Maternal effects, reciprocal differences and combing ability study for yield and its component traits in maize (*Zea mays* L.) through modified diallel analysis.

Commented [Ma1]: ...... , and combining ability..... (for a better title suggestion). The author wrote "combing." Please check.

Commented [Ma2]: Blue and Red-colored words or marks are suggestions I made within the manuscript. Otherwise, review comments by the side follow.

Bonipas Antony J[1], Rajashekhar M. Kachapur[2*], Gopalakrishna Naidu[3], Sidaramappa C. Talekar[2], Zerka Rashid[4], Vivek S. Bindiganavile[4*], Nagesh S. Patne [4]Shiddappa R. Salakinkop[2] and Prema G U[2]

[1]Department of Genetics and Plant Breeding,Tamil Nadu Agricultural University,Coimbatore - 641 003, India

[2]AICRP on Maize, MARS, University of Agricultural Sciences, Dharwad – 580 005, India

[3]AICRP on Soybean, MARS, University of Agricultural Sciences,Dharwad – 580 005, Karnataka, India

[4]International Maize and Wheat Improvement Centre (CIMMYT), ICRISAT Campus,Patancheru, Greater Hyderabad-502324, Telangana, India

Corresponding authors*:*

Rajashekhar M. Kachapur[2], Vivek S. Bindiganavile[4]

kachapurr@uasd.in(RM), B.Vivek@cgiar.org (BSV)

Abstract

Combining ability status of the inbred lines is a crucial information for hybrid breeding program. Diallel or line x tester mating designs are frequently used to evaluate the combining ability. In the current study, a modified diallel model was used wherein the Griffing's combining ability effects were divided to assess the maternal and reciprocal impacts of combining ability. To do this, a full diallel of 8 x 8 crosses in maize was made, and the field data gathered was analyzed using both Griffing's and the modified model to determine how well the parents' and F_1 hybrids combined. For each of the features, a sizable reciprocal and maternal variance was observed. The number of kernel rows per cob variable had a ratio of additive variance to dominance variance greater than one, whereas all other traits, including grain yield, had a ratio close to zero, suggesting that non-additive gene action was primarily responsible for the genetic control of most of the traits. The narrow sense of heritability was low to moderate for all variables, apart from the number of kernel rows per cob. With the help of the improved model, it was possible to choose superior parents and cross-parent pairings with accuracy. Based on the modified GCA effects and maternal effects, the parental line P5 was recognized as a potential seed parent and P7 as a good pollen parent for grain yield and yield-attributing characteristics. The P8xP1 cross had the highest SCA effect on grain yield, whereas the P5xP6 cross combination had the highest reciprocal effect. According to the correlation experiments, Griffing's GCA and SCA effects were not as good at predicting F_1 performance as the total of the partitioned GCA and SCA effects from the updated model.

Key words: Maize, combining ability, maternal effect, reciprocal effect, diallel

1. Introduction

The most widely cultivated and adaptable cereal is maize (*Zea mays* L.), which is used for a variety of purposes, including human nutrition, poultry and animal feed, and a number of industrial uses (Gupta et al., 2015). In order to meet the country's continuously rising demand, India will need to double its maize production by the year 2050 (Mehta et al., 2021). The creation of hybrids with more productive traits and desirable agronomic and physiological characteristics is a major goal of global maize breeding (Andorf et al., 2019). In-depth research is being done to create superior hybrids with high yielding capacities and resistance to biotic and abiotic stresses in order to accomplish this. The productivity of hybrids depends on the genetic performance of their parents, and the most difficult aspects of hybrid breeding are testing the inbred parents and finding the best cross combinations that result in productive hybrids (Patil et al., 2021). Based on an individual's performance as a whole, the line's adaptability and stability, and combining ability, the ideal parents could be found (Bertan et al., 2007). For a hybrid combination and figuring out inheritance patterns, combining ability is crucial (Fashat et al., 2016). The performance of cross combinations is the specific combining ability (SCA), whereas the general combining ability (GCA) is defined as the average performance of a line in a series of crosses (Sprague and Tatum, 1942). The relative importance of advantageous alleles within a line is determined by the GCA effect, a measurement of a line's breeding value. The difference in allele frequencies

Commented [Ma3]: The Journal has promised to format the references during the production period.

between the lines in a cross combination is indicated by the SCA effect (Zhang et al., 2012). The ability of the hybrid to combine, the presence of advantageous alleles, and the genetic separation between the parents all influence performance (Acquaah, 2009). Another factor to take into account is the reciprocal effect (Jumbo et al., 2008). Which may result from the cytoplasm's constituents or from interactions between its genes and nuclear genes. Certain lines produce superior combinations, whether male or female, because this type of interaction would vary in different materials (Fleming et al., 1960). Regarding its relative significance and methodical exploitation in hybrid development, there is not much agreement, though. Because they do not exhibit a uniform sign between two germplasm groups and are not consistently observed across environments (Gonzalo et al., 2007 and Mukanga et al., 2010).

Several maize breeding studies did not include reciprocal crosses because of a lack of funding and understanding of reciprocal differences and their use. Despite this, endosperm regulates maize grain yield, so understanding reciprocal effects (RECs), which have been thoroughly researched in maize ever since hybrids were created (Fleming et al., 1960, Pollmer et al., 1979 and Santos et al., 2017) is crucial. Additionally, it has been shown (Mahgoub, 2011 and Yao et al., 2013) that estimates of the SCA and GCA effects are influenced by the maternal and reciprocal effects. A better comprehension of maternal effects would also enable a better selection response (Falconer, 1996). Griffing suggested use of diallel method to estimate the combined effects of combining ability and genetic variance. Griffing's methods 1 and 3 have the distinction of allowing estimation of the reciprocal and maternal effects. However, this method (1 and 3) assumes that they are likely to be similar, as suggested by Yates~~,~~ (1947) and estimates the general and specific combining ability effects based on their average effect of parents when used as seed or pollen parents or in cross combinations. Regardless of whether a parent is used as a seed or pollen parent, the fixed model of diallel analysis estimates one GCA effect for each parent. Similar to that, each cross combination has one SCA effect. The contributions of each parent are included in this estimate as a whole.

When used as a seed or pollen parent, the partitioning of the GCA and SCA effects would offer more details about each parent. Additionally, it offers precise details regarding the nature of the interactions between the ideal parent combinations. It also reveals how the estimation of the GCA and SCA effects is impacted by the inclusion of reciprocal crosses in the diallel. As a result, the current study's main objective is to (i) compare the effects of GCA and SCA before and after partitioning. Estimate the maternal and RECs and their relationship to GCA and SCA, as well as the relative contributions of the seed and pollen parents in the cross combinations.

2. Materials and methods

2.1 Field evaluation of diallel crosses

Sixteen parental inbred lines along with 56 F_1 hybrids with a CIMMYT / UASD genetic background made up the study's sample (Table 1). These 56 F_1 hybrids were created using the 8 x 8 full diallel method (including reciprocal crosses) during the rabi season of

2019–2020 at All India Co-ordinated Maize Improvement Project, UAS, Dharwad and evaluated these hybrids and their parents in a randomized block design with three replications during kharif 2020, along with four checks: 900-MG, NK-6240, GH-0727, and GH-150125. Table 2 lists the specific weather conditions for the growing season. Vertic Inseptisol, a medium-deep black soil, made up the experimental plot and evaluation was under optimal situation. There was not enough F_1 seed to grow for another season as a result the entries were grown in two rows of four meters each, spaced 60 cm apart by 20 cm, and all the recommended maize package practices were followed to grow a robust crop.

Commented [Ma4]: It will be of interest to the reader to know the extent or basic requirements for the good practices in India to grow maize through the insertion of a reference that explicitly spells out those basic good practices for maize production. Therefore, I suggest at least one reference for the purposes of the international community.

2.2 Data collection

Eight quantitative traits were measured across all replications, including days to 50% tasseling (DTT), days to 50% silking (DTS), number of kernel rows per cob (NKRC), number of kernels per row (NKR), cob girth (CG) (cm), cob length (CL) (cm), hundred grain weight (HGW) (g), and grain yield (GY) (q/ha). Below is a detailed description of the method used to measure observation.

Days to 50 per cent tasseling (DTT)- Number of days from the day of sowing to the day on which 50 per cent of the plants in a treatment showed anthesis was recorded as days to 50 % tasseling.

Days to 50 per cent silking (DTS) – Number of days from the day of sowing to the day on which 50 per cent of the plants in the treatment showed silk emergence was recorded as days to 50 % silking.

Number of kernels per row (NKR) – It is the average number of kernels per row from 5 cobs from the base to tip of ear counted physically and recorded.

Number of kernel rows per cob (NKRC) – It is the number of kernel rows counted physically and recorded from five cobs and averaged.

Cob girth (CG)(cm)- Average cob girth of five cobs measured using vernier caliper after removing the husk at the middle portion of ear measured in centimeters (cm).

Cob length (CL)(cm) – Average length of five cobs in centimeters (cm) after harvest measured from the base to the tip of the ear.

Hundred grain weight (HSW) (g) -Weight of hundred grains drawn from a random sun-dried sample and measured in grams (g).

Grain yield (GY) (q/ha) - Weight of the de-husked ears/plot recorded at the time of harvest and then converted to grain yield at 15 per cent moisture and expressed in quintals per hectare (q/ha).

2.3 Statistical Analysis

With the aid of the statistical software package R studio version 2022.07.1 and Microsoft Excel, the data gathered for the traits was put together and examined according to

Griffing (1956a). The diallel analysis R package (Yaseen, 2018) from R studio was used to examine various effects and combining capability Model I of the diallel analysis method. The model used was: make sure this text above isn't mentioned in a different way.

$$Y_{ij} = \mu + g_i + g_j + s_{ij} + r_{ij} + \frac{1}{c}\sum ke_{ij}$$

Where, Y_{ij} was the observed measurement of parents i and j; μ was the population mean; gi and gj are the GCA effects of parent i and j, respectively; s_{ij} the SCA effect of the cross between parents i and j; r_{ij} RECs and e_{ij} the random environmental effects associated with ijth individual. The restrictions imposed on the combining ability effects were: $\sum g_i = 0$ and $\sum s_{ij} = 0$ for each j (Griffing, 1956b).

According to ~~(~~Singh and Chaudry~~,~~ (1985), the genetic components, or variance due to GCA (σ^2_{GCA}), SCA (σ^2_{SCA}), and RCA (σ^2_{RCA}), were estimated. Also, calculated was the ratio of GCA variance to SCA variance, with ratios greater than unity indicating additive gene action and ratios less than unity indicating dominance genetic effect (i.e., non-additive gene action) for the particular trait.

The additive and dominant variances, heritability was also calculated from σ^2_{GCA}, σ^2_{SCA}, σ^2_{RCA} as follows,

$$\sigma^2_P = 2\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_{RCA} + \frac{\sigma^2 error}{r}$$

$$\sigma^2_A = 2\,\sigma^2_{GCA}$$

$$\sigma^2_D = \sigma^2_{SCA}$$

$$H^2_{bs} = \frac{\sigma^2_A + \sigma^2_D}{\sigma^2_P}$$

$$h^2_{ns} = \frac{\sigma^2_A}{\sigma^2_P}$$

Where, r = Number of replications, σ^2_{GCA} = Variance due to GCA, σ^2_{SCA} = Variance due to SCA, σ^2_{RCA} = Reciprocal variance, σ^2error = Error variance, σ^2_P = Phenotypic variance, σ^2_A = Additive variance, σ^2_D = Dominance variance, H^2_{bs}= Broad sense heritability, h^2_{ns} = Narrow sense heritability (Singh and Chaudry, 1985).

Formatted: Indent: First line: 1.27 cm

According to Baker's formula, baker's ratio was used to determine the relative importance of GCA and SCA effects for each trait (Baker, 1978).

$$\text{Baker's ratio} = \frac{2\sigma^2_{GCA}}{[2\sigma^2_{GCA} + \sigma^2_{SCA}]}$$

Griffing's model formula

Griffing's method of combining ability effects was estimated using the following model,

Formatted: Indent: First line: 1.27 cm

$$g_i = \frac{1}{2n}(x_{i.} + x_{.i}) - \frac{1}{n^2}(x_{..})$$

$$\hat{s}_{ij} = \frac{1}{2}(x_{ij} + x_{ji}) - \frac{1}{2n}(x_{i.} + x_{.i} + x_{j.} + x_{.j}) + \frac{1}{n^2}(x_{..})$$

$$r_{ij} = \frac{1}{2}(x_{ij} - x_{ji})$$

Modified model formula

For the precise estimation, the GCA effect is g_i partitioned according to Mahgoub~~,~~ (2011) to estimate GCA effect for the parent when it is used as a female in its hybrid combination g_{fi} and GCA effect for the same parent when it is used as a male in its hybrid combination g_{mi} as follows;

Formatted: Indent: First line: 1.27 cm

$$g_{fi} = \frac{1}{n}(x_{i.}) - \frac{1}{n^2}(x_{..})$$

$$g_{mi} = \frac{1}{n}(x_{.i}) - \frac{1}{n^2}(x_{..})$$

$$g_i = \frac{1}{2}\left(g_{fi} + g_{mi}\right)$$

Where, $\sum g_{fi} = 0, \sum g_{mi} = 0$ and $\sum g_i = 0$

$$\frac{1}{2}\left(g_{fi} - g_{mi}\right) = \frac{1}{2}\left[\frac{1}{n}(x_{i.}) - \frac{1}{n^2}(x_{..}) - \frac{1}{n}(x_{.i}) + \frac{1}{n^2}(x_{..})\right]$$

$$\frac{1}{2}\left(g_{fi} - g_{mi}\right) = \frac{1}{2}\left[\frac{1}{n}(x_{i.}) - \frac{1}{n}(x_{.i})\right] = \frac{1}{2}(x_{i.} - x_{.i})$$

$$m_i = \frac{1}{2}\left(g_{fi} - g_{mi}\right)$$

Where, $\sum m = 0$

The average difference between the g_{fi} and g_{mi} was proved to be equal to of maternal effects. It is exactly equal to m~~M~~aternal effect estimated according to Cockerham

Formatted: Indent: First line: 1.27 cm

[26] $m = \left(\frac{x_{i.} - x_{.i}}{2n} \right)$. Thus, it proves the $g_{fi} - g_{mi}$ estimate provides the precise estimation of maternal effects.

Specific combining ability effect is partitioned to estimate SCA effect for the cross s_{ij} and for its reciprocal s_{ji} as follows:

$$s_{ij} = x_{ij} - \frac{1}{2}\left(x_{i.} + x_{.i} + x_{j.} + x_{.j}\right) + \frac{1}{n^2}\left(x_{..}\right)$$
$$s_{ji} = x_{ji} - \frac{1}{2}\left(x_{i.} + x_{.i} + x_{j.} + x_{.j}\right) + \frac{1}{n^2}\left(x_{..}\right)$$

Where, $\sum s_{ij} + s_{ji} = 2\ Griffing's\ s_{ij}$

Reciprocal effects were calculated from partitioned specific combining ability as follow,

$$r_{ij} = \frac{1}{2}\left(s_{ij} - s_{ji}\right) and\ r_{ji} = -r_{ij}$$

As a result, the difference between the SCA effect of a cross and its reciprocal equals the estimated reciprocal effect. Therefore, this difference provides a precise estimate of the reciprocal effect. Testing the significance differences was estimated according to Griffing's method.

Where,

g_i = Griffing's GCA effect of ith parent,

g_{fi} = Mean deviation of the ith parent as a female, averaged over a set of n males, from the grand mean,

g_{mi} = Mean deviation of the ith parent as a male, averaged over a set of n females, from the grand mean,

m_i = Maternal effect of ith parent,

s_{ij} = SCA effect of the cross combination with ith female and the jth male parent,

s_{ji} = SCA effect of the cross combination with jth female and the ith male parent,

Commented [Ma5]: This reference is not even mentioned in the reference list. Please either remove or include it in the reference list below and justify it like others, not by list numbering but by year of publication.

Formatted: Indent: First line: 1.27 cm

Formatted: Indent: First line: 1.27 cm

r_{ij} = reciprocal effect involving the i^{th} female and the j^{th} male parent,

x_{ij} = The mean of cross resulting from crossing the i^{th} female with the j^{th} male,

x_{ji} = The mean of cross resulting from crossing the j^{th} female with the i^{th} male,

$x_{i.}$ = The sum of i^{th} female over all males,

$x_{.i}$ = The sum of i^{th} male over all females,

$x_{j.}$ = The sum of jt^{h} female over all males,

$x_{j.}$ = The sum of j^{th} male over all females,

$x_{..}$ = Grand total.

~~2.2~~ Correlation analysis

The mean values, mid-parent, and better-parent heterosis were correlated with the Griffing's GCA, SCA, and adjusted GCA and SCA effects. The heterosis values of straight hybrids (S3-4) and the mean performance of straight and reciprocal hybrids (S1-2) were listed in the supporting files. Using MS-Excel, the correlation analysis was carried out.

3. Results

3.1 Analysis of variance for combining ability

Commented [Ma6]: All the abbreviations in Table 3 should be spelled out under the table footnote.

Formatted: Indent: First line: 1.27 cm

To understand source of variability and how it is manifested in the experimental material the analysis of variance was computed (Table 3). The results of the statistical analysis of variance showed that treatments were significant for each of the traits, which suggests that the experimental material was varied. The GCA was significant for all the examined traits, but for the traits DTT, DTS, NKR, and NKRC, it was higher than the SCA, indicating that these traits are regulated by additive gene action. SCA was also significant for all the traits, but for NKR, CL, TW, and GY, it was higher than GCA, indicating the significance of non-additive gene action in regulating these traits. Even though they were significant for cob girth (CG), GCA and SCA were both very low. The value of the maternal effect is demonstrated by the significance of RECs in every trait. Maternal and non-maternal components make up the reciprocal effect but it is the maternal component that is important.

Commented [Ma7]: This was not as true as others in Table 3 (GCA, 51.93** and SCA, 102.80**). Please remove.

3.2 Genetic parameters

Commented [Ma8]: All the abbreviations in Table 4 should be spelled out under the table footnote.

Formatted: Font: Not Bold

Formatted: Font: Not Bold

Formatted: Indent: First line: 1.27 cm

The estimated genetic parameters are shown in Table 4 with their estimates. The σ^2e was significantly lower than the σ^2P, indicating that all of the traits have less of an impact from the environment. The number of kernel rows per cob had a σ^2A value higher than a σ^2D value, indicating that additive genes were primarily responsible for this trait. The fact that

SCA variance for all traits is greater than GCA variance shows that non-additive gene action governs all traits primarily (Fig. 1). The additive to dominance variance ratio for NKRC, however, was greater than unity, indicating additive gene action. Fig. 2 depicts the broad and narrow sense heritability observed for the traits. The trait DTS (H^2bs = 94.54) showed the greatest heritability in the broadest sense. All other traits also demonstrated high broad sense heritability. The narrow sense heritability of all other traits was low, except for the number of kernel rows per cob (h^2ns = 45.26), which had a medium narrow sense heritability. The relative significance of GCA and SCA effects in predicting progeny performance was examined using Baker's ratio. For traits like days to the NKRC, the Baker's ratio was greater than 0.5. Baker's ratio was less than 0.5 and close to zero in the NKR, CL, HSW, and GY, in contrast.

3.3~~2~~ General combining ability

Griffing's method was used to estimate the GCA effects and Table 5 shows the adjusted GCA values following partitioning. The parental lines P1 (-1.43, -0.72) and P3 (-2.47, -1.66) are good general combiners for earliness, according to Griffing's GCA effects (g_i) for the DTT and DTS, respectively. For grain yield, parental lines P3 (2.65) and P4~~3~~ (1.75) were in front of parental line P7, which had significant positive GCA for GY (4.98), NKR (2.01), NKRC (0.94), CL (0.69), and CG (0.11). These three lines, P7, P3, and P4, can therefore be used as effective general combiners to increase grain yield. P5 and P4 were also discovered to be effective general combiners for TW (1.86) and (1.2), respectively.

How a particular line will behave as pollen and seed parent in the hybrid combination can be determined by comparing the adjusted GCA values after partitioning into male (g_{mi}) and female GCA (g_{fi}) effects. P7 had a significant GCA effect for GY (3.42 and 6.54), NKR (2.11 and 1.91), NKRC (0.80 and 1.08), ~~NKR~~CG (0.05 and 0.17), and CL (0.45 and 0.93) based on the adjusted values. The parental line P5 recorded negative g_{mi} (-12.20) high and significant breeding value for GY when used as a seed parent, g_{fi} (13.90) as opposed to gi (0.85), indicating that it is a potential line when used as a seed parent for grain yield as opposed to other crops.

Similar to this, on the GY, the parental lines P6, P4, and P3 recorded significant g_{mi} in a positive direction as compared to g_i (~~2.65, 1.75, and~~ -0.38, 1.75, and 2.65), respectively. These values were 7.21, 6.55, and 5.10, respectively. Parents P5 (3.02), P2 (0.83), and P8 (0.83) recorded high GCA as females compared to g_{mi} (~~-0.92,~~ 0.70, -0.92, and -0.05), ~~respectively),~~ and g_i (~~-0.05,~~ 1.86, -0.05, and 0.39), respectively, among the yield-contributing traits, for test weight (TW). For test weight, however, the P4 had the highest GCA as a male parent (1.70), indicating that it contributes more when used as a pollen parent.

3.4~~3~~ Maternal effect

The adjusted maternal effects, which are shown in Table 6, were determined by averaging the g_{fi} and g_{mi} differences. The average of the female over all the males is typically used to estimate the maternal effect. Estimating maternal effects for some specific cross combinations might be more crucial than using the ratio of all females to all associated males

Commented [Ma9]: All the abbreviations in Table 5 should be spelled out under the table footnote. Footnote at Table 5: gfi-Adjusted GCA after partition when parent used as **male**. I think it should be female instead.

Formatted: Font: Not Bold

Formatted: Font: Not Bold

Formatted: Indent: First line: 1.27 cm

Commented [Ma10]: Please remain consistent with the statement. Here, you mean HSW, right? If yes, please change back.

Commented [Ma11]: This change of text from HSW to TW has resulted in more ambiguity. Please stick with one conformity.

Commented [Ma12]: All the abbreviations in Table 6 should be spelled out under the table footnote. And remember the TW justification as suggested above.

Formatted: Font: Not Bold

Formatted: Font: Not Bold

Formatted: Indent: First line: 1.27 cm

as a baseline. If it estimates taking into account all males over all females, it may understate the maternal effect of a few cross combinations. The estimation of the reciprocal effects follows the partitioning of the maternal effects, which results in the estimation of the maternal effects on a hybrid combination basis rather than on the average of all associated male parents.

The findings (Table 6) indicated that all of the traits for the parental line P3 had significant maternal effects, but in an unfavorable negative direction. For grain yield and other yield-related traits, P5 recorded significantly the highest maternal effect among the other parental lines in a desirable positive direction. All other lines had a significant maternal impact on GY, with the exception of parental line P1. Only two parents P3 (-1.17 and -1.08) and P6 (0.88 and 0.88) showed a significant maternal effect for DTT and DTS, and only the maternal effect observed in P3 was in a desirable direction.

3.5~~4~~ Specific combining ability

Commented [Ma13]: All the abbreviations in Table 7 should be spelled out under the table footnote. And remember the TW justification as suggested above.

Formatted: Font: Not Bold

Formatted: Font: Not Bold

Formatted: Indent: First line: 1.27 cm

The partition provides additional information, such as the SCA of the straight cross and its reciprocal cross, whereas the Griffing's SCA estimation assumes a single SCA value for a cross combination. Griffing's SCA effect (30.56) on grain yield was the highest among the cross combinations P4xP7 (Table 7). There was no difference between Griffing's value and the adjusted straight and reciprocal cross SCA values. Despite this, after partitioning, many crosses revealed noticeable variations between Griffing's GCA and SCA values. The reciprocal crosss$_{ji}$ P5xP2 had the highest SCA effect for CL (2.11), HSW~~TW~~ (3.77), and GY (38.25) when compared to the straight crosss$_{ji}$. For NKR~~C~~ (7.17), HSW~~TW~~ (7.89), and GY (45.07), the reciprocal P8xP1 also displayed a higher SCA than its straight cross. On the other hand, the direct cross P5xP6 had greater SCA effects for CL (0.97), CG (0.28), and GY (35.30) than its reciprocal.

3.6~~5~~ Reciprocal effects

Commented [Ma14]: All the abbreviations in Table 8 should be spelled out under the table footnote. And remember the TW justification as suggested above.

Formatted: Font: Not Bold

Formatted: Font: Not Bold

Estimates of RECs are given by the difference between the straight cross and its reciprocal based on SCA effects. Griffing's reciprocal effect is the same, but the partitioned value ($r_{ij} = -r_{ji}$) is in two directions (- and/or +). The cross-combination of P5 and P6 was found to have the greatest reciprocal effect on grain yield (+27.46). Meanwhile, the cross combination between P1 and P8 had the highest reciprocal effect for ~~TW~~HSW, NKR, DTT, and DTS (+5.64, +5.82, -~~+~~2.88 and -~~+~~2.15, respectively) (Table 8). The cross between P1 and P2 for CL had the greatest reciprocal effect (+2.40), and the cross between P5 and P8 for CG had the greatest reciprocal effect (+0.52).

Commented [Ma15]: This value is in a negative direction in Table 8. Please verify if this is what you wanted to report or if it is still under P1xP8 (+0.41).

3.7~~6~~ Correlation between heterosis, mean performance and combining ability

Commented [Ma16]: All the abbreviations in Table 9 should be spelled out under the table footnote. And remember the TW justification as suggested above.

Formatted: Font: Not Bold

Formatted: Font: Not Bold

Formatted: Indent: First line: 1.27 cm

Mean performance, mid-parent heterosis, and better-parent heterosis (Table 9) were found to be strongly correlated with Griffing's SCA effect and adjusted SCA effect after partitioning. It is therefore appropriate to identify potential hybrids based on the adjusted SCA effects after partition, which had the highest correlation with hybrid performance and heterosis. Establish the facts and include a reference. While the sum of the adjusted GCA effects (g_{fi} and g_{mi}) and mean performance are strongly correlated, Griffing's GCA effect (g_i) was not consistently correlated with the phenotypic performance of hybrids, mid-parent heterosis, and better-~~-~~parent heterosis. In light of this, the adjusted GCA effect sum is more accurate at predicting hybrid performance than the sum after dividing the GCA into male and female GCA.

4. Discussion

The fundamental concepts in plant breeding, general combining ability (GCA) and specific combining ability (SCA), proposed by Sprague and Tatum~~,~~ (1942) have an impact on inbred line selection, hybrid breeding programs, and population development. Along with combining ability, the maternal and its ~~(~~RECs~~)~~ are crucial for the choice of inbred lines as seed or pollen parents in hybrid development. According to reports, there are reciprocal differences between maize grain yield and other quantitative traits (Fan et al., 2014 and 2018, Dosho et al., 2021). Additionally, it has been noted that the estimation of both general and specific combining ability effects is impacted by the presence of maternal and RECs (Yao et al., 2013).

One of the most popular mating designs for combining ability effects in parents and hybrids is the diallel analysis proposed by Griffing~~,~~ (1956a). Reciprocal crosses are taken into account in the traditional Griffing's analysis methods 1 and 3, but they cannot accurately estimate maternal, REC, or combining ability effects (Mahgoub et al., 2004). The modified model proposed by Mahgoub et al. (2011) can give more accurate estimates of GCA and SCA as well as information on maternal and RECs (Gareeb and Fares, 2016) by partitioning the combining ability effects. The results of the analysis of variance for combining ability showed that SCA variance was greater than GCA variance, indicating that these characters have non-additive gene action. Numerous researchers (Khan and Dubey, 2015, Yerva et al., 2016, and Bharat et al., 2020) also reported similar results. However, for NKRC, additive variance was higher than dominance variance, indicating that this trait is controlled by additive gene action. The importance of heterosis breeding in maize crop improvement is demonstrated by the predominance of non-additive gene action for grain yield and other yield contributing characters.

The broad-sense heritability was high for all the quantitative characters studied. In contrast, narrow-sense heritability was low for all other traits, including grain yield, while it was moderate for N~~R~~KRC. The Baker's ratio for grain yield and other yield-attributing traits was less than 0.5 and almost zero, indicating that SCA was a more reliable predictor of hybrid performance. A lower baker's ratio value for grain yield was also noted by Kayaga et al. (2014). The correlation study suggests, however, that the prediction based on GCA would be more accurate. The current study found significant combining ability effects and RECs for all the traits, both generally and specifically. The selection of female parents in cross combinations is much more important in the hybrid program to produce superior hybrids, according to earlier research work by Kumar et al. (2016), Sadalla et al. (2017), Onejeme et al. (2020), and Suyadi et al. (2021) that found significant reciprocal variance for the majority of maize traits. Given the importance of both the maternal and non-maternal components, it is crucial to carefully choose both male and female parents for a cross-combination.

The observed differences between straight and reciprocal crosses were used to estimate maternal effects (Grami et al., 1977). Because, cytoplasmic genes are responsible for maternal effects. While the interaction between nuclear and cytoplasmic genes may help to explain non-maternal effects (Evans and Kermicle, 2001). Additionally, it has been stated that non-maternal effects are caused by non-additive gene action, whereas maternal effects are caused by additive genetic variance (Mukunga et al., 2010). Because of this, the current study also suggests that all of the quantitative traits under investigation are influenced by both additive and non-additive gene action, as well as reciprocal differences. Despite this, a number of scientists, including Fleming et al. (1960), Crane and Nyquist~~,~~ (1967), and Bhat and Dhawan (~~,~~1942) had previously reported the cytoplasmic effect in maize quantitative trait inheritance. Therefore, choosing the right pollen parent and seed parent is crucial for the development of heterotic hybrids. Which could be accomplished by taking into account elements like maternal effects and RECs and combining them while making a choice. GCA effects were partitioned into g_{mi} and g_{fi}, revealing which line is more effective as a seed or pollen parent. Griffing's method overestimated the breeding values of parental lines P5 and P7 when used as pollen parents for grain yield and underestimated them when used as seed parents (Fig. 3). They could thus be utilized as female parents in the development of hybrids. The parental lines P3, P4, and P6 could also be used as pollen parents because they had high g_{mi} values relative to g_i and g_{fi}. The line P5 could be used as a seed parent because it had high g_{fi} for the genes NKR, NKRC, CL, CG, TW, and GY.

In contrast, the g_{mi} for NKR, NKRC, CL, and GY in line P7 were high. Additionally, P5 had a significant positive maternal effect, and P7 had a significant negative maternal effect for yield attributes. This suggests that the estimation of GCA is impacted by the presence of maternal effects (Fan et al., 2014). In the meantime, the P6 was a better parent for pollen and seeds in terms of breeding value. These findings suggest that P5 could be used as a seed parent, P7 as a pollen parent, and P6 as both a seed and pollen parent in the development of hybrids. Griffing's method's SCA effects overestimated the effects of the crosses P1 x~~-~~P8 and P4 x P5, while underestimating the effects of their reciprocal crosses for GY (Fig. 4). The reciprocal cross P8 x P1 had the highest SCA effects among the test hybrids, according to the partitioning. It should be noted that these crosses showed extremely important RECs for GY. As can be seen in the example above (Yao et al., 2013 and Mahagoub, 2004) the RECs have a significant impact on the estimation of the SCA effects. A lower selection response results from the presence of maternal and reciprocal effects (Roach and Wulff, 1987). The majority of the crosses showed significant reciprocal differences, suggesting that cytoplasmic factors and their interactions with nuclear factors influence the traits that contribute to maize GY and yield.

Additionally, only a few crosses exhibit reciprocal and maternal effects, indicating that the breeding material used to produce these effects may vary, i.e., it may be highly genotype-specific (Fleming et al., 1960). —The maternal and RECs differ based on environmental factors in addition to genotypes (Kalsy and Sharma, 1972).~~)~~ In order to choose

Commented [Ma17]: Treat ask others above.

Formatted: Indent: First line: 1.27 cm

Formatted: Not Highlight

the better~~st~~ base material, it is necessary to precisely estimate the combining ability, maternal, and RECs. By partitioning the effects as mentioned here, this could be done. In contrast to Griffing's GCA effects, the adjusted GCA effects after partitioning had a strong correlation with mean performance. As a result, according to Worku et al. (2008), the sum of adjusted GCA effects may be a trustworthy predictor of mean performance. Despite this, heterosis and total GCA effects did not significantly correlate. Yu et al. (2020) came to the conclusion that heterosis and sum of GCA were either negatively correlated or not correlated in Yu's study comparing combining ability with heterosis pattern in a wide variety of materials. The current study's findings, in contrast, show a stronger correlation between the phenotypic performance of the hybrid and the sum of the parental GCAs. Therefore, with additional validation, the sum of parental GCA, in particular the sum of adjusted GCA values, could be used to forecast F1 mean performance. The adjusted SCA effects after partitioning showed an even stronger correlation with mean performance and heterosis than Griffing's SCA effects, which already showed a significant correlation with them.

Thus, compared to Griffing's SCA effects, adjusted SCA effects more accurately predicted heterosis. Non-additive gene action in the majority of the traits accounts for the strong correlation between SCA effects and heterosis over the sum of parental GCA. SCA effects can therefore be used to accurately predict mid-parent and better-parent heterosis, and they are more significant for heterosis than GCA effects (Devi and Singh, 2011 and Tian et al., 2017)~~[47, 48]~~. While SCA values were less accurate and less useful in predicting hybrid performance than the sum of GCA values (Technow, 2019 and Liu et al., 2021)~~[49, 50]~~.

5. Conclusion

Based on these results, it has been established that maternal and reciprocal effects have an impact on maize's quantitative traits, as well as how these effects affect combining ability estimates. However, more investigation is required to ascertain the extent to which these effects affect traits in maize and GCA, according to SCA. To create hybrids with the greatest potential, it would be advantageous to estimate these effects. Griffing's diallel's effects on ability, maternal, and RECs can be precisely estimated by partitioning their GCA and SCA effects. By taking into account the maternal and reciprocal effects on hybrid performance, suitable male and female parents can be found in order to increase heterosis.

Formatted: Indent: First line: 1.27 cm

Acknowledgement

The All India Coordinated maize improvement project at University of Agricultural Sciences, Dharwad provided all of the logistical support for the experiment's conduct, and the authors thank CIMMYT for sharing their genetic material. The authors would also like to express their gratitude to Drs. S. S. Patil and Dr. N. G. Hanumaratti for sharing their expertise on combining ability analysis. For field research and data collection, the technical staff at AICRP-Maize is also acknowledged.

Commented [Ma18]: Please cross-check well. Do you mean Dr. (Mrs.) or just Dr.

Supporting information

S1 Table. Mean performances of straight crosses

S2 Table. Mean performances of reciprocal crosses

S3 Table. Mid-parent heterosis of straight crosses

S4 Table. Better parent heterosis of straight crosses

Author Contributions:

Conceptualization, RMK; methodology, BAJ and RMK; resources, ZR and VSB; investigation, BAJ, SCT, GKN, and SRS; writing—original draft preparation, BAJ; writing—review and editing, RMK and NSP; All authors have read and agreed to the published version of the manuscript.

Formatted: Indent: First line: 1.27 cm

Funding

The authors also declare that the present study has not received any funding from any of the outside funding source and the study was carried out using in-house funds.

Formatted: Indent: First line: 1.27 cm

Declaration of conflict of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Formatted: Indent: First line: 1.27 cm

Reference

1. Acquaah,G. 2009. Principles of plant genetics and breeding. 2nd eds. *John-Wiley publications*, DOI: https://doi.org/10.1002/9781118313718.fma
2. Andorf C, Beavis WD, Hufford M, Smith S, Suza WP, Wang K, Woodhouse M, Yu J, Lubberstedt T. 2019. Technological advances in maize breeding:past,present and future. *Theoretical and Applied Genetics* 132:817-849 DOI: doi.org/10.1007/s00122-019-03306-3
3. Baker RJ. 1978. Issues in diallel analysis. *Crop Sciences* **18**(4):533-536.DOI: doi.org/10.2135/cropsci1978.0011183X001800040001x
4. Bertan I, Carvalho Fide, Oliveira ACD. 2007. Parental selection strategies in plant breeding programs. *Journal of Crop Science Biotechnology* **10**(4):211-222.
5. Bharat GB, Wadikar PB, Dhuppe MV, Thakur NR. 2020. Combining Ability Analysis for Yield and Yield Contributing Traits in Maize (*Zea mays* L.) Hybrids. *International Journal of Current Microbiology and Applied Sciences* 9(6): 1234-1241 DOI: doi.org/10.20546/ijcmas.2020.906.152
6. Bhat BK, Dhawan NL. 1971. The role of cytoplasm in the manifestation of quantitative characters of maize. *Genetica* 42:165-174 DOI: https://doi.org/10.1007/BF00154847
7. Cockerham CC. 1963. Estimation of genetic variances. In: Hanson WD, Robinson HF (eds) Statistical genetics and plant breeding. National Academy of Sciences, National Research Council, Publication 982, Washington, D.C. pp 53–93
8. Crane PL, Nyquist WE. 1967. Effects of different gene-cytoplasm systems on quantitative characters in reciprocal F_2 crosses of Maize (*Zea mays* L.). *Crop Science* 7(4):376-378 DOI: https://doi.org/10.3389/fpls.2023.1154905
9. Devi P, Singh NK. 2011. Heterosis, molecular diversity, combining ability and their interrelationships in short duration maize (*Zea mays* L.) across the environments. *Euphytica* 178:71-81 DOI: doi.org/10.1007/s10681-010-0271-3
10. Dosho BM, Ifie BE, Asante IK, Danquah EY, Zelekhe H. 2021. Combining ability of quality protein maize inbred lines under low and optimum soil nitrogen environments in Ethiopia. *African Journal of Plant Science* 15(8):237-249 DOI: doi.org/10.5897/AJPS2021.2145
11. Evans MM, Kermicle JL. 2002. Interaction between maternal effect and zygotic effect mutations during maize seed development. *Genetics* 159(1):303-315 DOI: https://doi.org/10.1093%2Fgenetics%2F159.1.303
12. Falconerv DS. 1996. Introduction to quantitative genetics. 4th eds. Longman Scientific and Technical, UK pp.1-448.
13. Fan X, Bi Y, Zhang Y, Jeffers D, Yin, Xing Fu, Kang M. 2018. Improving breeding efficiency of a hybrid maize breeding program using a three heterotic-group classification. *Agronomy Journal* 110(4):1209-1216 DOI: https://doi.org/10.2134/agronj2017.05.0290
14. Fan XM, Zhang YD, Yao WH, Bi YQ, Liu L, Chen HM, Kang MS. 2014. Reciprocal diallel crosses impact combining ability, variance estimation, and heterotic group classification. *Crop Science* 54(1): 89-97 DOI: doi.org/10.2135/cropsci2013.06.0393
15. Fasahat P, Rajabi A, Rad JM, Derera J. 2016. Principles and utilization of combining ability in plant breeding. *Biometrics & Biostatistics International Journal* **4**(1):1-24 DOI: 10.15406/bbij.2016.04.00085

16. Fleming AA, Kozelnicky GM, Browne EB. 1960. Cytoplasmic effects on agronomic characters in a Double-Cross maize hybrid. *Agronomy Journal* 52(2):112-115 DOI: https://doi.org/10.2134/agronj1960.00021962005200020017x
17. Ghareeb ZE, Fares WM. 2016. Modified model for assessment of maternal effects in first generation of faba bean. *Annals of Agricultural Sciences* 61(1):77-85 DOI: https://doi.org/10.1016/j.aoas.2016.01.004
18. Gonzalo M, Vyn TJ, Holland JB, McIntyre LM. 2007. Mapping reciprocal effects and interactions with plant density stress in *Zea mays* L. *Heredity* 99(1):14-30 DOI:https://doi.org/10.1038/sj.hdy.6800955
19. Grami B, Stefansson BR, Baker RJ. 1997. Genetics of protein and oil content in summer rape: heritability, number of effective factors, and correlations. *Canadian Journal of Plant Science* 57(3):937-943.
20. Griffing B. 1956a. Concept of general and specific combining ability in relation to diallel crossing systems. *Australian Journal of Biological Sciences* **9:**463-493 DOI: https://doi.org/10.1071/BI9560463
21. Griffing B. 1956b. A generalized treatment of the use of diallel crosses in quantitative inheritance. *Journal of Heredity* **10:**31-50 DOI: https://doi.org/10.1038/hdy.1956.2
22. Gupta HS, Hossain F, Muthuswamy V. 2015. Biofortification of maize: An Indian perspective. *Indian Journal of Genetics Plant. Breed*ing 75(1):1-22 DOI: doi.org/10.5958/0975- 6906.2015.00001.2
23. Jumbo MB, Carena MJ. 2008. Combining ability, maternal, and reciprocal effects of elite early-maturing maize population hybrids. *Euphytica*162:325-333 DOI: doi.org/10.1007/s10681-007-9618-9
24. Kalsy HS, Sharma D. 1972. Study of cytoplasmic effects in reciprocal crosses of divergent varieties of maize (*Zea mays* L.). *Euphytica* 21:527-533 DOI: https://doi.org/10.1007/BF00039351
25. Kayaga HN, Kagoda F, Ochwo-Ssemakula M, Alladassi BME, Godfrey A, Gibson P, Edema R. 2017. Inheritance of yield and yield-related traits in highland maize hybrids of Uganda. *Journal of Crop Science and Biotechnology*20: 255-262 DOI: http://dx.doi.org/10.1007/s12892-017-0110-0
26. Khan R, Dubey RB. 2015. Combining ability analysis for nutritional quality and yield in maize (*Zea mays* L.). *The Bioscan* 10(2):785-788.
27. Kumar V, Singh SK, Singh NP, Mahajan V. 2016. Combining ability studies for grain yield other agronomic traits in maize (*Zea mays* L.). *Electronic Journal of Plant Breeding* 7(3):544-554 DOI: http://dx.doi.org/10.5958/0975-928X.2016.00070.3
28. Liu Z. Jiang J, Ren A, Xiangyang Xu, Zhang He, Tingting Z, Xiuming J, Yaoguang S, Jingfu Li, Huanhuan Y. 2021. Heterosis and combining ability analysis of fruit yield, early maturity, and quality in tomato. *Agron*omy 11(4):807 DOI: https://doi.org/10.3390/agronomy11040807
29. Mahgoub GM. 2011. Partitioning of general and specific combining ability effects for estimating maternal and reciprocal effects. *The Journal of Agricultural Science* 3(2):213
30. Mahgoub GM. 2004. Modification of Griffing's methods 1 and 3 of diallel analysis for estimating general and specific combining ability effects for male and female parents. *Egyptian Journal of Plant Breeding* 8: 1-20
31. Mehta BK, Shashikumara P, Kumar A, Singh P, Priyadharshini P. 2021. Biofortified maize: a nutritious food for poor people of India.*Krishi Science* 2(1):17-20. www.krishiscience.in

32. Mukanga M, Derera J, Tongoona P. 2010. Gene action and reciprocal effects for ear rot resistance in crosses derived from five tropical maize populations. *Euphytica*174, 293-301 DOI: http://dx.doi.org/10.1007/s10681-010-0178-z
33. Onejeme FC, Okporie EO, Eze CE. 2020. Combining ability and heterosis in diallel analysis of maize (*Zea mays* L.) lines. *International Annals of Science* **9**(1):188-200 DOI: https://doi.org/10.21467/ias.9.1.188-200
34. Patil NL, Kachapur RM, Nair SK. 2021. Genetic evaluation for understanding combining ability effects and Heterotic grouping in Maize (*Zea mays* L.). *Maydica***66**(1):1-13 DOI: https://journals-crea.4science.it/index.php/maydica/article/view/2260/1344
35. Pollmer WG, Klein D, Dhillon BS. 1979. Differences in reciprocal crosses of maize inbred lines diverse for protein content. *Euphytica* 28(2):325-328 DOI: https://doi.org/10.1007/BF00056590
36. Roach DA, Wulff DA. 1987. Maternal effects in plants. *Annual Review of Ecology, Evolution, and Systematics* 18(1):209-235 DOI: https://doi.org/10.1146/annurev.es.18.110187.001233
37. Sadalla HA, Barznji MO, Kakarash SA. 2017. Full diallel crosses for estimation of genetic parameters in maize. *Iraqi Journal of Agricultural Sciences* 48 :30-40
38. Santos JF, Dirk LM, Downie AB, Sanches MFG, Vieira RD. 2017. Reciprocal effect of parental lines on the physiological potential and seed composition of corn hybrid seeds. *Seed Science Research* 27(3): 206-216.
39. Singh RK, Chaudhary BD. 1985. Biometrical methods in quantitative genetic analysis Kalyani publishers, New Delhi pp 1-318
40. Sprague GF, Tatum LA. 1942. General vs specific combining ability in single crosses of corn.*Agronomy Journal* 34: 923-932 DOI: doi.org/10.2134/agronj1942.00021962003400100008x
41. Suyadi S, Saptadi D, Sugiharto AN. 2021. Combining ability of Indonesian tropical maize in two different seasons. *AGRIVITA, Journal of Agricultural Science* 43(2):347-357 DOI: https://doi.org/10.17503/agrivita.v43i2.2915
42. Technow F. 2019. Use of F_2 bulks in training sets for genomic prediction of combining ability and hybrid performance. *G3: Genes Genomes Genetics* 9(5):1557-1569 DOI: https://doi.org/10.1534/g3.118.200994
43. Tian HY, Channa SA, Hu SW. 2017. Relationships between genetic distance, combining ability and heterosis in rapeseed (*Brassica napus* L.). *Euphytica*213: 1-11 DOI: http://dx.doi.org/10.1007/s10681-016-1788-x
44. Worku M, Banziger M, Friesen D, Erley GSA, Worst H, Vivek BS. 2008. Relative importance of general combining ability and specific combining ability among tropical maize (*Zea mays* L.) inbreds under contrasting nitrogen environments. *Maydica* 53:279-288 DOI: http://hdl.handle.net/10883/3086
45. Yao WH, Zhang YD, Kang MS, Chen H, Liu Li, Yu LJ, Fan X. 2013. Diallel analysis models: A comparison of certain genetic statistics. *Crop Science* 53(4):481-1490 DOI: https://doi.org/10.2135/cropsci2013.01.0027
46. Yaseen M. 2018. Diallel Analysis R https://cran.r-project.org/web/packages/DiallelAnalysisR/index.html.
47. Yates F. 1947. Analysis of data from all possible reciprocal crosses between a set of parental lines. *Heredity* 1(3):287-301 DOI: https://doi.org/10.1038/hdy.1947.19
48. Yerva SR, Sekhar TC, Allam CR, Krishnana V. 2016. Combining ability studies in maize (*Zea mays* L.) for yield and its attributing traits using Griffing's diallel approach. *Electronic Journal of Plant Breeding* **7**(4):1046-1055. https://ejplantbreeding.org/index.php/EJPB/article/view/1185

Formatted: Font: Not Bold

49. Yu K, Wang H, Liu X, Cheng Xu, Zhiwei Li, Xiaojie Xu, Jiacheng, Liu, ZhenhuaW, Yunbi Xu. 2020. Large-scale analysis of combining ability and heterosis for development of hybrid maize breeding strategies using diverse germplasm resources. *Frontiers in Plant Science* 11: 660 DOI: https://doi.org/10.3389/fpls.2020.00660

50. Zhang AZ, Lv H, Zhang ZX, Tao YS, Bing Y, Lian ZY. 2012. Conversion of the statistical combining ability into a genetic concept. *Journal of Integrative Agriculture* 11(1):43-52 DOI: https://doi.org/10.1016/S1671-2927(12)60781-0