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Understanding the genetics of important quality traits in maize (*Zea mays* L.) using diverse germplasm by generation mean analysis

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ABSTRACT

The information about gene actions and interactions would most likely to direct and reinforce the crop breeding programs. With this objective, the present investigation was undertaken by using six generations P_1, P_2, F_1, F_2, BC_1, and BC_2 derived from six different crosses in maize, evaluated at CCS Haryana Agricultural University, Regional Research Station Karnal from Kharif 2015 to 2016. The study underscores the significance of additive–dominance model, gene action involved in the inheritance of grain yield and quality traits. Both the scaling test and the joint scaling test detected nonallelic interactions affecting the traits, showing the inadequacy of the additive–dominance model alone in describing the manifestation of complex traits like yield and quality traits except for oil content in cross HKI 325-17AN × HKI 1128. Both additive genetic effects and dominance effects were found significant with positive and negative magnitude in all the crosses. On the note, different types of interallelic interactions (i, j, l) contributed to the inheritance of traits in the given crosses. And among them, the dominance × dominance component (l) gene effect also played a major role in the inheritance of the studied traits. Duplicate epistasis was prevalent in all the crosses for grain yield and also for protein, tryptophan, oil, and starch content in some crosses whereas a complementary type of interaction was reported for protein content in cross HKI 325-17AN x HKI 1128 and oil content in cross HKI 209 x HKI 163. In view of the diverse gene actions, i.e. additive, dominant, and epistasis, playing important roles in the manifestation of complex traits like yield and quality traits, we advocate the implementation of population improvement techniques in particular reciprocal recurrent selection to improve productivity gains in maize in terms of both yield and quality. It is concluded that crosses, where dominant gene action was found predominant, should be effectively utilized in hybrid maize programs for improved grain yield and quality traits.

Keywords: *Additive × additive, dominant, epistasis, gene effects, grain yield, quality protein maize*

INTRODUCTION

Maize is a multi-faceted crop used as a food, feed, and industrial crop globally. Maize has a very prominent role to play in the Indian economy too. Currently, this coarse grain is cultivated in about 10.2 Million hectares in India. It is an economically and nutritionally important cereal crop being cultivated in different agricultural zones under diverse situations of rainfall and altitude around the world. Because of its high starch content, it acts as an energy source, but its protein content is weak and has a low average level (about 10 percent) [1]. Enhancing the yield of protein, oil, and carbohydrate in maize grain can be achieved either by increasing grain contents of these constituents or by increasing grain yield per land unit area. While significant efforts have been made to increase maize productivity, further research is needed to fully exploit maize's genetic potential in terms of grain quality. A classic example that has resulted in dramatically reducing malnutrition is the quality protein maize with higher lysine and tryptophan. Hence genetic modification is now considered a noble objective for enhanced nutritional value, especially protein quality. The type and relative amount of genetic components are all important factors in maize genetic improvement. Hence, phenotypic characterization is essential for selecting genetically diverse lines for maize breeding [2]. The quantification of diverse germplasm contributes in the development of new germplasm, broadening the genetic base and also filling the gap between available genetic resources and their utilization in maize breeding programs [3]. Many researchers have also reported significant variations among genotypes, environments and their interactions for yield, yield-related traits, and quality traits in maize.

A large number of genetic studies have been made in the past to explore the genetic basis of yield and yield components in maize cultivars but there was very little emphasis on the quality traits such as protein content, lysine content, tryptophan content, oil content, and starch

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content which are usually considered to have substantial contribution towards increasing grain quality. In addition to gene effects, breeders are interested in how much of a crop's variation is genetic and how much of it is heritable because the effectiveness of selection is mostly influenced by additive genetic variance, environmental factors, and interactions between genotype and environment [4]. The information on these aspects will help in the selection and adoption of breeding approaches suitable for improving grain yield and quality. Therefore, the current study has been designed to understand the nature and inheritance of grain yield, its component traits, and quality traits for different traits by using P1, P2, F1, F2, BC1, and BC2 generations of six crosses that are necessary for proper choice of breeding procedures for developing QPM hybrids with increased grain yield and improved quality.

MATERIALS AND METHODS

Genetic Materials and Experimental Procedure

The present investigation was carried out at the experimental area of CCSHAU, Regional Research Station Karnal, Haryana from *Kharif* 2013 to 2016. During *Kharif* 2013, three inbred lines used as females (HKI 209, HKI 1332, and HKI 325-17AN) and two inbred lines used as males (HKI 1128 and HKI 163) were crossed with each other to produce six F_1 crosses. F1s were sown with five parental inbred lines and self-pollinated to grow F2 seeds in *Rabi* 2013-2014 and *Kharif* 2014. Under the time limit, backcrosses BC1 and BC2 of six crosses were also completed. The experiment comprised six generations (P1, P2, F_1, F_2, BC_1, and BC_2) of the six crosses HKI 209 × HKI 1128 (C1), HKI 209 × HKI 163 (C2), HKI 1332 × HKI 1128 (C3), HKI 1332 × HKI 163 (C4), HKI 325-17AN × HKI 1128 (C5) and HKI 325-17AN × HKI 163 (C6), was laid out in randomized block design (RBD) with three replications during *Kharif* 2015 and 2016. The parents, F1's, F_2's, and backcrosses were randomized separately in each replication. The P1, P2, and F1 were planted in a single row, while the BC1, BC2, and F2 were planted in two rows and ten rows, respectively with planting geometry 75 x 20 cm.

Data Collection

The observations were recorded on the five quantitative characters *viz*., grain yield per plant (g) and for quality traits *viz*., protein content (%), tryptophan content (%), oil content (%), and starch content (%) on 10 random plants from parents and F1s; 20 plants from backcrosses and all the plants from F2s generations of all the six crosses in each replication by using the standard procedure as suggested by ICAR-IIMR, Ludhiana.

Grain Yield per Plant: Individual cobs were harvested, dried, and weighed for each plant.

Protein content (%): The protein content of the seeds was estimated by using Micro Kjeldahl's method given by ICAR-IIMR.

Tryptophan content (%): Calorimetric methods were used for the tryptophan content (%) content estimation.

Oil content (%): Soxhlet's ether extraction method was used for the estimation of oil content.

Starch content (%): The starch content was determined by the Anthrone Reagent method.

Statistical Analysis

Means of all the characters over the years were compared and pooled using OPSTAT software and Excell 2007. The "t" statistical test was applied to test the differences between parental genotypes for the studied characters before considering the biometrical analysis. Generation means analysis was performed using Mather and Jinks method. In this method the mean of each character is indicated as follows: Y= m + α[d] + β[h] + α2 [i] + 2αβ[j] + β2 [l] Where: Y = observed mean for a generation; m = the mean effect; d = average additive effects; h = average dominance effects; i = average interactions between additive effects; j = average interactions between additive and dominance effects; l = average interactions between dominance effects. The following quantities A, B, C, and D [5] and their variances [6] were calculated for the detection of digenic interactions or adequacy of the additive-dominance model in each case, using formulae:

$A = P_1 + F_1 - 2BC_1$

$B = P_2 + F_1 - 2BC_2$

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

$D = 2F_2 - BC_1 - BC_2$

The genetic parameters (m, [d], [h], [i], [j], and [l]) were tested by using a t-test to significance.

To estimate the parameters and to select the most suitable model the least squares method and the joint scaling test of Mather and Jinks were employed. For the generation mean analysis, at first, the additive-dominance model was conducted using weighted least squares. If the additive, dominance model did not fit the data, other models which included epistatic components were evaluated. The variance components, an average of gene dominance, dominance deviation, and dominance degree of the traits were performed using Mather and Jinks (1982).

The joint scaling test was carried out to verify the goodness of fit of the model [7]. According to this methodology, the following notation for gene effects was used: [m]-mean, [d]-additive, [h]-dominance, [i]-additive x additive, [j]-additive x dominance, [l]-dominance x dominance effect.

Estimates using six parameter models of Jinks and Jones (1958) were derived by the perfect fit solution as:

$$m = 1/2\,\bar{P}_1 + 1/2\,\bar{P}_2 + 4\bar{F}_2 - 2\overline{BC}_1 - 2\overline{BC}_2$$

$$(d) = 1/2\,\bar{P}_1 + 1/2\,\bar{P}_2$$

$$(h) = 6\overline{BC}_1 + 6\overline{BC}_2 - 8\bar{F}_2 - \bar{F}_1 - 1/2\,\bar{P}_1 - 1/2\,\bar{P}_2$$

$$(i) = 2\overline{BC}_1 - \bar{P}_1 - 2\overline{BC}_1 + \bar{P}_2$$

$$(j) = 2\overline{BC}_1 - \bar{P}_1 + 2\overline{BC}_1 + \bar{P}_2$$

$$(l) = \bar{P}_1 + \bar{P}_2 + 2\bar{F}_1 + 4\bar{F}_2 - 4\overline{BC}_1 - 4\overline{BC}_2$$

The type of epistasis was determined only when dominance [h] and dominance x dominance [l] effects were significant. When these effects had the same sign, the type of epistasis was complimentary, while different signs indicated duplicate epistasis.

The significance of genetic components was tested using "t" test as follows:

$$\pm t = \frac{\text{effect}}{\sqrt{\text{variance of effect}}}$$

RESULTS AND DISCUSSION

Generation Means for yield and quality traits

The means and standard errors of the six generations of each cross for eleven traits presented in Table 1 indicated significant variation existed among the parents imply the divergent nature of both the parents (P_1 and P_2) for all the characters. Higher mean values of F_1 than the better parent (parent with the highest value) revealed positive heterobeltiosis for these characters except for the phenological characters (days to 50% tasselling,

days to 50 % silking, and days to maturity) where the condition was mostly reversed because most of the F_1 means were lower than the better parent (parent with the lowest value) and thus, indicated desirable negative heterobeltiosis. The results indicated over-dominance or partial dominance towards the respective parents for most studied traits, as well as, transgressive segregation was also observed in the F_2 generation. The mean values of F_2 generation were lower than F_1 means in all the crosses showing partial dominance and inbreeding depression for all the characters except for phenological traits. The backcross progenies, in general, tended towards their respective recurrent parents in all the crosses and for all the characters.

Estimation of Genetic Components for yield and quality traits

The estimates of gene effects derived from generation mean of all the six crosses for all the characters, by an individual (A, B, C and D) and joint scaling test depicted the presence of epistasis (Table 2). Scaling tests showed good fit for the non-epistatic model and indicated failure of simple additive-dominance model for different traits in all the crosses. Further, significant chi-square (χ^2) value observed from three parameters m, (d) and (h) through joint scaling test predicted inadequacy of the model in the majority of the traits except for oil content in cross 5 that indicated the presence of epistasis (non-allelic interaction), which was also inferred from the generation means. The failure of three-parameter model may be either due to digenic or higher-order interactions on account of the presence of linkage between interacting genes. Hence, most of the individual scaling tests and joint scaling tests were in complete agreement with each other in reflecting the presence of epistasis.

In the inadequacy of three-parameter model the estimates of the mean (m), additive effect (d), dominance effect (h), additive x additive I additive x dominance (j), and dominance x dominance (l) interactions from six generations (P1, P2, F1, F2, BC1, and BC2) were estimated on digenic epistatic model (Table 3). The significant magnitudes of both d (additive) and h (dominance) with significant gene interactions (i, j and l) in cross 2, cross 4 and cross 5 , played an important role in the inheritance of grain yield per plant. The dominance gene action and duplicate type of epistasis is more pronounced as the magnitude of h (dominance) is higher than d (additive) in all the crosses for grain yield per plant. The results corroborate to [8, 9, 10 and 11].

Protein content: The significant magnitudes of both d (additive), h (dominance) and nonallelic interaction i, j, and l in cross 2, l (dominance x dominance) in cross 5, and i (additive x additive), l (dominance x dominance) in cross 6 revealed that additive, dominance and epistatic interactions played a significant role in the inheritance of this character. The magnitude of h (dominance) was found to be higher than d (additive) thus indicating the importance of dominance gene action in the inheritance of protein content in these crosses. The complementary type of epistasis was shown by cross 5 as the magnitude of h and l was found to be of similar sign and in cross 2 and cross 6 the duplicate type of epistasis was observed as the magnitude of h and l was of opposite sign. Additive effects were significant for cross 1, cross 3 and cross 4 as well as epistatic interactions played a significant role in the inheritance of this trait it was also revealed that the significant magnitude of l and nonsignificant magnitude of h indicated the dispersal of alleles in the parents.

Tryptophan content: The significant magnitude of d (additive) and l (dominance x dominance) genetic components in cross 1 and cross 2 and d (additive) and j (additive x dominance) in cross 4 indicates the prevalence of additive gene action as well as epistatic interactions played a significant role in the inheritance of this character. The significant magnitudes of both d (additive) and h (dominance) and nonallelic interaction (i, j, and l) in cross 3 and cross 6 played a significant role in inheritance of tryptophan content. In cross 5 the significant magnitude of h (dominance), as well as i (additive × additive) and l (dominance x dominance) type of interaction, indicates the prevalence of dominant gene action in inheritance of this character. The opposite signs of h (dominance) and l (dominance x dominance) indicate the presence of a duplicate type of epistasis in cross 3, cross 5 and cross 6.

Table 1: Generation means and standard error (S.E) of yield and quality characters in various maize crosses.

Characters	Crosses	Mean ±S.E					
		P1	P2	F1	F2	BC1	BC2
Grain yield per plant	HKI 209 × HKI 1128	58.22±1.91	45.96±2.12	108.25±2.58	83.21±5.00	46.80±1.84	60.708±1.77
	HKI 209 × HKI 163	65.29±0.50	53.65±0.76	120.10±2.16	91.94±2.75	65.810±0.38	55.22±0.59
	HKI 1332 × HKI 1128	55.22±0.84	55.42±0.44	115.57±2.20	78.42±2.72	59.20±0.61	55.60±0.72
	HKI 1332 × HKI 163	68.00±0.30	60.38±0.57	99.13±0.46	81.14±3.34	68.72±0.50	61.45±0.62
	HKI 325-17AN × HKI 1128	65.61±0.42	59.21±0.49	110.10±0.85	92.29±2.48	68.14±0.21	62.45±0.30
	HKI 325-17AN × HKI 163	75.44±1.13	66.20±0.97	116.16±2.38	99.26±3.43	81.33±2.935	60.41±15.18
Protein content (%)	HKI 209 × HKI 1128	8.66±0.06	9.23±0.18	10.66±0.35	9.67±0.20	8.42±0.11	9.36±0.11
	HKI 209 × HKI 163	9.23±0.08	9.90±0.06	11.33±0.21	10.90±0.31	9.32±0.07	9.98±0.03
	HKI 1332 × HKI 1128	9.30±0.07	9.84±0.09	11.30±0.14	10.10±0.18	9.67±0.05	9.93±0.07
	HKI 1332 × HKI 163	9.23±0.02	8.55±0.03	9.82±0.17	9.04±0.14	9.16±0.02	8.70±0.02
	HKI 325-17AN × HKI 1128	8.52±0.04	10.04±0.05	11.30±0.07	9.09±0.08	8.80±0.08	9.59±0.14
	HKI 325-17AN × HKI 163	8.40±0.03	8.78±0.18	10.30±0.02	9.80±0.21	8.42±0.03	8.94±0.03
Tryptophan content (%)	HKI 209 × HKI 1128	0.49±0.01	0.41±0.02	0.61±0.01	0.49±0.01	0.52±0.01	0.41±0.005
	HKI 209 × HKI 163	0.44±0.02	0.33±0.02	0.61±0.02	0.44±0.02	0.45±0.01	0.38±0.02
	HKI 1332 × HKI 1128	0.41±0.02	0.34±0.01	0.62±0.02	0.56±0.01	0.46±0.01	0.39±0.02
	HKI 1332 × HKI 163	0.59±0.01	0.80±0.01	0.74±0.02	0.68±0.01	0.57±0.01	0.81±0.02

	HKI 325-17AN × HKI 1128	0.53±0.01	0.49±0.009	0.60±0.01	0.59±0.012	0.52±0.012	0.50±0.005
	HKI 325-17AN × HKI 163	0.54±0.004	0.60±0.006	0.78±0.003	0.69±0.013	0.56±0.006	0.62±0.002
Oil content (%)	HKI 209 × HKI 1128	3.97±0.04	4.49±0.13	4.87±0.04	4.32±0.07	3.96±0.02	4.67±0.052
	HKI 209 × HKI 163	3.55±0.04	3.85±0.04	4.96±0.03	3.63±0.08	3.59±0.02	3.84±0.02
	HKI 1332 × HKI 1128	3.93±0.05	3.61±0.02	4.70±0.06	4.20±0.11	3.84±0.02	3.64±0.03
	HKI 1332 × HKI 163	4.37±0.02	3.77±0.08	4.49±0.01	4.141±0.07	4.36±0.01	3.81±0.02
	HKI 325-17AN × HKI 1128	4.57±0.02	4.21±0.03	4.93±0.02	4.62±0.07	4.56±0.15	4.52±0.02
	HKI 325-17AN × HKI 163	4.64±0.01	4.80±0.016	5.25±0.018	4.52±0.097	4.95±0.041	4.94±0.017
Starch content (%)	HKI 209 × HKI 1128	69.65±0.45	67.18±0.51	73.25±0.19	70.11±0.40	70.20±0.13	67.45±0.755
	HKI 209 × HKI 163	68.73±0.09	73.54±0.04	78.52±0.01	76.98±0.97	67.83±0.00	73.72±0.01
	HKI 1332 × HKI 1128	72.26±0.05	73.60±0.06	79.05±0.41	76.16±0.70	71.69±0.50	74.03±0.33
	HKI 1332 × HKI 163	72.15±0.13	73.24±0.29	81.87±0.75	75.61±0.86	71.23±1.68	73.62±0.04
	HKI 325-17AN × HKI 1128	74.68±0.12	76.41±0.05	78.62±0.06	77.12±0.17	67.83±0.03	73.72±0.01
	HKI 325-17AN × HKI 163	76.66±0.21	75.42±0.154	77.55±0.149	71.90±0.839	74.66±0.075	76.50±0.015

Oil content: The adequacy of three-parameter models (additive-dominance model) is obvious from the nonsignificant estimates of χ^2 for oil content in cross 5 (Table 2). Both d (additive) and h (dominance) were found significant for this cross, however, the magnitude of h (dominance) was higher than d (additive). Additive effects as well as j (additive x dominance) and l (dominance x dominance) type of interaction were significant for cross 1 and cross 4 whereas h (dominance) effect with i (additive x additive) and l (dominance x dominance) type of interaction were favored in cross 6 for the inheritance of oil content. Also in cross 1 and cross 4 the significant estimates of l (dominance x dominance) and nonsignificant estimates of h (dominance) indicated the dispersal of alleles in the parents. In cross 2 and cross 3 the significant magnitudes of both d (additive) and h (dominance) and nonallelic interaction (j and l in cross 2, i and l in cross 3) revealed that additive, dominance and interactions played a significant role in the inheritance of this character in these crosses however the magnitude of dominance effect was more pronounced. A duplicate type of epistasis was observed in cross 3 and cross 6, whereas, a complementary type of epistasis was recorded for cross 2.

Starch content: Additive effects were significant for cross 1 and cross 2 as well as epistatic interactions of all types *i.e* i (additive × additive), j (additive x dominance) and l (dominance x dominance) played a significant role in the inheritance of this trait (Table 4). Also in cross 1 and cross 2, the nonsignificant estimates of h (dominance) and the significant estimates of l (dominance x dominance) indicated the dispersal of alleles in the parents. The significant magnitudes of both d (additive) and h (dominance) and all nonallelic interactions (i, j and l) in cross 4, cross 5 and cross 6 revealed that additive, dominance and interactions played a significant role in the inheritance of this character in these crosses. Whereas, dominance gene action was evident in cross 3 where the magnitude of h (dominance) and i (additive × additive) and l (dominance x dominance) type of nonallelic interactions were found significant. In 4 crosses *viz.,* cross 3, cross 4, cross 5 and cross 6, the magnitudes for genetic components of dominance (h) and dominance x dominance (l) were exhibited with opposite signs and of significant nature. It could, therefore, be concluded that the involvement of duplicate types of non-allelic gene interactions was prominent to explain the inheritance of starch content.

For the characters, in individual crosses, where the relative magnitude of additive estimates was smaller as compared to dominance effects, suggested that additive gene effects made only a minor contribution to the inheritance of those characters. The prevalence of dominant genetic effects is more helpful in the formation of superior maize hybrids. For traits, in cases where dominance was of major importance, the trait could be successfully utilized in the development of hybrids. The frequent appearance of epistasis (additive x additive [i], additive x dominance [j] and dominance x dominance [l]) was observed for most of the characters and in most of the crosses, thus, indicating the greater genetic diversity in the parents involved in the formation of these crosses. The preponderance of additive x additive (i-type) epistasis or gene interaction is indicative of good potential in the improvement of this particular parameter in the breeding material for a similar type of environment which further suggested that these traits in the population may be improved through random mating of the selected desirable plants followed by selection. This approach will lead to the exploitation of additive (d); additive x additive (i-type) of gene effects and interactions in the populations. The high frequency of occurrence of dominance (h) and dominance x dominance (l-type) gene effects and interactions may paradoxically suggest the exploitation of heterosis. However, a close examination for the sign of 'h' and 'l' type of epistasis revealed that the magnitude of the two if found in opposite directions imply thereby antagonistic effects in heterosis expression because the opposite signs of h and l counterbalance each other, thus leading to reduced heterosis [12].

Along with grain yield, the quality of maize crops is equally important, because of the increasing demand for quality protein maize day by day. Therefore it can be concluded that, the present study indicated the presence of favourable epistatic gene combinations in all the crosses for all the traits. All types of gene actions and interactions were found to be important in controlling the inheritance of grain yield in these crosses. Among these effects, dominance and duplicate type of epistatic effects were found to contribute more to the inheritance of this trait than additive effects alone. In crosses where dominance was of major importance, the trait could be successfully utilized for the exploitation of hybrid vigor during the formation of hybrids. Some additive and additive x additive effects were seen in all of these crosses and they were of significant magnitude,

and therefore gain from selection could be possible. For protein content, additive effects were significant as well as epistatic interactions played a significant role in the inheritance of this trait. Both additive and dominant gene effects played a significant role but the predominance of the dominance gene effect was observed thus, indicated inheritance was governed by dominant gene action along with digenic interactions. The nonallelic interaction of duplicate type and complementary type was also observed where continuous directional selection can lead to the evolution of complementary gene action in genetically diverse inbred lines. Both additive and h dominance and non allelic interactions (i, j and l) were observed for tryptophan content, thus, indicating a significant role in the inheritance of this trait. The prevalence of additive gene effects was observed in three crosses. Nonallelic interactions of duplicate type was also reported in three crosses, where dominance component (h) and dominance x dominance (l) had opposite signs. The presence of duplicate epistasis in all three crosses for the trait can hinder progress and make it difficult to fix genotypes at a high level of manifestation.

For oil content, the prevalence of additive gene effects was observed as well as dominance gene effects were also observed with the duplicate type of digenic nonallelic interaction. Both d (additive) and h (dominance) and digenic nonallelic interactions of complementary type and duplicate type were observed. The adequacy of three-parameter models (additive-dominance model) was obvious from the nonsignificant estimates of χ^2 for oil content in HKI 325-17AN × HKI 1128, indicating that for those characters wherever the digenic model has been found as adequate, for the most part the characters are ascertained wherever there has been a preponderance of both 'additive' and 'dominance' components and among epistatic components mostly 'i' type (additive × additive) and 'l' type (dominance × dominance) epistatis contributed significantly towards the gene effects. Additive effects were significant for two crosses for starch content, as well as epistatic interactions of all the 3 types (i, j and l) played a significant role in the inheritance of this trait. Both d (additive) and h (dominance) and digenic nonallelic interaction of duplicate type were observed in four crosses. However, the predominance of additive gene effect was observed in one cross and a dominant gene effect was observed in three crosses. For all the traits studied, all types of gene action effects (d, h and epistasis) were highly significant or significant, while dominance × dominance component (l) gene effect also played a major role in the inheritance of the studied traits. Among the individual epistatic gene effects, additive × additive (i) and dominance × dominance (l) effects appear to contribute more to the performance of most traits and crosses than do the additive × dominance (j) gene effect except for starch content where all the three types (i, j, and l) played a significant role in the inheritance of this trait.

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Conflict of interest

No potential conflict of interest was reported by the author.

Table 2: Estimates of different scaling tests for yield and quality traits in different generations of maize hybrids

	Crosses	Scaling Tests				Joint Scaling Test (Three Parameter Model)			
		A	B	C	D	m	d	h	χ^2 (df = 3)
Grain yield per plant	HKI 209 × HKI 1128	72.87*±4.88	32.80*±4.88	-12.14±20.85	58.91*±10.32	45.83*±1.33	-2.10±1.24	40.30*±2.70	241.53**
	HKI 209 × HKI 163	53.77*±2.35	63.32*±2.58	-8.63±11.87	62.86*±5.55	57.10*±0.44	-7.07*±0.38	13.42*±1.01	744.82**
	HKI 1332 × HKI 1128	56.39*±2.69	59.78*±2.67	32.09*±11.78	42.04*±5.28	55.35*±0.45	-1.03*±0.43	14.19*±1.22	599.26**
	HKI 1332 × HKI 163	29.69*±1.15	36.60*±1.46	2.07±13.42	32.11*±6.73	75.36*±0.20	-1.61*±0.12	2.14*±0.41	164.41**
	HKI 325-17AN × HKI 1128	39.44*±1.05	44.42*±1.16	-24.11*±10.10	53.98*±4.98	57.88*±0.31	-3.74*±0.25	20.94*±0.65	1878.4**
	HKI 325-17AN × HKI 163	28.95*±6.43	61.55*±30.49	-28.14*±14.60	56.78*±16.92	184.39*±33.85	4.62*±0.74	-272.30*±96.85	28.874**
Protein content	HKI 209 × HKI 1128	2.48*±0.42	1.18*±0.45	0.50±1.09	1.58*±0.44	9.00*±0.08	0.40*±0.08	0.24±0.21	46.09**
	HKI 209 × HKI 163	1.92*±0.27	1.21*±0.23	-1.83±1.34	2.51*±0.64	9.47*±0.05	0.41*±0.04	0.63*±0.11	62.41**
	HKI 1332 × HKI 1128	1.25*±0.19	1.28*±0.23	1.31±0.82	0.61±0.39	9.44*±0.06	0.28*±0.05	1.07*±0.12	50.23**
	HKI 1332 × HKI 163	0.73*±0.19	0.96*±0.19	1.39*±0.69	0.22±0.29	8.87*±0.02	-0.37*±0.02	0.17*±0.05	28.3**
	HKI 325-17AN × HKI 1128	2.22*±0.18	2.16*±0.30	4.79*±0.39	-0.20±0.24	9.15*±0.03	0.78*±0.03	1.46*±0.08	274.73**
	HKI 325-17AN × HKI 163	1.85*±0.08	1.19*±0.20	-1.78*±0.88	2.22*±0.43	8.00*±0.04	-0.03±0.04	2.06±*0.05	579.9**
Tryptophan content	HKI 209 × HKI 1128	0.06*±0.03	0.20*±0.03	0.15*±0.07	0.05±0.03	0.38*±0.01	-0.11*±0.01	0.20*±0.02	44.86**
	HKI 209 × HKI 163	0.16*±0.05	0.19*±0.06	0.23±0.13	0.06±0.07	0.36*±0.02	-0.04*±0.01	0.19*±0.03	15.21**
	HKI 1332 × HKI 1128	0.12*±0.05	0.19*±0.04	-0.25*±0.08	0.28*±0.04	0.38*±0.01	-0.04*±0.01	0.23*±0.02	55.32**
	HKI 1332 × HKI 163	0.20*±0.04	-0.09±0.05	0.15±0.09	-0.02±0.05	0.69*±0.01	0.12*±0.01	0.00±0.02	38.18**

	HKI 325-17AN × HKI 1128	0.09*±0.03	0.10*±0.02	-0.14*±0.05	0.16*±0.03	0.50*±0.01	-0.03*±0.01	0.08*±0.01	63.38**
	HKI 325-17AN × HKI 163	0.19*±0.01	0.14*±0.01	-0.07±0.05	0.20*±0.03	0.54*±0.003	0.01*±0.003	0.21*±0.005	462.7**
Oil content	**HKI 209 × HKI 1128**	0.92*±0.08	0.01±0.17	0.91*±0.35	0.01±0.16	4.14*±0.05	0.49*±0.04	0.46*±0.07	151.29 **
	HKI 209 × HKI 163	1.33*±0.07	1.13*±0.08	2.79*±0.36	-0.16±0.17	3.37*±0.02	0.25*±0.02	1.07*±0.05	472.5 **
	HKI 1332 × HKI 1128	0.96*±0.10	1.03*±0.01	0.12±0.50	0.93*±0.24	3.66*±0.03	-0.01*±0.02	0.39*±0.06	147.99 **
	HKI 1332 × HKI 163	0.14*±0.04	0.64*±0.09	0.57±0.31	0.10±0.15	3.78*±0.02	-0.55*±0.01	0.66*±0.03	58.2 **
	HKI 325-17AN × HKI 1128	0.38±0.30	0.09±0.06	0.15±0.32	0.16±0.22	4.37*±0.02	-0.19*±0.02	0.55*±0.03	3.47**
	HKI 325-17AN × HKI 163	-0.01±0.08	0.17*±0.04	1.86*±0.40	-0.85*±0.20	4.71*±0.01	0.07*±0.01	0.50*±0.02	37.6**
Starch content	**HKI 209 × HKI 1128**	2.50*±0.56	5.52*±1.61	2.87±1.80	2.57*±1.11	67.36*±0.27	-71.00*±0.27	5.51*±0.37	30.05**
	HKI 209 × HKI 163	11.57*±3.45	7.87*±0.81	1.18±4.18	9.13*±2.56	72.17*±0.15	0.02±0.15	2.96*±0.42	107.34**
	HKI 1332 × HKI 1128	7.93*±1.09	4.59*±0.78	-0.66±2.95	6.59*±1.54	72.92*±0.04	0.67*±0.04	4.26*±0.33	75.35**
	HKI 1332 × HKI 163	11.60*±0.11	4.61*±0.06	-3.15±3.46	9.68*±1.73	66.25*±0.03	5.11*±0.03	11.45*±0.04	165.90**
	HKI 325-17AN × HKI 1128	3.98*±0.204	2.05*±0.09	-0.15±0.70	3.08*±0.35	74.64*±0.06	1.04*±0.05	2.86*±0.08	794.46**
	HKI 325-17AN × HKI 163	0.38±0.43	1.68*±0.39	19.61*±3.38	-8.77*±1.69	75.86*±0.12	-0.72*±0.11	1.37*±0.20	49.70**

df = degrees of freedom, calculated as the number of generations minus the number of estimated genetic parameters
**, **- significant by the t-test at the 5% and 1% probability level, respectively.*

Table 3: Estimates of genetic effects for yield and quality traits in different generations of maize

hybrids OR Table 3: Estimates of generation mean parameters, mean (m), additive (d), dominance (h), additive ×additive (i), additive × dominance (j) dominance × dominance (l) for yield and quality traits in different generations of maize hybrids

Crosses		Components							
		m	**d**	**h**	**i**	**j**	**l**	**χ^2 (df = 3)**	**Type of Epistasis**
Grain yield per plant	**HKI 209 × HKI 1128**	83.21*±5.001	-13.90*±2.559	-61.66*±20.859	-117.81*±20.649	4.77±5.863	223.49*±23.24	241.53**	Duplicate
	HKI 209 × HKI 163	91.95*±2.755	10.58*±0.706	-65.09*±11.328	-125.73*±11.109	4.77*±1.683	242.82*±12.21	744.82**	Duplicate
	HKI 1332 × HKI 1128	78.42*±2.721	3.59*±0.969	-23.82*±11.284	-84.08*±11.056	3.49±2.16	196.25*±12.40	599.26**	Duplicate
	HKI 1332 × HKI 163	81.14*±3.343	-7.27*±0.805	-29.28*±13.48	-64.22*±13.469	-11.07*±1.73	130.52*±13.80	164.41**	Duplicate
	HKI 325-17AN × HKI 1128	92.29*±2.485	-5.69*±0.373	-60.28*±10.01	-107.97*±9.967	-8.89*±0.99	191.82*±10.22	1878.4**	Duplicate
	HKI 325-17AN × HKI 163	99.26*±3.431	20.92*±15.47	-68.23*±33.94	-113.56*±33.847	16.30±30.97	204.06*±63.58	28.874**	Duplicate
Protein content	**HKI 209 × HKI 1128**	9.68*±0.20	-0.94*±0.16	-1.40±0.95	-3.12*±0.88	-0.82*±0.37	6.81*±1.26	46.09**	-
	HKI 209 × HKI 163	10.91*±0.32	-1.66*±0.08	-4.73*±1.30	-7.00*±1.28	-0.82*±0.19	11.19*±1.38	62.41**	Duplicate
	HKI 1332 × HKI 1128	10.11*±0.19	-0.26*±0.01	0.51±0.79	-1.22±0.78	0.01±0.23	3.75*±0.90	50.23**	-
	HKI 1332 × HKI 163	9.04*±0.15	0.45*±0.04	0.49±0.62	-0.44±0.59	0.23*±0.08	2.13*±0.70	28.3**	-
	HKI 325-17AN × HKI 1128	9.01*±0.09	-0.79*±0.16	2.43*±0.48	0.41±0.48	-0.03±0.33	3.97*±0.76	274.73**	Complementary
	HKI 325-17AN × HKI 163	9.71*±0.21	-0.52*±0.05	-2.74*±0.87	-4.44*±0.86	-0.33±0.22	7.49*±0.90	579.9**	Duplicate
Tryptophan content	**HKI 209 × HKI 1128**	0.50*±0.01	0.11*±0.01	0.06±0.02	-0.11±0.06	0.02±0.04	0.37*±0.08	44.86**	-
	HKI 209 × HKI 163	0.44*±0.03	0.07*±0.03	0.12±0.14	-0.10±0.13	0.01±0.07	0.46*±0.18	15.21**	-
	HKI 1332 × HKI 1128	0.57*±0.01	0.20*±0.02	-0.13*±0.08	-0.30*±0.08	0.09±0.05	0.50*±0.13	55.32**	Duplicate
	HKI 1332 × HKI 163	0.68*±0.02	-0.25*±0.03	0.10±0.09	0.04±0.09	-0.14*±0.06	0.06±0.14	38.18**	-
	HKI 325-17AN × HKI 1128	0.60*±0.01	0.02±0.01	-0.23*±0.05	-0.33*±0.05	0.00±0.03	0.52*±0.07	63.38**	Duplicate
	HKI 325-17AN × HKI 163	0.696*±0.013	-0.06*±0.01	-0.19*±0.05	-0.40*±0.05	-0.03*±0.01	0.72*±0.06	462.7**	Duplicate
	HKI 209 × HKI 1128	4.32*±0.08	-0.72*±0.057	0.61±0.34	-0.03±0.33	-0.40*±0.18	0.96*±0.42	151.29 **	-

Oil content	HKI 209 × HKI 163	3.64*±0.09	-0.25*±0.03	1.59*±0.35	0.34±0.35	-0.40*±0.09	2.13*±0.38	472.5 **	Complementary
	HKI 1332 × HKI 1128	4.2*1±0.12	0.32*±0.04	-2.08*±0.49	-2.91*±0.48	-0.58±0.01	6.14*±0.52	147.99 **	Duplicate
	HKI 1332 × HKI 163	4.14*±0.07	0.55*±0.02	0.22±0.30	-0.20±0.30	0.25*±0.09	0.98*±0.32	58.2 **	-
	HKI 325-17AN × HKI 1128	4.63*±0.08	0.04±0.15	0.22±0.44	-0.32±0.44	-0.14±0.31	0.79±0.69	3.47**	-
	HKI 325-17AN × HKI 163	4.52*±0.01	-0.09±0.04	2.03*±0.40	1.50*±0.40	-0.01±0.09	-1.15*±0.43	37.6**	Duplicate
Starch content	HKI 209 × HKI 1128	70.11*±0.40	2.75*±0.77	-0.30±2.26	-5.13*±2.23	-8.30*±1.68	13.1*5±3.55	30.05**	-
	HKI 209 × HKI 163	76.98*±0.97	-5.89*±1.68	-17.43±5.19	-18.25*±5.13	-8.30*±3.38	41.02*±7.91	107.34**	-
	HKI 1332 × HKI 1128	76.16*±0.71	-2.34*±0.60	-7.06*±3.11	-13.18*±3.08	-1.67±1.21	25.70*±3.82	75.35**	Duplicate
	HKI 1332 × HKI 163	75.62*±0.86	-2.39*±0.03	-3.60*±3.46	-19.36*±3.46	-1.84*±0.12	32.20*±3.47	165.90**	Duplicate
	HKI 325-17AN × HKI 1128	77.12*±0.17	-5.90*±0.08	-3.09*±0.70	-6.17*±0.70	-5.03*±0.20	50.60*±0.77	794.46**	Duplicate
	HKI 325-17AN × HKI 163	71.89*±0.84	-2.03*±0.24	17.05*±3.40	17.54*±3.39	-1.45*±0.54	-11.46*±3.51	49.70**	Duplicate

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