



# Generation Mean Analysis using Six Parameters Genetic Model for Quantitative Traits in Quality Protein Maize (*Zea mays* L.)

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## ABSTRACT

**Background:** Discovery of maize mutants in the mid-1960s containing the opaque-2 gene which enhances levels of lysine and tryptophan in the endosperm protein opened a new era in breeding for improvement of quality in maize.

**Methods:** The present study aimed to perform a generation mean analysis of two quality protein maize (QPM) (*Zea mays* L.) crosses CML332 × CML145 and CML167 × CML330 during *zaid*, 2023 P.G research farm, MSSSoA, Paralakhemudi. To, determine the genetic effects along with nature of gene action.

**Result:** Dominance variance showed more importance than additive variance and the presence of duplicate form of non-allelic gene interaction was prevalent for all the characters studied except days to 50% tasseling in CML332 × CML145 and catalase in CML167 × CML330 which showed complementary gene action. Characters with duplicate gene interactions, grain yield per plant in CML167 × CML330 and number of kernels row<sup>-1</sup> in CML332 × CML145 showed strong dominance and dominance × dominance gene interaction. Selection could be rewarding for consecutive populations followed after bi-parental mating design to improve these traits.

**Key words:** Additive and dominance effect, Generation mean analysis, Non-allelic interactions, Quality protein maize.

## INTRODUCTION

Maize is one of the most important cereal crops globally valued for its high yield potential and diverse uses in food, feed and industrial products. Enhancing its grain yield and nutritional quality particularly in quality protein maize is a key objective in breeding programs. Since yield and quality traits are quantitatively inherited understanding their genetic architecture is crucial for effective improvement (Lahane *et al.*, 2015).

Generation mean analysis (GMA) is a powerful tool for dissecting gene action governing quantitative traits. By estimating additive, dominance and epistatic effects with helps breeders determine the most suitable selection strategies. The significance of epistasis in trait inheritance has been widely reported and its role in improving heterosis and inbreeding tolerance is well recognized. This study applies GMA to analyze the genetic basis of physiological, biochemical and agronomic traits in QPM providing insights for developing high-yielding, nutritionally superior maize hybrids (Murugesan *et al.*, 2024).

The genetic improvement of crops relies on understanding the nature of gene action for traits like yield and quality. Genetic variances, dominance levels and genetic effects are key to understanding heterosis (Ayyanna *et al.*, 2023).

As polygenic traits grain yield and its components depend on dominant, additive and epistatic gene action. The significance of epistasis for the inheritance of quantitative traits was reported by Attri *et al.* (2021). Therefore, the study helps to understand the nature of inheritance for various physiological, biochemical, grain yield and its attributing traits in maize (Patel *et al.*, 2024).

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## MATERIALS AND METHODS

### Plant genetic material

The experimental materials comprising four parents CML332, CML145, CML167, CML330, two F<sub>1</sub> hybrids CML332 × CML145 and CML167 × CML330 and the corresponding F<sub>2</sub> populations, BCP<sub>1</sub> and BCP<sub>2</sub> populations of the two crosses were evaluated using a compact family block design (CFBD) in two replications during the *zaid* (February to June, 2023) at the P.G. Research Farm, MSSSoA, Paralakhemudi, Gajapati, Odisha.

This investigation evaluated six populations (P<sub>1</sub>, P<sub>2</sub>, F<sub>1</sub>, F<sub>2</sub>, BCP<sub>1</sub> and BCP<sub>2</sub>) of two elite hybrids, CML332 (P<sub>1</sub>) ×

CML145 ( $P_2$ ) and CML167 ( $P_1$ )  $\times$  CML330 ( $P_2$ ), which exhibited superior performance in terms of grain yield plant<sup>-1</sup>. The parents,  $F_1$ s,  $F_2$ s and backcrosses were randomized separately in each replication. The  $F_2$  populations were space-planted in 25 rows with a total plant population of 250. The planting geometry was maintained at 60 cm  $\times$  20 cm.

Observations were recorded on days to 50 % tasseling and days to 50% silking, plant height (cm), ear height (cm), ear length (cm), ear girth (cm), number of kernels row<sup>-1</sup>, number of kernels cob<sup>-1</sup>, 100-grain weight (g), grain yield plant<sup>-1</sup> (g), canopy temperature (°C), SPAD meter, membrane stability index (%), protein content (%), oil content (%), catalase activity (Umg<sup>-1</sup>) and peroxidase activity (Umg<sup>-1</sup>). Leaf firing, tassel blast, root lodging were also recorded based on scoring (Raj *et al.*, 2020 and Teja *et al.*, 2024). To evaluate predominant gene effects in maize, analysis were carried out by fitting the data into a six-parameter model.

### Statistical analysis

#### Generation mean analysis

The generation mean analysis six parameter model was applied to estimate the genetic parameters to determine epistatic interaction. Mean data were first tested to determine non-allelic interaction through individual scaling tests A, B, C and D proposed by Mather, (1949).

$$\begin{aligned}\text{Scale A} &= 2BCP_1 - P_1 - F_1 \\ \text{Scale B} &= 2BCP_2 - P_2 - F_1 \\ \text{Scale C} &= 4F_2 - 2F_1 - P_1 - P_2 \\ \text{Scale D} &= 2F_2 - BCP_1 - BCP_2\end{aligned}$$

Where,

$P_1, P_2, F_1, F_2, BCP_1$  and  $BCP_2$  = Means from distinct generations. The variances of the values A, B, C and D were determined using the corresponding variances of different populations, as given below:

$$\begin{aligned}VA &= 4V(BCP_1) + V(P_1) + V(F_1) \\ VB &= 4V(BCP_2) + V(P_2) + V(F_1) \\ VC &= 16V(F_2) + 4V(F_1) + V(P_1) + V(P_2) \\ VD &= 4V(F_2) + V(BCP_1) + V(BCP_2)\end{aligned}$$

Where,

VA, VB, VC and VD are the variances of respective scales A, B, C and D;  $VP_1, VP_2, VF_1, VF_2, VBCP_1$  and  $VBCP_2$  are the Variances of  $P_1, P_2, F_1, F_2, BCP_1$  and  $BCP_2$  populations respectively. Standard error for A, B, C and D scales were calculated by estimating the square root of the respective variances.

If any scaling tests were found to be significant, the genetic effects were estimated by fitting the data into a six-parameter model for generation mean analysis as suggested by Hayman, (1958) to estimate the genetic parameters *viz.*, mean (m), additive gene effects (d), dominance gene effects (h) and three types of non-allelic gene interactions *viz.*, additive  $\times$  additive (i), additive  $\times$  dominance (j) and dominance  $\times$  dominance (l).

Following the analysis of the estimation were calculated by using the following formula:

- (1)  $m$  = Mean =  $F_2$
- (2)  $d$  = Additive effect =  $BCP_1 - BCP_2$
- (3)  $h$  = Dominance effect =  $F_1 - 4F_2 - (1/2)P_1 - (1/2)P_2 + 2BCP_1 + 2BCP_2$
- (4)  $i$  = Additive  $\times$  Additive effect =  $2BCP_1 + 2BCP_2 - 4F_2$
- (5)  $j$  = Additive  $\times$  Dominance effect =  $BCP_1 - (1/2)P_1 - BCP_2 + (1/2)P_2$
- (6)  $l$  = Dominance  $\times$  Dominance effect =  $P_1 + P_2 + 2F_1 + 4F_2 - 4BCP_1 - 4BCP_2$
- (7)  $\sqrt{H/D} VI = V(P_1) + V(P_2) + 4V(F_1) + 16V(F_2) + 16V(BCP_1) + 16V(BCP_2)$

Where,

$V(P_1), V(P_2), V(F_1), V(F_2), V(BCP_1)$  and  $V(BCP_2)$  = Variances of  $P_1, P_2, F_1, F_2, BCP_1$  and  $BCP_2$  populations respectively.

The estimation of (h) and (l) along with their sign were utilized to understand the nature of epistasis Mather and Jinks, (1971) *viz.* if (h) and (l) were of same sign, the gene action was referred to as complementary type and where (h) and (l) had opposite sign the same was referred to as duplicate type.

The degree of dominance, expressed as the square root of the ratio of dominance variance (H) to additive variance (D), was determined according to Robinson *et al.* (1949).

$$\text{Degree of dominance} = \sqrt{H/D}$$

## RESULTS AND DISCUSSION

The generation mean analysis provides insight into the genetic control of morphological and biochemical traits in all the crosses. This method allows the partitioning of genetic effects into additive, dominance and epistatic components which are crucial for understanding the inheritance of traits. Generation mean analysis for characters reveal significant variations ( $P \leq 0.05$ ) among the populations. Analysis of variance depicts the variation among the populations. Sharma *et al.* (2023); Vidadala *et al.* (2024) observed significant dominance effects in maize.

#### Means analysis

Generation mean analysis relies on different populations ( $P_1, P_2, F_1, F_2, BCP_1, BCP_2$ ) in a cross using the mean values of these populations to assess gene action for a specific trait. The results showed in CML332  $\times$  CML145 that  $F_1$  means were higher than either of the parents only for traits plant height, ear height (Table 1 and 2). The results indicated that in cross CML167  $\times$  CML330  $F_1$  means were higher than both parents only for traits plant height, ear height, ear length, number of kernels row<sup>-1</sup>, number of kernel rows cob<sup>-1</sup>, grain yield plant<sup>-1</sup>, SPAD meter, canopy temperature, membrane stability index and catalase (Table 3 and 4). The above two crosses showing different responses in terms of considered characters in the present investigation. Moreover, it is noted that (CML167  $\times$  CML330) shows superior heterotic performance respect to grain yield plant<sup>-1</sup> compared to (CML332  $\times$  CML145). The  $F_1$  population performing superiority over other populations indicates the

**Table 1:** Generation mean for yield attributes in six generation of CML332 × CML145.

| Character                                      | Days to 50% tasseling (days) | Days to 50% silking (days) | Anthesis-silking interval (days) | Plant height (cm) | Ear height (cm) | Ear length (cm) | Number of kernels row <sup>-1</sup> | Number of rows cob <sup>-1</sup> | Ear girth (cm) | Grain yield plant <sup>-1</sup> (g) | 100 grain weight (g) |
|------------------------------------------------|------------------------------|----------------------------|----------------------------------|-------------------|-----------------|-----------------|-------------------------------------|----------------------------------|----------------|-------------------------------------|----------------------|
| CML332 (P <sub>1</sub> )                       | 65                           | 66                         | 2                                | 163               | 52              | 22              | 28                                  | 11                               | 10             | 297                                 | 21                   |
| CML145 (P <sub>2</sub> )                       | 67                           | 68                         | 1                                | 148               | 52              | 19              | 32                                  | 16                               | 11             | 525                                 | 30                   |
| CML332 × CML145 (F <sub>1</sub> )              | 67                           | 68                         | 2                                | 186               | 60              | 20              | 28                                  | 15                               | 10             | 427                                 | 25                   |
| CML332 × CML145 (F <sub>2</sub> )              | 58                           | 60                         | 2                                | 175               | 81              | 16              | 21                                  | 13                               | 9              | 275                                 | 21                   |
| [CML332 × CML145 (CML332)] (BCP <sub>1</sub> ) | 59                           | 62                         | 3                                | 204               | 55              | 19              | 38                                  | 14                               | 8              | 524                                 | 30                   |
| [CML332 × CML145 (CML145)] (BCP <sub>2</sub> ) | 60                           | 62                         | 1                                | 158               | 93              | 20              | 33                                  | 17                               | 11             | 562                                 | 23                   |

**Table 2:** Generation mean for quality attributes in six generation of CML332 × CML145.

| Character                                      | SPAD meter | Canopy temperature (°C) | Protein content (%) | Oil content (%) | Membrane stability index (%) | Catalase (U mL <sup>-1</sup> ) | Peroxidase (U mL <sup>-1</sup> ) | Leaf firing | Tassel blast | Root lodging (%) |
|------------------------------------------------|------------|-------------------------|---------------------|-----------------|------------------------------|--------------------------------|----------------------------------|-------------|--------------|------------------|
| CML138 (P <sub>1</sub> )                       | 38         | 31                      | 7                   | 2               | 37                           | 0                              | 1                                | 0           | 0            | 0                |
| CML145 (P <sub>2</sub> )                       | 27         | 31                      | 9                   | 5               | 47                           | 0                              | 1                                | 0           | 0            | 0                |
| CML138 × CML145 (F <sub>1</sub> )              | 29         | 31                      | 9                   | 3               | 47                           | 0                              | 1                                | 0           | 0            | 0                |
| CML138 × CML145 (F <sub>2</sub> )              | 35         | 31                      | 8                   | 3               | 41                           | 0                              | 1                                | 0           | 0            | 0                |
| [CML138 × CML145 (CML138)] (BCP <sub>1</sub> ) | 40         | 31                      | 7                   | 4               | 45                           | 0                              | 1                                | 1           | 1            | 0                |
| [CML138 × CML145 (CML145)] (BCP <sub>2</sub> ) | 38         | 31                      | 9                   | 2               | 56                           | 0                              | 1                                | 1           | 1            | 0                |

**Table 3:** Generation mean for yield attributes in six generations of CML167 × CML330.

| Character                                   | Days to 50% tasseling (days) | Days to 50% silking (days) | Anthesis-silking interval (days) | Plant height (cm) | Ear height (cm) | Ear length (cm) | Number of kernels row <sup>-1</sup> | Number of kernel rows cob <sup>-1</sup> | Ear girth (cm) | Grain yield plant <sup>-1</sup> (g) | 100 grain weight (g) |
|---------------------------------------------|------------------------------|----------------------------|----------------------------------|-------------------|-----------------|-----------------|-------------------------------------|-----------------------------------------|----------------|-------------------------------------|----------------------|
| CML334 (P <sub>1</sub> )                    | 65                           | 72                         | 7                                | 166               | 61              | 8               | 13                                  | 10                                      | 9              | 142                                 | 21                   |
| CML330 (P <sub>2</sub> )                    | 66                           | 70                         | 5                                | 173               | 59              | 15              | 21                                  | 14                                      | 10             | 309                                 | 18                   |
| CML334 × CML330 (F <sub>1</sub> )           | 65                           | 68                         | 3                                | 202               | 87              | 16              | 31                                  | 15                                      | 7              | 463                                 | 19                   |
| CML334 × CML330 (F <sub>2</sub> )           | 66                           | 69                         | 2                                | 189               | 84              | 16              | 13                                  | 12                                      | 8              | 169                                 | 18                   |
| [CML334 × CML330 (CML334)] BCP <sub>1</sub> | 62                           | 64                         | 2                                | 205               | 88              | 19              | 39                                  | 14                                      | 7              | 543                                 | 26                   |
| [CML334 × CML330 (CML330)] BCP <sub>2</sub> | 62                           | 63                         | 1                                | 207               | 94              | 17              | 38                                  | 14                                      | 8              | 525                                 | 27                   |

**Table 4:** Generation mean for quality attributes in six generation of CML167 × CML330.

| Character                                   | SPAD meter | Canopy temperature (°C) | Protein content (%) | Oil content (%) | Membrane stability index (%) | Catalase (U mL <sup>-1</sup> ) | Peroxidase (U mL <sup>-1</sup> ) | Leaf firing | Tassel blast | Root lodging (%) |
|---------------------------------------------|------------|-------------------------|---------------------|-----------------|------------------------------|--------------------------------|----------------------------------|-------------|--------------|------------------|
| CML334 (P <sub>1</sub> )                    | 34         | 31                      | 7                   | 1               | 31                           | 0                              | 1                                | 1           | 1            | 1                |
| CML330 (P <sub>2</sub> )                    | 35         | 31                      | 9                   | 4               | 53                           | 0                              | 1                                | 0           | 0            | 0                |
| CML334 × CML330 (F <sub>1</sub> )           | 39         | 32                      | 8                   | 2               | 54                           | 0                              | 1                                | 1           | 1            | 1                |
| CML334 × CML330 (F <sub>2</sub> )           | 38         | 31                      | 8                   | 3               | 45                           | 0                              | 1                                | 0           | 0            | 0                |
| [CML334 × CML330 (CML334)] BCP <sub>1</sub> | 32         | 31                      | 8                   | 3               | 41                           | 0                              | 1                                | 1           | 1            | 1                |
| [CML334 × CML330 (CML330)] BCP <sub>2</sub> | 32         | 30                      | 9                   | 2               | 52                           | 0                              | 1                                | 1           | 1            | 1                |

**Table 5:** Estimates of different scaling tests and genetic effects for quantitative and qualitative parameters in two QPM crosses (cont.).

| Character                               | Cross           | Scaling test |         |          |          | Gene effects |          |            |          |        |           |               | Type of epistasis | $\sqrt{H/D}$ |
|-----------------------------------------|-----------------|--------------|---------|----------|----------|--------------|----------|------------|----------|--------|-----------|---------------|-------------------|--------------|
|                                         |                 | A            | B       | C        | D        | m            | d        | h          | i        | j      | l         |               |                   |              |
| Days to 50% tasseling (days)            | CML332 × CML145 | -13**        | -13.4** | -33.36** | -3.4**   | 57.9**       | -1       | 7.9**      | 6.9**    | 0.2    | 19.4**    | Complementary | -2.8              |              |
|                                         | CML167 × CML330 | -6.6**       | -7.2**  | 4.168    | 8.9**    | 66.1**       | 0.2      | -18.6**    | -17.9**  | 0.3    | 31.7**    | Duplicate     | -9.7              |              |
| Days to 50% silking (days)              | CML332 × CML145 | -10.6**      | -13.6** | -31.5**  | -3.6**   | 59.9**       | 0.4      | 8.4**      | 7.3**    | 1.5    | 16.8**    | Complementary | 4.6               |              |
|                                         | CML167 × CML330 | -8.6**       | -9.2**  | 3.4      | 10.6**   | 68.5**       | 0.8      | -21.7**    | -21.2**  | 0.3    | 39.04**   | Duplicate     | -5.2              |              |
| Anthesis-silking interval (days)        | CML332 × CML145 | 2.4**        | -0.2    | 1.8**    | -0.2     | 2**          | 1.4**    | 0.5        | 0.4      | 1.3**  | -2.6      | Duplicate     | 0.6               |              |
|                                         | CML167 × CML330 | -2**         | -2**    | -0.7     | 1.6**    | 2.3**        | 0.6      | -3.08**    | -3.2**   | 0      | 7.2**     | Duplicate     | -2.3              |              |
| Plant height (cm)                       | CML332 × CML145 | 58.9**       | -18.2   | 16.7     | -11.9    | 174.8**      | 46       | 54.7       | 23.9     | 38.5   | -64.6     | Duplicate     | 1.1               |              |
|                                         | CML167 × CML330 | 41.8**       | 40.4**  | 13.4     | -34.3**  | 188.9**      | -2.6     | 101.2**    | 68.7**   | 0.7    | -150.9**  | Duplicate     | -6.2              |              |
| Ear height                              | CML332 × CML145 | -1.3         | 74.2**  | 98.9**   | 13.04    | 80.9**       | -38      | -18.03     | -26.08   | -37.7  | -46.8     | Complementary | 0.7               |              |
|                                         | CML167 × CML330 | 27.6*        | 42.8**  | 43.6**   | -13.4    | 84.2**       | -6.2     | 53.4**     | 26.8     | -7.6   | -97.2**   | Duplicate     | -2.9              |              |
| Ear length (cm)                         | CML332 × CML145 | -3*          | 0.2     | -17.9**  | -7.58*   | 15.6**       | -0.4     | 14.1**     | 15.1**   | -1.6   | -12.3**   | Duplicate     | -6.0              |              |
|                                         | CML167 × CML330 | 12.9**       | 3.1     | 9.8**    | -3.09*   | 16.3**       | 1.4      | 10.3**     | 6.1*     | 4.9**  | -22.1**   | Duplicate     | 2.7               |              |
| Number of kernels row <sup>-1</sup>     | CML332 × CML145 | 19.6**       | 7       | -32.6**  | -29.6**  | 20.6**       | 4.2      | 57.1**     | 59.2**   | 6.3*   | -85.8**   | Duplicate     | 3.7               |              |
|                                         | CML167 × CML330 | 33.4**       | 22.4**  | -44.2**  | -50.04** | 13.1**       | 1.2      | 114.3**    | 100.1**  | 5.5*   | -155.8**  | Duplicate     | 9.8               |              |
| Number of kernel rows cob <sup>-1</sup> | CML332 × CML145 | 2            | 2.6     | -4.2     | -4.4**   | 13.1**       | -2.8**   | 11.1**     | 8.8**    | -0.3   | -13.4**   | Duplicate     | -2.0              |              |
|                                         | CML167 × CML330 | 3.2          | -1      | -4.8     | -3.5**   | 12.2**       | -        | 9.3**      | 7.02**   | 2.1    | -9.2      | Duplicate     | -                 |              |
| Ear girth (cm)                          | CML332 × CML145 | -3.8**       | 1.4     | -6.01**  | -1.8*    | 8.6**        | -3.2**   | 3.6*       | 3.61*    | -2.6** | -1.2      | Duplicate     | -1.1              |              |
|                                         | CML167 × CML330 | -2.1**       | 0       | 1.02     | 1.5      | 8.4**        | -1.4     | -5.5**     | -3.1     | -1.05  | 5.2       | Duplicate     | 2.0               |              |
| Grain yield plant <sup>-1</sup> (g)     | CML332 × CML145 | 324.8**      | 170.4   | -576.2** | -535.7** | 275.1**      | -37.2    | 1087.8**   | 1071.4** | 77.2   | -1566.6** | Duplicate     | -5.4              |              |
|                                         | CML167 × CML330 | 480.6**      | 277.2** | -702.5** | -730.1** | 168.7**      | 18       | 1698.004** | 1460.3** | 101.7  | -2218.1** | Duplicate     | 9.7               |              |
| 100 grain weight (g)                    | CML332 × CML145 | 15.2**       | -9.6    | -17.3**  | -11.4**  | 20.8**       | 7.6**    | 22.1**     | 22.9**   | 12.4** | -28.5*    | Duplicate     | 1.7               |              |
|                                         | CML167 × CML330 | 12**         | 17.2**  | -3.07    | -16.1**  | 18.3**       | -1.6     | 31.6**     | 32.2**   | -2.6   | -61.4**   | Duplicate     | -4.4              |              |
| SPAD meter                              | CML332 × CML145 | 12.9         | 20.3    | 16.8     | -8.1     | 34.7**       | 1.72     | 12.2       | 16.3     | -3.6   | -49.6     | Duplicate     | 2.7               |              |
|                                         | CML167 × CML330 | -8.1         | -10.04  | 6.9      | 12.5*    | 38.3**       | 0.12     | -21.01     | -25.1*   | 0.9    | 43.3      | Duplicate     | -13.2             |              |
| Canopy temperature (°C)                 | CML332 × CML145 | 0.4          | -0.2    | -0.4     | -0.3     | 31.04**      | 0.4      | 1.1        | 0.6      | 0.3    | -0.8      | Duplicate     | 1.7               |              |
|                                         | CML167 × CML330 | -1           | -3.2*   | -0.2     | 1.9*     | 31.2**       | 1        | -3.03      | -3.9*    | 1.1    | 8.1*      | Duplicate     | -1.7              |              |
| Protein content (%)                     | CML332 × CML145 | -1.1         | 0.3     | -1.1     | -0.1     | 8.2**        | -1.9**   | 1.3        | 0.3      | -0.7   | 0.4       | Complementary | -0.8              |              |
|                                         | CML167 × CML330 | -0.3         | 1.03**  | -0.5     | -0.6**   | 8.1**        | -1.572** | 1.1**      | 1.2**    | -0.6** | -1.9*     | Duplicate     | -0.9              |              |
| Oil content (%)                         | CML332 × CML145 | 3.2*         | -2.4*   | 0.7      | -0.01    | 3.09**       | 1.4      | -0.5       | 0.03     | 2.8**  | -0.8      | Complementary | -0.6              |              |
|                                         | CML167 × CML330 | 2.7*         | -3.1**  | -0.08    | 0.1      | 2.5**        | 1**      | -1.3       | -0.3     | 2.9**  | 0.7       | Duplicate     | -0.9              |              |
| Membrane stability index (%)            | CML332 × CML145 | 5.4          | 18.7    | -14.7*   | -19.4**  | 40.6**       | -11.7    | 44.02**    | 38.8**   | -6.6   | -63.08*   | Duplicate     | -1.9              |              |
|                                         | CML167 × CML330 | -2.7         | -1.8    | -9.6*    | -2.51    | 45.4**       | -11.2**  | 16.5**     | 5.03     | -0.4   | -0.4      | Duplicate     | -1.2              |              |
| Catalase (U mL <sup>-1</sup> )          | CML332 × CML145 | 0.03         | -0.03   | -0.01    | -0.008   | 0.05**       | 0.02     | 0.05       | 0.01     | 0.03   | -0.01     | Duplicate     | 1.5               |              |
|                                         | CML167 × CML330 | 0.05         | -0.08   | 0.02     | 0.02     | 0.1**        | 0.07     | 0.03       | -0.05    | 0.06   | 0.09      | Complementary | 0.6               |              |

Table 5: Continue....

Table 5: Continue....

|                                                                                                                      |                 |       |       |      |        |       |      |       |        |       |        |               |      |
|----------------------------------------------------------------------------------------------------------------------|-----------------|-------|-------|------|--------|-------|------|-------|--------|-------|--------|---------------|------|
| Peroxidase (U mL <sup>-1</sup> )                                                                                     | CML332 × CML145 | 0.4   | -0.2  | 0.3  | 0.05   | 0.8** | 0.1  | -0.07 | -0.1   | 0.3   | -0.1   | Complementary | -0.5 |
|                                                                                                                      | CML167 × CML330 | 0.04  | 0.1   | -0.7 | -0.4** | 1.1** | -    | 0.7   | 0.9**  | -0.06 | -1.1   | Duplicate     | -    |
| Leaf firing                                                                                                          | CML332 × CML145 | 1     | 1     | 0.09 | -0.9** | 0.1** | -    | 1.7*  | 1.9**  | -     | -3.9** | Duplicate     | -    |
|                                                                                                                      | CML167 × CML330 | -1**  | -0.6* | -0.8 | 0.3**  | 0.1** | -    | -0.3  | -0.7** | -0.2  | 2.3**  | Duplicate     | -    |
| Tassel blast                                                                                                         | CML332 × CML145 | 0.8   | 0.8   | -0.1 | -0.8*  | 0.1** | -    | 1.7*  | 1.7*   | -     | -3.3*  | Duplicate     | -    |
|                                                                                                                      | CML167 × CML330 | -1**  | -0.6* | -0.8 | 0.3**  | 0.1*  | -    | -0.3  | -0.7** | -0.2  | 2.3**  | Duplicate     | -    |
| Root lodging (%)                                                                                                     | CML332 × CML145 | -     | 0.2   | -0.5 | -0.3   | 0.1** | -0.2 | 1.08  | 0.7    | -0.1  | -0.9   | Duplicate     | -2.3 |
|                                                                                                                      | CML167 × CML330 | -0.8* | -0.6* | -0.5 | 0.4**  | 0.2** | -    | -0.3  | -0.8** | -0.1  | 2.2**  | Duplicate     | -    |
| Mean (m); additive (d); dominance (h); additive × additive (i); additive × dominance (j); dominance × dominance (l). |                 |       |       |      |        |       |      |       |        |       |        |               |      |

\*Significant at p = 0.05% level; \*\*Significant at p = 0.01% level.

predominance of dominance and non-additive gene action in QPM Elmyhun *et al.* (2024); Godasara *et al.* (2025).

#### Assessment of genetic components for biochemical, grain yield and its attributing traits

The scaling test is used to detect epistasis which is crucial for estimating genetic parameters. Epistasis can result in over-dominance or under-dominance. The scaling test of the generation mean for various traits in the crosses revealed the presence of non-allelic interactions. It showed that the simple additive-dominance model was inadequate for traits like SPAD meter, canopy temperature, protein, catalase, peroxidase and root lodging in CML332 × CML145 and catalase in CML167 × CML330 indicating epistasis.

In number of kernels row<sup>-1</sup> and number of kernel rows cob<sup>-1</sup> significant magnitude of (h) and epistatic effects (i, j and l) indicate the role of dominance and non-allelic gene action in their inheritance. Duplicate epistasis was noted for both traits in CML332 × CML145 and CML167 × CML330 (Table 5). These findings align with Attri *et al.* (2021); Sharma *et al.* (2022); Shankar *et al.* (2022); Mistry *et al.* (2025) and Nagarajan *et al.* (2022) previously reported dominance and epistatic effects for this trait in maize.

In grain yield plant<sup>-1</sup> significant magnitude of (h) as well as interaction effects (i and l) in both the crosses indicates the prevalence of dominance and non-allelic gene interaction in character inheritance. Duplicate type of epistasis was observed in both crosses (Table 5). In maize, Sharma *et al.* (2023) previously observed that non additive gene effects functioned for this trait. Jayalakshmi and reddy *et al.* (2024) previously observed that non additive gene effects functioned for the traits in groundnut.

Opposite signs of gene effects (h) and (l) indicate duplicate epistasis for CML332 × CML145 in catalase and CML167 × CML330 in peroxidase. While complementary epistasis was noted for CML167 × CML330 in catalase and CML332 × CML145 in peroxidase. Teja *et al.* (2024) also reported non-additive gene effects for these traits in maize stress tolerant.

Duplicate type of epistasis interaction was observed for protein and oil content in CML167 × CML330 and complementary type of epistasis was noted in cross CML332 × CML145 for protein and oil content. Sharma *et al.* (2023) previously observed in maize non-additive gene effects for both the traits in maize.

A duplicate type of epistasis interaction was observed for leaf firing, tassel blast and root lodging in both the crosses CML332 × CML145 and CML167 × CML330 indicating that the gene interaction involves the masking of one gene's effect by another gene at different loci (Table 5). A duplicate type of epistasis is observed for SPAD meter, canopy temperature and membrane stability index in both the crosses (Table 5). These results were in accordance with Teja *et al.* (2024) and Kumar *et al.* (2023) in quality protein maize and noticed the function of non additive gene effects for the trait.

The degree of dominance among the two crosses showed considerable variation. For the cross CML332 × CML145



it ranged from as low as -6.0 for the trait ear length to as high as 4.6 for days to 50% silking. Similarly, for the cross CML167 × CML330 the degree of dominance ranged from -13.2 for SPAD meter to 9.7 for number of kernels per row. Particularly for number of kernels per row the degree of dominance reached 9.7 in the cross CML167 × CML330 indicating significant non-additive genetic effects as previously observed (Murugesan *et al.*, 2024).

For most of the traits: ASI, plant height, number of kernels row<sup>-1</sup>, number of kernal rows cob<sup>-1</sup>, ear girth, ear length, grain yield plant<sup>-1</sup>, 100 grain weight, SPAD meter, leaf firing, tassel blast, canopy temperature, membrane stability index and root lodging the inheritance was mainly controlled by duplicate gene action in both the crosses suggesting that significant genetic gain can be noted under selection using existing variability along with better resilience to varied environmental conditions as observed previously in rice by Kumar *et al.* (2023).

Traits that function with complementary gene action in either of the crosses for traits: catalase activity, days to 50% tasseling, days to 50% silking, ear height, protein content, oil content and peroxidase activity, the focus may be emphasizing to enhance genetic gain by assessing genetic worth of the selected plant for better improvement of population performance and selection intensity than under duplicate gene interaction as previously observed by Patil *et al.* (2020) and Peer *et al.* (2022).

## CONCLUSION

The greater prevalence of dominance gene effect and dominance × dominance interaction effect might provide insight on the exploitation of heterosis. Some additive × additive effects were observed in both the crosses suggesting potential to gain from selection. Dominance and dominance × dominance effect were found to have considerable role in both the crosses evaluated under study indicating the presence of duplicate gene action for traits: ASI, plant height, number of kernels row<sup>-1</sup>, number of kernal rows cob<sup>-1</sup>, ear girth, ear length, grain yield plant<sup>-1</sup>, 100 grain weight, SPAD meter, leaf firing, tassel blast, canopy temperature, membrane stability index and root lodging. Therefore biparental mating could be promising approach to handle the segregating populations and break the undesirable linkage.

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## Disclaimer

The authors are responsible for the accuracy and completeness of the information provided.

## Conflict of interest

The authors declare that there is no conflict of interest regarding the publication of this paper.

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