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Research Article

Generation mean analysis in quality protein maize (*Zea mays* L.) for yield and quality attributes

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Abstract
Maize (*Zea mays* L.), the world's most significant cereal crop, provides a pivotal roles for the supply of food for humans and forage for livestock. The present study aimed to perform a Generation mean analysis of two quality protein maize (QPM) (*Zea mays* L.) crosses [(CML149 x CML330) and (CML143 x CML193)] in order to determine the genetic effects along with the nature of gene action controlling morphological and biochemical traits underlying inheritance. All four components of scaling testing revealed significant differences with the parameter model, indicating the importance of the additive, dominance and epistatic modes of gene action for the inheritance of physiological, biochemical, grain yield and its attributing traits. 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% silking in CML149 × CML330 ([h] = 2.064, [l] = 1.536) and membrane stability index in CML143 × CML193 ([h] = 4.055, [l] = 17.362) which showed complementary gene action. Characters with duplicate genes, grain yield per plant in CML149 × CML330 ([h] = 1545.776, [l] = -2126.616) and plant height in CML149 × CML330 ([h] = 113.336, [l] = -104.376) showed strong dominance and dominance x dominance gene action. The significant role of dominance variance and duplicate epistasis was noted in the inheritance of the aforementioned characters. Selection could be rewarding for consecutive populations, followed by a bi-parental mating design to improve these traits.

Keywords: Additive and dominance effect, Generation mean analysis, Non-allelic interactions, Quality protein maize

INTRODUCTION

Maize (*Zea mays* L.), the world's most significant cereal crop, provides a pivotal roles for the supply of food for humans and forage for livestock, earning it the title of the "Queen of Cereals". Cultivated on 197.20 million hectares globally, it yields 1,148.48 million tonnes. In India, maize covers 9.03 million hectares, producing 27.7 million tonnes with an average productivity of 3,070 kg per hectare FAOSTAT (2022). 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 Vidadala *et al.* (2024). Quality Protein Maize (QPM) is a genetically enhanced variety to overcome the nutritional limitations of traditional maize. Enriched with essential amino acids like lysine and tryptophan, QPM improves protein synthesis and overall health, making it a crucial crop for enhancing dietary quality and combating protein malnutrition. Its high biological value and adaptability make QPM a promising solution for improving food security and meeting nutritional needs, especially in regions where maize is a staple crop Vidadala *et al.* (2024).

The genetic improvement of any crop species depends upon the nature of gene action for various traits, including yield and quality attributing traits, which helps to determine an appropriate breeding strategy. Understanding genetic variances, levels of dominance, and the significance of genetic effects has led to a better knowledge on the gene action contributing to heterosis (Ayyanna *et al.,* 2023). Grain yield is the most significant characteristic in maize and starch content in grain has become more attractive because of its value as food/feed consumption and biofuel production (Yadav *et al.,* 2018). Grain yield and its components are quantitative in nature; therefore, they are polygenic in inheritance. The phenotypic expression of these characters mostly depends upon the type of gene governing them, i.e., dominant or, additive or epistasis. However, digenic gene actions can be ascertained using Generation mean analysis and scaling test that precisely find epistasis, whether complementary or duplicates. As a result, Generation mean analysis is an effective tool for estimating the key genetic factors involved in the development of quantitative traits like yield and quality components. The significance of epistasis for the inheritance of quantitative traits is reported by Attri *et al.* (2021). Therefore, the present study was designed to understand the nature of inheritance for various physiological, biochemical, grain yield and its attributing traits in maize in the election of appropriate breeding procedures for hybrid maize development.

MATERIALS AND METHODS

Plant genetic material

The present investigation was conducted at the P.G. Research Farm, M.S. Swaminathan School of Agriculture, CUTM, Paralakhemudi, Gajapati, Odisha. The soil of the experimental site was red sandy loam in texture, non-saline and neutral in pH 6.5. Nine parents were selected based on morphological characters in the pedigree. Six female lines (three heat tolerant lines CML 149, CML 334 and CML 143 and three heat susceptible lines CML 138, CML 332 and CML 167) were crossed to three male resistant testers (CML 145, CML 193, and CML 330) in a line × tester mating design during *summer* (Mid-February to Mid-June, 2022) to produce 18 F_1 hybrids. These 18 F_1 hybrids and parental lines were evaluated using randomized block design (RBD) for various agronomic traits during the *kharif* season (Mid-July to Mid-October, 2022).The crossing program was conducted during the *kharif* season of 2022 to develop segregating populations, including backcross (BCP_1 and BCP_2) and second filial (F_2) populations. The BCP_1 population was produced in each cross combination by crossing F_1 individuals with the respective parent P_1. Likewise the BCP_2 population progeny was obtained by crossing F_1 individuals with parent P_2. F_2 populations for each cross were developed by selfing of respective F_{1s}.

Among the 18 F_1 hybrids, CML149 × CML330 and CML143 × CML193 were identified as superior crosses based on early flowering, yield-attributing traits showing significant per se performance and standard heterosis for grain yield per plant and other traits Teja *et al.* (2024). These hybrids also differed in performance for important agronomic traits: early flowering, yield-attributing characters and antioxidant status. These two F_1 hybrids were forwarded for Generation mean analysis to study the nature of gene action.

For developing the BCP_1 and BCP_2 populations, both P_1 and P_2 plants were used as pollen sources, with F_1 plants serving as the female parent. Pollen collected from P_1 plants was used to pollinate F_1 plants to develop the BCP_1 population progeny, while pollen from P_2 plants was used to pollinate F_1 plants to develop the BCP_2 population. The bagging of male and female line plants was performed daily. At the full tasseling stage, pollen from the male parents (P_1 and P_2) was collected in tasselling bags and dusted into the female lines (F_1) by gentle tapping in the morning hours between 08:00 A.M. to 11:30 A.M. Soon after pollination. The crossed silks were covered with tasseling bags to avoid foreign pollen contamination. The plants were appropriately labeled, harvested at maturity, sun-dried for more than 15 days, and shelled to collect hybrid seeds.

Field evaluation

The experimental materials comprising four parents, CML149, CML330, CML143, CML193, two F_1 hybrids CML149 × CML330 and CML143 × CML193, and the corresponding F_2 populations, BCP_1, and BCP_2 populations of the two crosses were evaluated using a compact family block design (CFBD) in two replications during the summer season (Mid-February to Mid-June 2023) at the P.G. Research Farm, M.S. Swaminathan School of Agriculture, Paralakhemudi, Gajapati, Odisha.

This investigation evaluated six populations (P_1, P_2, F_1, F_2, BCP_1, and BCP_2) of two elite hybrids, [CML149 (P1) x CML330 (P2)] and [CML143 (P1) x CML193 (P2)], which exhibited superior performance in terms of grain yield plant^{-1}.

The parents, F_1s, F_2s, and backcrosses were randomized separately in each replication. The P_1, P_2, and F_1 populations were space-planted in one row, with 10 plants each, whereas the BCP_1 and BCP_2 populations were space-planted in two rows, with 20 plants each. 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 × 20 cm. Standard agronomic practices were followed during the crop period to ensure good phenotypic expression of characters.

Observations were recorded on a whole plot basis for days to 50% tasseling and days to 50% silking by counting the number of days from sowing to the emergence of tassels and silks in 50% of the plants. Additional observations were recorded for characters such as plant height (cm), ear height (cm), ear length (cm), ear girth(cm), number of kernels row^{-1}, number of kernels cob^{-1}, 100-grain weight (g), grain yield plant^{-1} (g), estimation of canopy temperature (°C) was done using infrared thermal, estimation of chlorophyll content (%) was done using SPAD502 chlorophyll meter, membrane stability index (%) with fresh leaf sample, following the method of Premachandra *et al.* (1990), Sairam (1994), estimation of protein content (%) from grains using Lowry method Shen *et al.* (2019), estimation of oil content (%) was done using soxhlet apparatus extraction methods, Catalase activity (U mL^{-1}) and peroxidase activity (U mL^{-1}) were estimated using Labman UV-VIS spectrophotometer model (LMSP-UV1900) from fresh leaf samples as described previously (Sadasivam and Manickam 1996). Observations for leaf firing, tassel blast, root lodging (%) were recorded based on scoring. These data were recorded from 10 plants of the parents and F_1 populations, 20 plants of the backcross populations, and 250 plants of the F_2 populations, respectively Raj *et al.* (2020), Teja *et al.* (2024). The genetic effects were estimated using Generation mean analysis, following the methods earlier reported by Pujar *et al.* (2022) in pearl millet. To evaluate predominant gene effects in maize, analysis was carried out by fitting the data into a six-parameter model to assess the additive and non-additive types of genetic effects.

Statistical analysis

Generation mean analysis

The Generation mean analysis six-parameter model was applied to estimate the genetic parameters and test the presence of a type of epistatic interaction. Characters with substantial variances ($P \leq 0.05$) across the populations were analyzed using Generation mean analysis. To verify generational differences, data were subjected to compute analysis of variance. Mean data were first tested to determine non-allelic interaction through individual scaling tests A, B, C and D proposed by Mather (1949).

Scale A = $2BCP_1 - P_1 - F_1$

Scale B = $2BCP_2 - P_2 - F_1$

Scale C = $4F_2 - 2F_1 - P_1 - P_2$

Scale D = $2F_2 - BCP_1 - BCP_2$

Where P_1, P_2, F_1, F_2, BCP_1, and BCP_2 represent 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:

$VA = 4V(BCP_1) + V(P_1) + V(F_1)$

$VB = 4V(BCP_2) + V(P_2) + V(F_1)$

$VC = 16V(F_2) + 4V(F_1) + V(P_1) + V(P_2)$

$VD = 4V(F_2) + V(BCP_1) + V(BCP_2)$

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 was calculated by estimating the square root of the respective variances. The t-test has been used to test of deviation from the hypothetical value of zero. The calculated t-values were compared with "t" table values at 5 and 1% level of significance at their respective degrees of freedom.

After conducting scaling tests, if any of the 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 × additive (i), additive × dominance (j), and dominance × dominance (l). Six parameters model was calculated by using following formula:

m = Mean = F_2 Eq. 1

d = Additive effect = $BCP_1 - BCP_2$ Eq. 2

h = Dominance effect = $F_1 - 4F_2 - (1/2)P_1 - (1/2)P_2 + 2BCP_1 + 2BCP_2$ Eq. 3

i = Additive × Additive effect = $2BCP_1 + 2BCP_2 - 4F_2$ Eq. 4

j = Additive × Dominance effect = $BCP_1 - (1/2)P_1 - BCP_2 + (1/2)P_2$ Eq. 5

l = Dominance × Dominance effect = $P_1 + P_2 + 2F_1 + 4F_2 - 4BCP_1 - 4BCP_2$ Eq. 6

Where,

Variances of genetic effects were calculated after the following formula:

$Vm = V(F_2)$ Eq. 7

$Vd = V(BCP_1) + V(BCP_2)$ Eq. 8

$Vh = V(F_1) + 16V(F_2) + (1/4)V(P_1) + (1/4)V(P_2) + 4V(BCP_1) + 4V(BCP_2)$ Eq. 9

$Vi = 4V(BCP_1) + 4V(BCP_2) + 16V(F_2)$ Eq. 10

$\sqrt{H/D}$ $Vl = V(P_1) + V(P_2) + 4V(F_1) + 16V(F_2) + 16V(BCP_1) + 16V(BCP_2)$ Eq.11

Where, $V(P_1)$, $V(P_2)$, $V(F_1)$, $V(F_2)$, $V(BCP_1)$, and V

(BCP_2) were the variances of P_1, P_2, F_1, F_2, BCP_1, and BCP_2 populations, respectively. The significance for the above genetic parameters was tested using the t-test. First, standard error is worked out for each component separately by taking the square root of the variance of the respective components. The significance of the genetic effect was tested using the t-test in a similar manner as in the case of the scaling test. 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).

Degree of domicance = $\sqrt{\mathrm{H/D}}$

RESULTS AND DISCUSSION

The Generation mean analysis provides insight into the genetic control of morphological and biochemical traits in both 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. Yadav *et al.* (2018) and Sharma *et al.* (2023) observed significant dominance effects in maize.

Generation mean analysis for characters reveals significant variations ($P \le 0.05$) among the populations. Analysis of variance depicts the variation among the populations. The mean performance of six populations (P_1, P_2, F_1, F_2, BCP_1 and BCP_2), scaling test (A, B, C and D) and the genetic parameters (m, d, h, i, j, l) calculated for two crosses *viz.,*(CML149 x CML330) and (CML143 x CML193) using six-parameter model.

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. In the present study, the means of the six population of crosses [CML149(P_1) x CML330 (P_2)] and [CML143(P_1) x CML193 (P_2)] for 21 traits were evaluated. The results showed in (CML149 x CML330) that F_1 means were higher than either of the parents for all traits under study except for days to 50% tasseling, days to 50% silking, 100 grain weight (g), leaf firing(%), tassel blast (score), root lodging (score), chlorophyll content(%), canopy temperture (□), membrane stability index (%), catalase activity (U mL^{-1}) and peroxidase activity (U mL^{-1}) (Table-1 and 2). The results showed that in cross (CML143 x CML193) F_1 means were higher than both parents only for traits plant height (cm), cob height (cm), cob girth (cm), grain yield plant^{-1} (g), Chlorophyll content (%), membrane stability index (%) (Table-3 and 4).The above two crosses show different responses regarding considered characters in the present investigation. Moreover, it is noted that (CML143 x CML193) shows superior heterotic performance respect to grain yield plant^{-1} compared to (CML149 x CML330). The F_1 population performing superiority over other populations indicates the predominance of dominance and non-additive gene action in maize (Shahrokhi *et al.*, 2013; Elmyhun *et al*., 2024).

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

The scaling test is employed to ascertain the presence or absence of epistasis, which is a crucial step before estimating various genetic parameters. Therefore, the scaling test serves as an indicator of the presence or absence of non-allelic interactions. Epistasis has the potential to impact the expression and performance of traits. Gene interactions can lead to non-additive effects, where the phenotype of a trait in a hybrid or population is not simply to the sum of individual gene effects. Epistasis may result in traits being over-dominant (hybrids outperform either parent) or under-dominant (hybrids perform inferior to either parent), influencing overall performance. The estimates of gene effect were derived from the Generation mean of the crosses for all the studied characters by an individual (A, B, C, D) scaling test that showed the presence of non-allelic interactions. Scaling test showed good fit for the non-epistatic model and indicated failure of the simple additive-dominance model for different traits in both the crosses. Further significant values observed from scaling test predicted inadequacy of the model in the majority of the traits except for cob height, number of kernels row^{-1} , number of kernel rows cob^{-1}, grain yield plant^{-1}, perioxidase activity in the cross CML149 x CML330 that indicated the presence of epistasis (non-allelic interaction), which was also inferred from the Generation mean.

Under the present investigation, duplicate type of epistasis was reported for crosses *viz*., CML149 x CML330 and CML143 x CML193 for various characters namely, days to 50% tasseling, plant height, ear height, ear length, ear girth, number of kernels row^{-1}, number of kernels row cob^{-1}, 100 grain weight, grain yield plant^{-1}, canopy temperature, protein content, oil content, peroxidase activity and root lodging as shown in Table 5.

The nature of epistasis in that cross CML149 x CML330 was the complementary type for the characters: days to 50% silking, leaf firing and tassel blast. Characters *viz*., chlorophyll content, membrane stability index and catalase activity showed complementary epistasis for the cross CML143 x CML193.

Table 1. Generation mean for yield attributes in six generation of CML 149 X CML 330

Population	**Days to 50% Tasseling**	**Days to 50% silking**	**Anthesis-silking interval (days)**	**Plant height (cm)**	**Cob height (cm)**	**Cob length (cm)**	**Number of kernels row^{-1}**	**Number of kernel rows cob^{-1}**	**Cob girth (cm)**	**Grain yield plant^{-1} (g)**	**100 grain weight (g)**	**Leaf firing**	**Tassel blast**	**Root lodging (%)**
CML 149 (P_1)	67.4	69	1.6	136.6	49.4	13.2	22.2	12.2	8.6	270.2	21.006	0.4	0.4	0.4
CML 330 (P_2)	65.6	66.6	1	166.4	61.5	16.9	23.2	14.2	8.6	330.8	24.008	0.2	0.2	0.2
CML 149 x CML 330 (F_1)	62.4	64.2	1.8	216.4	92.4	23.8	30.4	15	10.1	456.6	23.464	0.4	0.4	0.4
CML 149 x CML 330 (F_2)	60.98	62.78	1.8	186.0	82.10	15.76	16.32	12.95	8.51	215.39	32.91	0.11	0.11	0.12
[CML 149 x CML 330 (CML 149)] (Bc_1)	61.8	64.8	3	201.6	102.6	17.4	33.6	15.6	9	521.2	22.47	0.2	0.2	0
[CML 149 x CML 330 (CML 330)] (Bc_2)	61.6	63.6	2	194.6	99	18.8	35.8	16.8	9.8	604.4	23.812	0.2	0.2	0

Table 2. Generation mean for quality attributes in six generation of CML 149 X CML 330

Population	**Chlorophyll content (%)**	**Canopy temperature (℃)**	**Protein%**	**oil%**	**Membrane stability index (%)**	**Catalase (U mL^{-1})**	**Perioxidase (U mL^{-1})**
CML 149 (P_1)	34.1	34.42	8.57	3.768	39.354	0.156	0.506
CML 330 (P_2)	22.24	34.6	9.34	4.262	54.942	0.264	0.302
CML 149 x CML 330 (F_1)	21.54	31.6	9.448	4.854	52.17	0.13	0.458
CML 149 x CML 330 (F_2)	25.0512	32.404	6.8863	4.511	45.98	0.2063	0.3548
[CML 149 x CML 330 (CML 149)] (Bc_1)	30.94	31	8.876	4.548	43.412	0.268	0.304
[CML 149 x CML 330 (CML 330)] (Bc_2)	40.42	31.4	9.46	4.886	54.136	0.226	0.282

Anthesis-silking interval (ASI):

In temperate maize, grain yield and ASI exhibit highest phenotypic plasticities Silva *et al.* (2022). The significant magnitudes of h (dominance) effect as well as interaction effects i (additive x additive) and l (dominant × dominant) in both the crosses indicate that both dominance and epistatic interactions (additive × additive and dominant × dominant) play important roles in the expression of the traits in these crosses. The prevalence of h (dominance) over d (additive) indicates dominant gene action in the inheritance of this trait. The parameters (h) and (l) had opposite signs, suggesting that the duplicate epistasis was involved in the inheritance of this trait in CML149 x CML330 and CML143 x CML193, respectively (Table 5). These results are in accordance with Shankar *et al.* (2022) in maize across F_2 populations.

Plant height (cm):

Plant height has a direct, measurable impact on crop lodging resistance Stubbs *et al.* (2023). The significant magnitude of d (additive) effect for the cross CML143 x CML193 and the non significant j (additive × dominant) values in the crosses CML149 x CML330 and CML143 x CML193 indicate dispersal of alleles in the parents. The gene effects (h), (i), and (l) were significant in the crosses CML149 x CML330 and CML143 x CML193, indicating the influence of non-additive interactions on the expression of plant height. However, the magnitude of the dominance effect was more pronounced. In both crosses, the gene effects (h) and (l) were of opposite signs suggesting duplicate epistasis in the inheritance of this trait (Table 5). The findings on dominance and non-additive gene action for plant height concord with Haq *et al.* (2013) in maize.

Cob height (cm)

Cob height was measured from ground level to the primary cob's attachment node. Cob height indirectly influences maize grain yield (Arsyad *et al.* (2020). The significant magnitudes of h (dominant) effect, as well as interaction effects i (additive x additive) and l (dominant × dominant) in both the crosses CML149 x CML330 and CML143 x CML193, suggest dominance and epistatic interactions. The opposite signs of gene effects (h) and (l) suggest that duplicate epistasis is involved in the inheritance of this trait in both crosses (Table 5). These results in maize were in accordance with Dorri *et al.* (2014), where in cob height and yield-related traits exhibited duplicate gene action.

Cob length (cm)

The significant magnitudes of (h) and (i) in the cross CML 149 x CML 330 indicates the presence of dominance and additive × additive types of epistasis while, significant magnitudes of (h) as well as interaction effects (i) and (l) in cross CML143 x CML193 indicate the prevalence of dominant gene action as well as interaction effects in the inheritance of cob length. The opposite signs of gene effects (h) and (l) suggest that duplicate epistasis is observed in both the crosses (Table 5). These results followed maize's dominance and epistatic gene action (Shahrokhi *et al.*,2013).

Number of kernels row^{-1}:

The number of kernels row^{-1} directly affects grain yield plant^{-1} Teja *et al,* (2024). The significant magnitude of i (additive x additive) and l (dominance x dominance) in cross CML149 x CML330 indicated the predominant role of interacting gene effects in maize, obtained significant results, indicating epistatic gene effects. The significant magnitude of h (dominant), as well as interaction effects i (additive x additive) and l (dominant × dominant) in cross CML143 x CML193, indicates the prevalence of dominance as well as epistatic type of gene action for inheritance of this character. Duplicate type of epistasis was recorded for both the crosses (Table 5). Similar observations were also reported by Attri *et al*. (2021), Sharma *et al*. (2022) and Shankar *et al.* (2022), wherein duplicate gene interaction was noted for this trait in maize.

Number of kernel rows cob^{-1}:

Several kernel rows cob^{-1} directly influence grain yield plant^{-1} Teja *et al.* (2024). Number of kernel rows cob^{-1} was governed by significant magnitudes of h (dominance) as well as interaction effects i (additive x additive) and l (dominant × dominant) in both the crosses, indicating dominance and epistatic interactions have played a significant role in the inheritance of this trait. A duplicate type of non-allelic interaction was observed in both the crosses (Table 5). These results were in accordance with Rahangdale *et al*. (2019); Nagarajan *et al.* (2022) in maize.

Ear girth (cm):

The significant magnitudes of h (dominance) as well as interaction effects i (additive x additive) and l (dominant × dominant) in both the crosses indicate that dominance and non-allelic interactions played a significant role in the inheritance of ear girth. However, both the crosses exhibited duplicate types of epistasis (Table 5). Elmyhun *et al*. (2024) previously reported dominance and epistatic effects for this trait in maize.

Grain yield plant^{-1} (g)**:**

Grain yield plant^{-1} directly affects overall crop productivity Rahimi *et al*. (2021). The significant magnitude of i (additive x additive) and l (dominance x dominance) in cross CML149 x CML330 indicates that both additive epistatic interactions and dominant epistatic interactions play a crucial role in the expression of the trait and h (dominance) as well as interaction effects i (additive x additive) and l (dominant × dominant) in the cross CML143 x CML193 indicates the prevalence of dominance and non-allelic gene interaction in character inheritance. Duplicate type of epistasis was observed in both crosses (Table 5). Chiangmai *et al.* (2013) and Sharma *et al*. (2023) previously observed that non-additive gene effects functioned for the trait in maize.

100 grain weight (g)

The significant magnitudes of h (dominance) as well as interaction effects i (additive x additive) and l (dominant × dominant) in both the crosses indicate that dominance and epistatic interactions played a significant role in the inheritance of this trait. The type of epistasis was found to be duplicate in nature for both crosses (Table 5). These results were in accordance with the study of Moharramnejad *et al.* (2018) in maize and noticed that non-additive gene effects operated for this trait.

Chlorophyll content (%)

Chlorophyll content directly correlates with photosynthetic efficiency, ultimately leading to improved Grain yield plant^{-1} Li *et al*. (2024).The significant magnitude of d (additive), h (dominance) and non allelic interaction i (additive x additive) and l (dominant × dominant) in cross CML149 x CML330 revealed additive, dominance and non-allelic interactions contributing significantly to the character inheritance. However the magnitude of the dominance effect was more obvious. In the cross CML149 x CML330 duplicate type of epistasis was observed while complementary type of epistasis was noted for cross CML143 x CML193 as the magnitude of h and l was found to be in similar direction (Table 5). Said, (2014) reported duplicate gene action for chlorophyll content in wheat whereas Yadav *et al*. (2018) observed non-additive gene effects for the trait in maize.

Canopy temperature (℃)

Canopy temperature is directly related to plant growth and productivity, often reflected in grain yield plant^{-1}.Higher canopy temperatures can indicate stress conditions, negatively impacting maize productivity Zhai *et al.* (2024). The significant magnitude of h (dominance) and i (additive × additive) in cross CML149 x CML330 suggest contribution of both dominant and non-allelic interaction in trait inheritance. A duplicate type of epistasis is observed in both crosses (Table 5). These results were in accordance with Teja *et al.* (2024) in the quality protein of maize and noticed the function of non-additive gene effects for the trait.

Membrane stability index (%)

The Membrane Stability Index (MSI) assesses cell membrane integrity under stress conditions. A higher MSI indicates greater membrane stability crucial for maintaining cellular functions and overall plant health during stress conditions Abid *et al*. (2018). The significant magnitudes of d (additive) components were recorded in cross CML149 x CML330, indicating significant role of additive gene effects in the inheritance of the trait. The complementary type of epistasis was noted in cross CML143 x CML193 as the magnitude of (h) and (l) were found to be of similar sign. In cross CML149 x CML330 the duplicate type of epistasis was observed (Table 5). Yadav *et al.* (2018) earlier observed maize, where non-additive gene effects were noted for the trait.

Catalase activity (**U mL^{-1}**) :

High-yielding QPM lines with high antioxidant status (catalase and peroxidase) were preferred because of their ability to scavenge free radicals generated during stress conditions (Hamidi *et al.*, 2023). Duplicate type of epistatic interaction was observed for catalase activity in CML149 x CML330. The complementary type of epistasis was observed in the cross CML143 x CML193 (Table 5). Teja *et al.* (2024) previously observed in maize leaf samples and noticed that non additive gene effects operated for this trait.

Perioxidase activity (**U mL^{-1}**) **:**

The significant magnitudes of h (dominance), as well as interaction effects i (additive x additive) and l (dominant × dominant) type of interaction, were favored in CML149 x CML330, indicating that dominance and non-allelic interactions are favored in the inheritance of peroxidase activity. A duplicate type of non-allelic interaction was observed for this trait in both crosses (Table 5). Teja *et al.* (2024) previously observed in maize leaf samples the function of non-additive gene effects for this trait.

Root lodging (%)**:**

Root lodging damages the root system, disturbs the normal canopy structure, reduces photosynthetic performance, and reduces yield. Root lodging at the late growth stage results in ears touching the ground and promotes a sharp increase of grain rot leading to a decline in grain quality Wang *et al.* (2022). Non-allelic interaction i (additive x additive) and l (dominance × dominance) were significant in cross CML149 x CML330, implying the existence of non-allelic interaction for this trait, indicating the predominant role of interacting gene effects. A duplicate type of epistatic interaction was observed for this trait in both crosses (Table 5). These results agreed with Raj *et al*. (2020)

Table 3. Generation mean for yield attributes in six generation of CML 143 x CML 193

Population	Days to 50% tasseling	Days to 50% silking	Anthesis-silking interval (days)	Plant height (cm)	Cob height (cm)	Cob length (cm)	Number of kernels row^{-1}	Number of kernel rows per cob^{-1}	Cob girth (cm)	Grain yield plant^{-1}	100 grain weight (g)	Leaf firing	Tassel blast	Root lodging (%)
CML 143 (P_1)	67.4	71	3.6	146.2	56	14	18.6	10.2	8.8	190.6	36.524	0.4	0.4	0.2
CML 193 (P_2)	64	66.8	2.8	138.6	54	21	29.4	15	9.6	437.6	30.398	0.4	0.4	0.2
CML 143 x CML 193 (F_1)	64.2	67.2	3	218.4	80.8	19.4	36.8	18.4	10.4	673.2	26.152	0.2	0.2	0.2
CML 143 x CML 193 (F_2)	61.264	63.588	2.324	164.56	70.384	16.688	16.16	13.124	8.86	222.576	30.8453	0.344	0.304	0.252
[CML 143 x CML 193 (CML 143)] (Bc_1)	62.8	64.8	2	245.8	88.6	19.4	32.6	20.2	10	685	41.804	0.4	0.4	0.2
[CML 143 x CML 193 (CML 193)] (Bc_2)	66.2	67.4	1.2	178.6	71.2	18.8	35	17	10.8	596.4	36.524	0.2	0.2	0.2

Table 4. Mean for quality attributes in six generation of CML 143 x CML 193

Population	Chlorophyll content (%)	Canopy temperature (℃)	Protein%	oil%	Membrane stability index (%)	Catalase (U mL^{-1})	Perioxidase (U mL^{-1})
CML 143 (P_1)	42.9	31.8	8.54	2.89	30.17	0.044	0.502
CML 193 (P_2)	42.46	30.4	9.136	4.504	45.256	0.128	0.524
CML 143 x CML 193 (F_1)	47.6	31	8.806	3.59	49.104	0.09	0.5
CML 143 x CML 193 (F_2)	44.212	31.068	8.7222	3.8399	42.7361	0.0826	0.472
[CML 143 x CML 193 (CML 143)] (Bc_1)	47.6	31.4	9.074	3.786	37.756	0.098	0.472
[CML 143 x CML 193 (CML 193)] (Bc_2)	39.28	30.8	9.2	3.522	44.048	0.072	0.434

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)	CML 149 x CML 330	-6.2*	-4.8*	-13.8*	-1.4	60.9*	0.2	-1.2	2.864	-0.7	8.136	duplicate	-2.49
	CML 143 x CML 193	-6	4.2*	-14.7*	-6.4*	61.2*	-3.4	11.4*	12.944*	-5.1	-11.144*	duplicate	-1.83
Days to 50% silking (days)	CML 149 x CML 330	-3.6*	-3.6*	-12.8*	-2.8*	62.7*	1.2	2.064	5.664*	0*	1.536	complementary	1.31
	CML 143 x CML 193	-8.6*	0.8	-17.8*	-5.02*	63.5*	-2.6	8.348*	10.048*	-4.7	-2.248	duplicate	-1.79
Anthesis-silking interval (days)	CML 149 x CML 330	2.6*	1.2	1	-1.4*	1.8*	1	3.3*	2.8*	0.7	-6.6*	duplicate	1.82
	CML 143 x CML 193	-2.6*	-3.4*	-3.1*	1.4*	2.3*	0.8	-3.096*	-2.896*	0.4	8.896*	duplicate	-1.97
Plant height (cm)	CML 149 x CML 330	50.2	6.4	8.2	-24.1	186.01*	7	113.236*	48.336*	21.9	-104.93*	duplicate	4.02
	CML 143 x CML 193	127	0.2	-63.3	-95.2*	164.5*	67.2*	266.560*	190.560*	63.4	-317.76*	duplicate	1.99
Cob height (cm)	CML 149 x CML 330	63.4*	44.1*	32.7*	-37.3*	82.1*	3.6	111.734*	74.784*	9.65	-182.28*	duplicate	5.57
	CML 143 x CML 193	40.4*	7.6	9.9	-19.03*	70.3*	17.4	63.864*	38.064*	16.4	-86.064*	duplicate	1.92
Cob length (cm)	CML 149 x CML 330	-2.2	-3.1*	-14.6*	-4.6*	15.7*	-1.4	18.094*	9.344*	0.45	-4.044	duplicate	-3.60
	CML 143 x CML 193	5.4*	-2.8	-7.04*	-4.8*	16.6*	0.6	11.548*	9.648*	4.1	-12.248*	duplicate	4.39
Number of kernels row^{-1}	CML 149 x CML 330	14.6*	18*	-40.8*	-36.7*	16.3*	-2.2	81.188	73.488*	-1.7	-106.08*	duplicate	-6.07
	CML 143 x CML 193	9.8*	3.8	-56.9*	-35.2*	16.1*	-2.4	83.360*	70.560*	3	-84.160*	duplicate	-5.89
Number of kernel rows cob^{-1}	CML 149 x CML 330	4*	4.4*	-4.5*	-6.4*	12.9*	-1.2	14.792*	12.992*	-0.2	-21.392*	duplicate	-3.51
	CML 143 x CML 193	11.8*	0.6	-9.5*	-10.9*	13.1*	3.2	27.704*	21.904*	5.6	-34.304*	duplicate	2.94
Cob girth (cm)	CML 149 x CML 330	-0.7	0.9	-3.3*	-1.7*	8.5*	-0.8	5.028*	3.528*	-0.8	-3.728	duplicate	-2.51
	CML 143 x CML 193	0.8	1.6	-3.7*	-3.08*	8.8*	-0.8	7.360*	6.160*	-0.4	-8.560*	duplicate	-3.03

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

Table 5. Estimates of different scaling tests and genetic effects for quantitative and qualitative parameters in two qpm crosses

Character	**Cross**	**Scaling Test**				**Gene effects**						**Type of epistasis**	$\sqrt{H/D}$
		A	B	C	D	m	d	h	i	J	l		
Grain yield plant^{-1}(g)	CML 149 x CML 330	315.6*	421.4*	-652.6*	-694.8*	215.3*	-83.2	1545.716	1389.616*	-52.9	-2126.616*	duplicate	-4.31
	CML 143 x CML 193	452.2*	82	-1084.2*	-809.2*	222.5*	61.6	1977.596*	1618.496*	185.1	-2152.696*	duplicate	5.67
100 grain weight (g)	CML 149 x CML 330	0.47	0.15	39.7*	19.5*	32.9*	-1.3	-38.146*	-39.103*	0.159	38.481*	duplicate	5.33
	CML 143 x CML 193	20.9*	16.4	4.1	-16.6*	30.8*	5.2	25.966*	33.275*	2.217	-70.705*	duplicate	2.22
Chlorophyll content(%)	CML 149 x CML 330	6.2	37.06*	0.7	-21.2	25.05*	-9.4*	35.885*	42.515*	-15.41	-85.815*	duplicate	-1.95
	CML 143 x CML 193	4.7	-11.5	-3.7	1.5	44.2*	8.3	1.832	-3.088	8.1	9.888	complementary	0.47
Canopy temperature (℃)	CML 149 x CML 330	-4.02	-3.4	-2.6	2.4*	32.4*	-0.4	-7.726*	-4.816*	-0.31	12.236	duplicate	4.39
	CML 143 x CML 193	0.1	0.2	0.07	-0.06	31.06*	0.6	0.028	0.128	-0.1	-0.328	duplicate	0.22
Protein%	CML 149 x CML 330	-0.2	0.1	-9.2*	-4.5*	6.8*	-0.5	9.620*	9.127*	-0.199	-8.993*	duplicate	-4.06
	CML 143 x CML 193	0.8	0.5	-0.3	-0.8*	8.7	-0.1	1.747	1.779*	0.112	-3.159*	duplicate	-3.06
oil%	CML 149 x CML 330	0.4	0.6	0.3	-0.4	4.5*	-0.3	1.663*	0.824	-0.091	-1.954	duplicate	-2.22
	CML 143 x CML 193	1.09	-1.05	0.7	0.3	3.8*	0.2	-0.851	-0.744	1.071	0.702	duplicate	-1.79
Membrane stability index (%)	CML 149 x CML 330	-4.7	1.1	-14.7*	-5.5	45.9*	-10.7*	16.198	11.176	-2.93	-7.636	duplicate	-1.23
	CML 143 x CML 193	-3.7	-6.2	-2.6	3.6	42.7*	-6.2	4.055	-7.336	1.251	17.362	complementary	-0.80
Catalase (U mL^{-1})	CML 149 x CML 330	0.2	0.05	0.1	-0.08	0.2*	0.04	0.083	0.163	0.096	-0.471	duplicate	1.40
	CML 143 x CML 193	0.06	-0.07	-0.02	-0.005	0.08*	0.02	0.014	0.01	0.068	0.002	complementary	0.72
Perioxidase (U mL^{-1})	CML 149 x CML 330	-0.3*	-0.1*	-0.3*	0.1*	0.3*	0.02	-0.193*	-0.247*	-0.08	0.799*	duplicate	-2.96
	CML 143 x CML 193	-0.05	-0.1	-0.1	0.03	0.4	0.03	-0.089	-0.076	0.049	0.29	duplicate	-1.53
Leaf firing	CML 149 x CML 330	-0.4	-0.2	-0.9	-0.1	0.1*		0.436	0.336	-0.1	0.264	complementary	-
	CML 143 x CML 193	0.2	-0.2	0.1	0.08	0.3*	0.2	-0.376	-0.176	0.2	0.176	duplicate	-1.37
Tassel blast	CML 149 x CML 330	-0.4	-0.2	-0.9	-0.1	0.1*		0.436	0.336	-0.1	0.264	complementary	-
	CML 143 x CML 193	0.2	-0.2	0.01	0.008	0.3*	0.2	-0.216	-0.016	0.2	0.016	duplicate	-1.04
Root lodging (%)	CML 149 x CML 330	-0.8*	-0.6	-0.8	0.2	0.1*		-0.412	-0.512*	-0.1	1.912*	duplicate	-
	CML 143 x CML 193			0.2	0.1	0.2*		-0.208	-0.208		0.208	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 for quality protein maize, where heat tolerance did not show any symptoms of root lodging and noticed the function of non-additive gene effects for the trait.

Duplicate epistasis interaction was observed for this trait in both the crosses for protein and oil content (Table 5). Sharma *et al. (*2023)previously observed in maize non-additive gene effects for both traits in maize. A duplicate type of epistasis interaction was observed for leaf firing (%) and tassel blast (%) in the cross CML143 x CML193, indicating that the gene interaction involves masking one gene's effect above another gene at different loci. Complementary epistasis was observed in the cross CML149 x CML330 for leaf firing and tassel blast, indicating that both interacting genes contribute towards the expression of the character (Table 5). Similar observations were also reported by Raj *et al. (*2020) for quality protein maize, where heat tolerance did not reflect in symptoms of leaf firing as well as tassel blast and noticed that non-additive gene effects operated for both these traits.

Degree of dominance

The degree of dominance among the two crosses showed considerable variation. The cross CML 149 x CML 330 ranged from as low as -6.07 for the trait number of kernels per row to as high as 5.57 for cob height. Similarly, for the cross CML 143 x CML 193, the degree of dominance ranged from -5.89 for the number of kernels per row to 5.67 for grain yield per plant. Particularly for grain yield per plant, the degree of dominance reached 5.67 in the cross CML 143 x CML 193, indicating significant non-additive genetic effects as earlier reported by Pujar *et al.* (2022).

For most of the traits: ear length, number of kernels row^{-1}, number of kernal rows cob^{-1}, ear girth, ASI, cob height, cob length grain yield, 100 grain weight, protein content and perioxidase activity the inheritance was mainly controlled by dominance effects with 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 cowpea Dinesh *et al*. (2018). Traits that function with complementary gene action in either of the crosses: leaf firing, chlorophyll content, membrane stability index, catalase activity and tassel blast, the focus may be emphasizing to enhanced genetic gain by assessing the genetic worth of the selected plant for better improvement of population performance and selection intensity than under duplicate gene interaction as previously observed by Dinesh *et al*. (2018).

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Conclusion

The Generation mean analysis provided insights into the genetic control of traits, indicating the prevalence of dominance gene effect and epistatic interaction (duplicate gene action) in the inheritance of the majority of the traits of QPM (*Zea mays*). This information is valuable for designing effective breeding strategies and understanding the genetic basis of trait inheritance. Moreover, the greater prevalence of the dominance gene effect and the dominance x dominance interaction effect might provide insight into the exploitation of heterosis. Some additive x additive effects were observed in both the crosses, suggesting potential to gain from selection. Dominance and dominance x dominance effect were found to have a considerable role in both the crosses evaluated under study, indicating the presence of duplicate gene action for traits namely, ear length, number of kernels row^{-1}, number of kernal rows cob^{-1}, ear girth, grain yield, 100 grain weight, protein content and perioxidase activity. Therefore, biparental mating could be a promising approach to handling and segregating populations and breaking undesirable linkage.

Conflict of interest

The authors declare that they have no conflict of interest.

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