond what is observed in the parents. Such improvements are generally attributed to dominance interactions (25–28).

Morphological traits also showed notable SCA variation. Crosses including CML-141 \times PMS-116 and DMR-649 \times CML-141 exhibited favourable SCA effects for plant height, while PMS-116 \times CML-150 and IB-3012 \times PMS-100 showed desirable SCA effects for stem girth. These results indicate that plant architecture traits are influenced by non-additive genetic interactions, which may contribute to heterotic expression (29–31).

Cob-related traits exhibited particularly high SCA variance, especially for kernels per cob (88387.18). Cross combinations such as CML-141 \times DMR-649 and DMR-649 \times PMS-116 demonstrated positive SCA effects for kernel number, suggesting enhanced sink strength and improved assimilate partitioning. Since kernel number is a primary determinant of yield in maize, the predominance of non-additive gene action for these traits supports the strategic use of hybrid breeding (10, 25, 32).

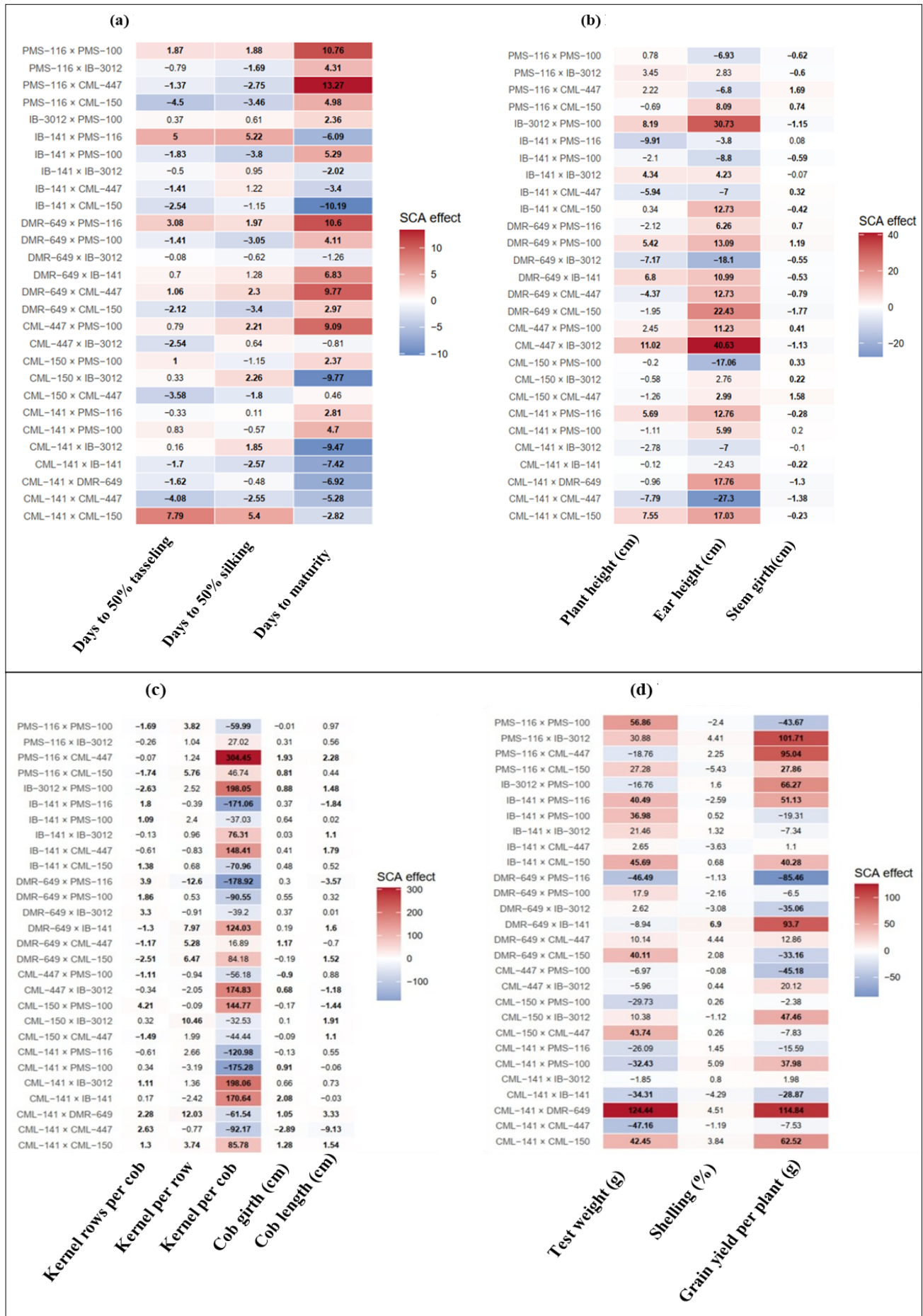


Fig. 3. Heatmap representation of specific combining ability (SCA) effects for (a) phenological; (b) morphological; (c) cob; (d) yield traits in direct maize crosses: Heatmap showing specific combining ability (SCA) effects of maize single crosses for phenological, morphological, cob and yield traits. Red and blue colour scales represent positive and negative SCA effects, respectively, with colour intensity indicating magnitude. Bold values denote statistically significant SCA effects, highlighting superior cross combinations governed by non-additive gene action.

The SCA effects for yield traits, namely test weight, shelling percentage and grain yield per plant (Fig. 3), revealed considerable variation among direct crosses, highlighting the decisive role of specific parental combinations in yield expression. Several direct crosses exhibited positive and significant SCA effects for test weight, indicating improved grain density and quality. Favourable SCA effects for shelling percentage were also observed in a few hybrids, reflecting efficient grain recovery and higher marketable yield. Comparable trends have been reported earlier, emphasising the importance of these traits in hybrid evaluation (33, 34).

For grain yield per plant, the higher SCA mean square relative to GCA indicates that dominance and interaction effects played a decisive role in yield expression. Crosses such as PMS-116 × CML-150 and IB-3012 × CML-150 exhibited favourable SCA effects, suggesting their potential for further multilocation evaluation. The importance of exploiting specific combining ability for yield enhancement has been consistently emphasised in maize breeding literature (28, 35).

Overall, the differential expression of SCA effects across trait groups demonstrates that hybrid performance in maize is largely governed by specific parental interactions. The identification of direct crosses with favourable SCA effects for earliness, plant architecture, cob traits and yield provides valuable information for hybrid development. These cross combinations can be effectively exploited in maize breeding programmes aimed at improving yield potential, stability and adaptation to diverse agro-climatic conditions.

Influence of cross direction on hybrid performance

The evaluation of reciprocal crosses (Fig. 4) showed that cross direction affected hybrid performance only in a limited number of combinations. For most hybrids, the reciprocal performed very similarly to its corresponding direct cross. In terms of grain yield per plant, differences between direct and reciprocal combinations were generally modest, mostly falling within a range of about 3–8 %. Only a few crosses showed larger differences exceeding 10 %, indicating that cross direction had a measurable effect in those specific cases. Overall, these results suggest that hybrid performance was primarily controlled by nuclear genetic effects, although directional influences were evident in certain parental combinations (Fig. 5).

For phenological traits, reciprocal differences were observed in selected combinations rather than across all crosses. The reciprocal DMR-649 × CML-141 flowered earlier than CML-141 × DMR-649, showing a reduction of approximately 2 to 3 days in tasselling. Likewise, the difference in days to maturity between IB-141 × CML-150 and its counterpart CML-150 × IB-141 ranged from 3 to 5 days. These observations indicate that maternal background contributed to phenological expression in specific crosses. Similar reciprocal responses for flowering and maturity have been reported in maize, although such effects are generally confined to combinations rather than being universal (36, 37). Under rainfed subtropical conditions, differences of a few days in flowering or maturity may influence crop escape from terminal stress and affect harvest timing.

Reciprocal effects were somewhat more noticeable for certain morphological traits, particularly ear height and stem girth. The cross IB-3012 × PMS-116 differed from PMS-116 × IB-3012 in ear height by roughly 6 to 9 %, indicating that cross direction influenced plant architecture in this combination. Differences in stem girth

between PMS-100 × CML-447 and its reciprocal were in the range of 5–7 %, suggesting a maternal contribution to stem development. Earlier studies have also reported that reciprocal effects for plant architectural traits may occur in maize, depending on the genetic background involved (38, 39). However, such differences were not consistently expressed across all hybrid combinations.

For yield and related traits, most reciprocal hybrids followed the same performance pattern as their corresponding direct crosses. In most cases, grain yield differences remained below 5 %, indicating minimal practical impact of cross direction. Nevertheless, certain combinations showed more pronounced deviations. The reciprocal IB-3012 × CML-150 produced about 11–13 % higher grain yield than CML-150 × IB-3012, suggesting a favourable directional effect. Conversely, PMS-100 × DMR-649 yielded approximately 8–10 % less than its direct counterpart, demonstrating that cross direction can either enhance or reduce performance depending on the parental combination. Similar patterns have been documented in maize, where reciprocal effects for grain yield are usually restricted to specific crosses rather than consistently expressed across all hybrids (40–43).

The overall comparison between direct and reciprocal crosses indicates that maternal or cytoplasmic influences were present but limited in magnitude. Reciprocal differences were observed in less than one-fourth of the total combinations evaluated and even in those cases, the variation was generally moderate. From a seed production standpoint, this suggests that for most hybrids, the choice of female parent may not substantially alter yield performance. However, in crosses such as DMR-649 × CML-141 and IB-3012 × CML-150, where yield differences exceeded 10 %, the direction of crossing becomes relevant for maximising commercial hybrid performance. Therefore, while routine evaluation of all reciprocals may not be necessary, cross-direction should be verified for promising hybrids before large-scale seed multiplication.

Conclusion

Substantial genetic variability was observed among the maize hybrids evaluated under rainfed subtropical conditions, with grain yield predominantly governed by non-additive gene action as evidenced by significant specific combining ability effects. The inbred lines CML-141, DMR-649, PMS-116 and IB-3012 emerged as reliable general combiners, while crosses such as IB-3012 × CML-150, CML-141 × DMR-649 and PMS-116 × CML-150 showed significant SCA effects for grain yield and CML-141 × CML-447 and IB-141 × CML-150 were promising for earliness. These elite parents may be strategically utilised in heterotic group formation and population improvement programmes and the identified superior crosses should be advanced to multi-location trials for stability assessment. Future research should focus on evaluating these hybrids under diverse stress scenarios and integrating molecular tools to validate combining patterns and accelerate hybrid development for the rainfed regions of Jammu and Kashmir.

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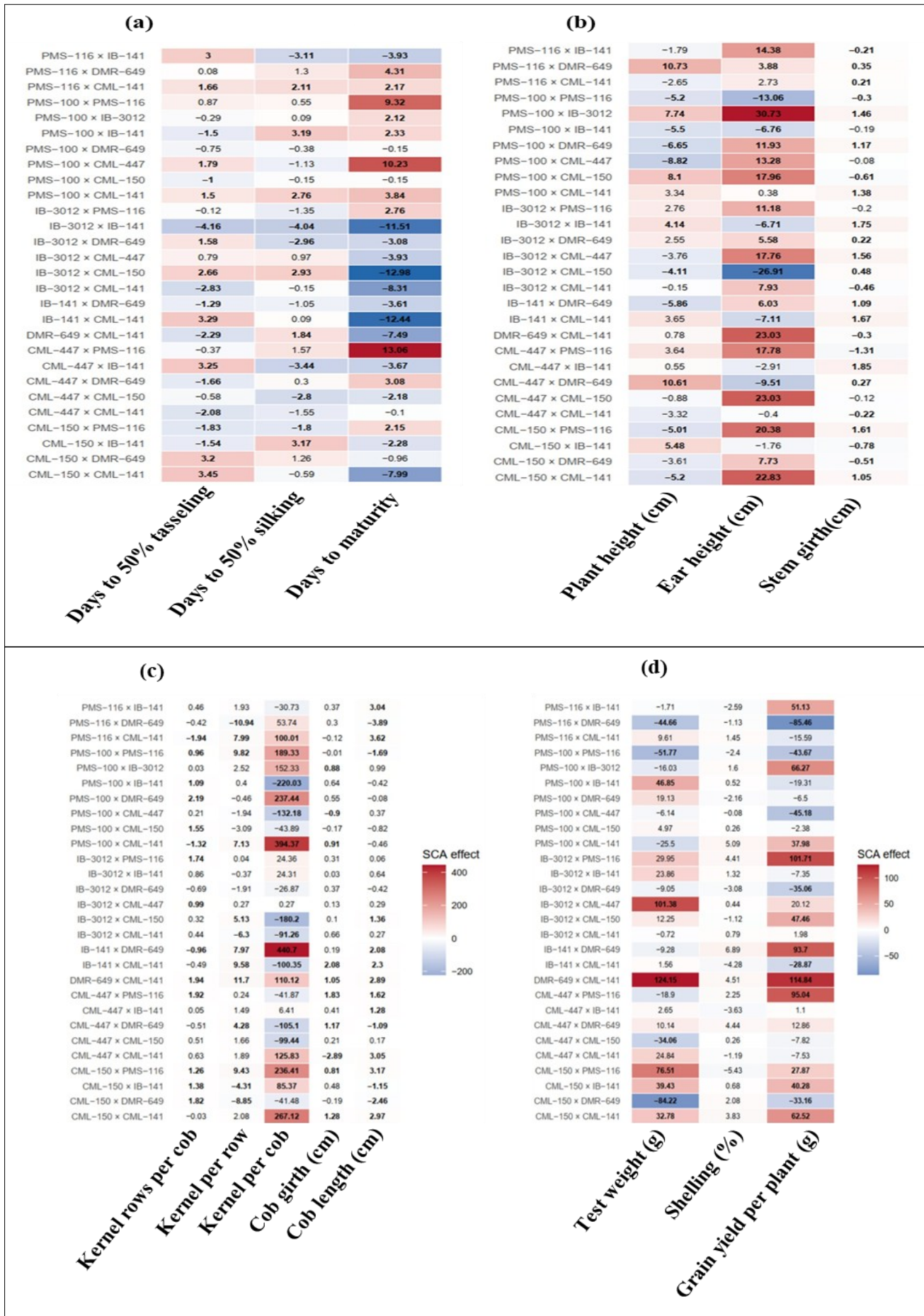


Fig. 4. Heatmap representation of specific combining ability (SCA) effects for (a) phenological; (b) morphological; (c) cob; (d) yield traits in reciprocal maize crosses: Heatmap showing specific combining ability (SCA) effects of maize single crosses for phenological, morphological, cob and yield traits. Red and blue colour scales represent positive and negative SCA effects, respectively, with colour intensity indicating magnitude. Bold values denote statistically significant SCA effects, highlighting superior cross combinations governed by non-additive gene action.

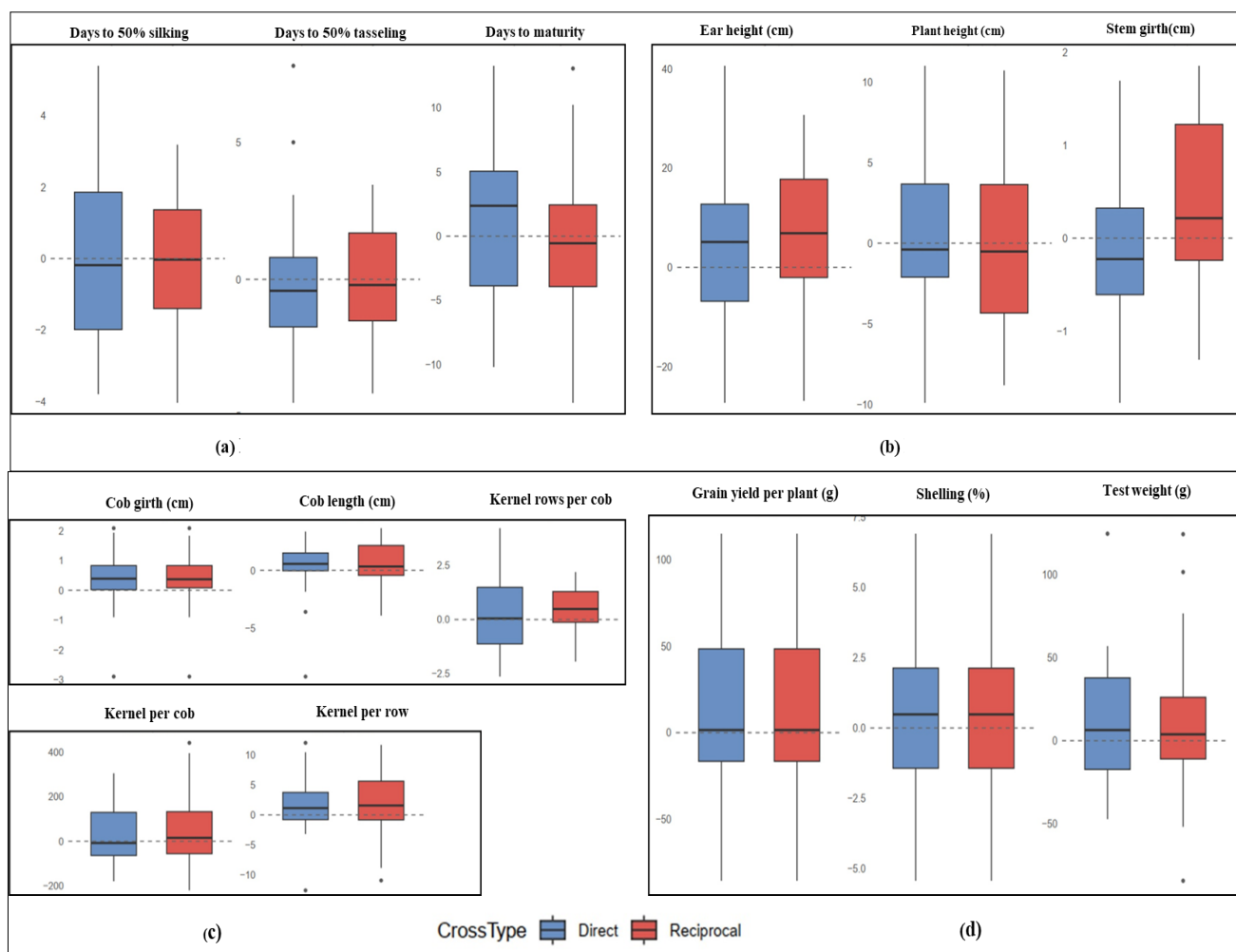


Fig. 5. Comparison of direct and reciprocal crosses for SCA effects across traits in maize hybrids: Boxplots comparing specific combining ability (SCA) effects of direct and reciprocal crosses for (a) phenological traits; (b) morphological traits; (c) cob traits; (d) yield traits in maize hybrids. Although SCA effects primarily represent non additive gene action, consistent differences between direct and reciprocal crosses around the zero SCA line indicate the prevalence of maternal (cross-direction) effects across traits.

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Authors' contributions

DMK conceived and designed the experiment, conducted field and laboratory investigations, performed data analysis and drafted the manuscript. PS assisted in experimental design, data interpretation and critical revision of the manuscript. RSS contributed to statistical analysis, interpretation of results and manuscript editing. AK supervised the research work, provided technical guidance and critically reviewed the manuscript. All authors have read and approved the final manuscript.

Compliance with ethical standards

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

Ethical issues: None

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this manuscript, the authors used Jenni AI as an AI-assisted writing tool to improve language clarity, grammar and overall readability. The tool was used solely for linguistic and editorial refinement. All scientific content, data, analyses, results and interpretations presented in this article are based on original research conducted by the authors. Following the use of this tool, the authors carefully reviewed, edited and validated the manuscript and take full responsibility for the accuracy, integrity and originality of the content.

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