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Generation mean analysis in maize (*Zea mays*) for yields and yield attributing traits

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ABSTRACT

The nature of gene action involved is mainly responsible for the genetic improvement of any crop. Generation means analysis for maize (*Zea mays* L.) yield and its traits for six generations, i.e. P_1, P_2 F_1, F_2, BC_1 and BC_2 of six crosses evaluated at Karnal. Significant individual and joint scaling tests indicated inadequacy of three parameter models and presence of epistasis in all characters indicating greater genetic variation in parents. However, only shelling percentage in HKI 209 × HKI 163 showed additive-dominance. The presence of duplicate form of non-allelic gene interactions was prominent, except for days to maturity and cob diameter in HKI 325-17AN × HKI 163, cob length in HKI 209 × HKI 163 and shelling percentage in HKI 1332 × HKI 163 where complementary gene action is recorded. It suggests selection from F_3 generation onwards for character improvement. Dominance and duplicate type of epistatic effects were found to be more prominent for inheritance than additive effects alone for grain yield/plant, grains/cob, and plant height suggesting the reciprocal recurrent selection or bi-parental mating design to improve in these characters. In crosses where dominance was of major importance, the trait could be successfully utilized for the exploitation of hybrid vigour. Some significant additive and additive × additive effects were recorded in all of these crosses, and therefore gain from selection could be possible, fixable and heritable epistasis could be effectively used in the selection of superior inbred lines.

Keywords: Additive-dominance effect, Generation means, Gene effects, Maize, Non-allelic interactions

In the genetic improvement of any crop, the nature of gene action involved is mainly responsible for implementation of breeding method for quantitative traits. In subsequent generations, causes of genetic variability may be examined to predict the genetic regulation of various multi-genetic parameters (Ali *et al*. 2019). For better understanding of the gene action involved in the expression of heterosis, the information on genetic variances, levels of dominance, and the importance of genetic effects have contributed significantly. However, the nature of gene action involved in the expression of heterosis for the grain yield of elite maize hybrids remains unresolved. The development of dominantce gene action would benefit the production of hybrids whereas additive gene action designating the standard procedures for selection would be effective in bringing about advantageous changes in character (Edwards *et al.* 1975, Ewool *et al.* 2020). In classical breeding systems, grain yield would be improved by efficient breeding procedures that make use of additive genetic variance and non-allelic interaction. The success of any breeding programme lies in thorough understanding of the genetic architecture of the genotypes and the nature of the gene action (Lingaiah *et al*. 2020). Therefore, understanding concerning genetic composition of a character helps the breeders to set up their breeding programs. To accomplish this, the breeder will need basic information on the inheritance of grain yield and its closely related components to exploit the current genetic variability present in breeding material for grain yield.

Many mathematical models for estimating gene effects presume that epistasis is of low significance. However, the presence or absence of epistasis can be defined by generation mean analysis using a scaling test that accurately tests epistasis, whether complementary or duplicate at the digenic level. Therefore, generation mean analysis is a valuable technique to estimate the key genetic effects involved in the expression of quantitative characteristics such as yield and its components. Therefore, present study has been designed to understand the nature and inheritance of grain yield and quality traits of maize (*Zea mays* L.) for proper choice of breeding procedures in developing maize hybrids

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with increased grain yield.

MATERIALS AND METHODS

The experiment was conducted at CCS Haryana Agricultural University, Research Station, Karnal, during 2013–2014 and 2015–2016. Six crosses, viz. 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) were attempted in *kharif* 2013 to produce the F_1 seeds where three inbred lines were used as female (HKI 209, HKI 1332 and HKI 325-17AN) and two inbred lines were used as male (HKI 1128 and HKI 163). In *rabi* 2013–2014 and *kharif* 2014, F_1s were sown along with five parental inbred lines and self pollinated to produce F_2 seeds. Backcrosses, BC_1 and BC_2 of six crosses were also made within the stipulated period.

The experiment was laid out in randomized complete block design (RCBD) with three replications during *kharif* 2015 and 2016. The experimental material consisted of five parents, six F_1, their F_2, BC_1 and BC_2, of six crosses. The parents, F_1's, F_2's, and back crosses were randomized separately in each replication. The P_1, P_2, F_1 were planted in one row whereas, the BC_1, BC_2 were planted in two rows and F_2 in 10 rows. The planting geometry was kept with 75 cm × 20 cm. Uniform agronomical standard practices were adopted in order to obtain the good phenotypic expression of characters. The observations were recorded on eleven quantitative characters, viz. days to 50% tasselling, days to 50% silking, days to maturity, plant height (cm), ear height (cm), cob length (cm), cob diameter (cm), grains/cob, 100 grain weight (g), grain yield/plant (g), shelling percentage, from 10 plants of parents and F_1; 20 plants of backcrosses and all the plants from F_2 generations.

Pooled mean data were first tested for non-allelic interaction by Individual scaling test- A, B, C and D given by Mather (1949). Further analysis of data was performed according to the method of "Joint scaling test" given by Cavalli (1952). To compute gene effects for grain yield and its components with six basic generations, Mather's (1949) three parameter model and Hayman's (1958) six parameter models were used in case of inadequacy of three parameter model. Generation mean analysis was performed for characters showing significant variations ($P \leq 0.05$) among generations.

RESULTS AND DISCUSSSION

Genetic analysis of generation means with individual and joint scaling test depicted presence of epistasis (Table 1). Significant chi square (χ^2) values and failure of simple additive-dominance model in majority of the traits except for shelling percentage in HKI 209 × HKI 163 showed the adequacy of three parameter model. The failure of three parameter model may be either due to digenic or higher order interaction. So, a six parameter model applied to accommodate epistatic and other interactions (Table 2). In three crosses (C2, C3, C5), the predominance of additive gene effect (negatively significant and desirable direction) was observed for days to 50% tasseling and hence it can be exploited effectively by selection. Significant additive effects (d) in C1, C4 and C6 showed that additive effects were found prominent in controlling inheritance of this trait and the results confirmed the earlier reports of Noor *et al*. (2018). However, C3 and C5 showed presence of both dominance as well as additive gene effects and there was partial agreement with the conclusions reached by Irshad-ul-haq *et al.* (2010). Frequent appearance of all types of epistasis (i, j and l) was observed for C2 to C5. Predominance of additive gene effects (negatively significant and desirable direction) was reported for days to 50% silking in all crosses except for C1 and C3. The dominance gene effects were also observed for days to 50% silking in C1, C3, C4 and C6. Prevalence of additive × dominance genes interaction was observed in all the crosses except C5. The additive effects observed for days to maturity were in close conformity with Sher *et al*. (2012). However, the dominance effect was more important than additive effects in governing the inheritance of this trait as there was prevalence of dominance effects in C1, C2, C3, C4 and C5.

Dominant gene effects for plant height were observed in all the crosses except C1 which is in agreement with Irshad-ul-haq*et al.* (2010). Whereas, additive gene effects were more pronounced for ear height in C1, C2 and C6. The dominance × dominance gene interactions and duplicate type of epistasis in all the crosses except C1 for plant height and C1 and C 6 for ear height showed dispersal of alleles that corroborates to Irshad-ul-haq *et al.* (2010). Dominant gene effects and additive × dominance genes interaction were observed for cob length in all the crosses except C1 and C3 (Shahrokhi *et al*. 2013). Duplicate type gene interactions in C4, C4 and C6 and complementary type in C2 were important for controlling inheritance of cob length which were in accordance with Alam*et al.* (2008). Complementary type of epistats is in C6 and dominance x dominance effects in all the crosses were of primary importance for controlling inheritance of cob diameter and that corroborated to Ali *et al*. (2007). Prevalence of dominant gene effects as well as digenic interactions of duplicate type were observed for number of grains per cob in all the crosses. Relative proportion of epistatic gene effects varied among six crosses for this trait suggesting importance of both additive and dominant effects, in conformity with Irshad-ul-haq *et al.* (2010). In three crosses (C1, C2, C4), the predominance of additive gene effect was observed for hundred grain-weight whereas dominance gene effect with duplicate type of epistasis was found in C5 and C6 that were in accordance with the reports of Noor *et al*. (2018). The additive x additive gene interactions in all the crosses except C1 indicated increase in 100-grain weight and is possible to fix during next generations.

All additive (C2, C3 and C6), dominant (C1, C4, and C5) and epistatic effects were important in controlling the inheritance of grain yield in all the crosses and corroborate to Noor *et al*. (2018). Prevalence of dominance effects with

Table 1 Estimates of different scaling tests for different traits of six maize crosses in different generations of maize hybrids

Trait	Cross	Scaling Test				Joint Scaling Test (Three Parameter Model)			
		A	B	C	D	m	d	h	χ^2 (df = 3)
Days to 50% tasselling	C1	-3.80* ± 0.80	-1.20 ± 1.20	-0.44 ± 2.23	-2.28 ± 1.21	55.90* ± 0.24	-2.09* ± 0.240	-2.32* ± 0.41	23.42**
	C2	-2.33* ± 0.81	-6.33* ± 0.81	-4.00 ± 2.16	-2.33 ± 1.10	55.96* ± 0.22	2.40* ± 0.211	-3.04* ± 0.40	62.7**
	C3	-1.20* ± 0.60	-5.40* ± 0.82	0.44 ± 1.36	-3.52* ± 0.75	55.74* ± 0.16	1.26* ± 0.160	-3.65* ± 0.29	47.16**
	C4	-0.40 ± 0.49	-6.40* ± 0.88	2.16 ± 1.20	-4.48* ± 0.69	55.88* ± 0.17	-0.27 ± 0.17	-3.88* ± 0.27	62.42**
	C5	-2.80* ± 0.67	-0.60* ± 0.29	2.52 ± 1.33	-2.96* ± 0.66	56.03* ± 0.21	-2.12* ± 0.204	-3.20* ± 0.352	29.46**
	C6	-2.20* ± 0.60	0.40 ± 0.66	-1.64 ± 1.49	-0.00 ± 0.72	54.64* ± 0.21	-2.07* ± 0.202	-1.95* ± 0.36	14.91**
Days to 50 % silking	C1	5.40* ± 0.70	0.20 ± 1.00	1.44 ± 2.20	2.08 ± 1.09	57.529* ± 0.291	-0.342* ± 0.276	-1.496* ± 0.467	18.99**
	C2	-2.33 ± 1.24	-5.66* ± 0.07	-2.80 ± 2.27	-2.60* ± 1.38	56.736* ± 0.303	2.460* ± 0.270	-0.053 ± 0.671	59.51**
	C3	-1.60 ± 0.92	-5.60* ± 1.04	1.12 ± 1.61	-4.16* ± 0.84	58.288* ± 0.299	2.269* ± 0.303	2.269* ± 0.479	39.12**
	C4	-1.80 ± 1.02	-5.60* ± 0.90	1.72 ± 1.34	-4.56* ± 0.87	58.666* ± 0.19	0.878* ± 0.195	-3.665* ± 0.289	47.11**
	C5	-3.00* ± 0.69	-0.40 ± 0.69	2.04 ± 1.48	-2.72* ± 0.69	58.682* ± 0.203	-1.882* ± 0.188	-2.373* ± 0.401	29.10**
	C6	-2.40* ± 0.53	1.40* ± 0.87	-2.52 ± 1.50	0.76 ± 0.79	57.44* ± 0.199	-1.526* ± 0.196	-1.397* ± 0.326	26.63**
Days to maturity	C1	2.00* ± 0.60	-3.80* ± 0.66	-1.08 ± 2.20	-0.36 ± 1.09	86.48* ± 0.22	-0.32 ± 0.20	-3.72* ± 0.36	50.88
	C2	-0.66 ± 2.62	-9.66* ± 2.28	9.80 ± 3.14	-10.06* ± 1.81	89.86* ± 0.62	3.37* ± 0.64	-4.65* ± 1.13	46.82
	C3	-0.60 ± 2.43	-5.40* ± 1.07	13.60* ± 2.02	-9.80* ± 1.51	89.18* ± 0.30	2.97* ± 0.30	-4.811* ± 0.53	101.07
	C4	4.40 ± 2.46	-7.80* ± 0.96	13.96* ± 2.24	-8.68* ± 1.59	89.46* ± 0.32	-0.33 ± 0.32	-3.91* ± 0.50	131.93
	C5	-4.40* ± 0.63	-0.20 ± 0.68	8.28* ± 1.63	-6.44* ± 0.81	89.50* ± 0.21	-2.38* ± 0.20	-3.75* ± 0.35	94.26
	C6	-1.00 ± 0.60	-0.40 ± 0.60	-6.28* ± 1.29	2.44* ± 0.66	85.13* ± .16	-1.56* ± 0.15	-1.27* ± 0.29	24.25
Plant height	C1	52.80* ± 5.93	73.80* ± 5.35	45.08 ± 30.65	40.76* ± 14.87	135.47* ± 1.73	-16.42* ± 1.43	31.91* ± 3.57	201.64
	C2	123.33* ± 6.62	63.33* ± 6.95	-74.80* ± 16.10	130.73* ± 7.76	107.39* ± 2.13	-5.93* ± 1.99	90.44* ± 3.93	517.22
	C3	85.80* ± 1.02	73.00* ± 1.00	-21.76* ± 10.20	90.28* ± 5.13	120.85* ± 0.23	8.66* ± 0.23	72.08* ± 0.40	135.31
	C4	57.00* ± 4.50	52.60* ± 7.16	-46.16* ± 15.00	77.88* ± 6.40	133.44* ± 1.87	10.74* ± 1.52	17.04* ± 3.25	307.572
	C5	75.80* ± 4.19	61.60* ± 3.61	-59.32* ± 16.32	98.36* ± 8.33	115.91* ± 0.96	5.06* ± 0.94	66.46* ± 1.68	593.57
	C6	71.80* ± 3.63	84.80* ± 2.65	-22.92 ± 19.24	89.76* ± 9.54	119.67* ± 0.96	-13.24* ± 0.87	55.59* ± 1.85	1179.37

Cond.

Table 1 (*Continued*)

Cross		Scaling Test				Joint Scaling Test (Three Parameter Model)			
		A	B	C	D	m	d	h	χ^2 (df = 3)
Ear height	C1	15.40* ± 3.72	39.20* ± 3.22	33.16* ± 13.80	10.72 ± 6.48	66.46* ± 1.09	-19.95* ± 0.88	7.27* ± 2.21	153.49**
	C2	50.66* ± 7.15	-12.00* ± 3.87	-40.53* ± 6.93	39.60* ± 4.08	64.41* ± 1.40	-8.66* ± 1.37	35.60* ± 2.60	117.58**
	C3	20.20* ± 3.92	24.00* ± 3.50	-0.44 ± 5.34	22.32* ± 3.68	64.16* ± 0.32	1.75* ± 0.32	22.21* ± 0.49	73.09**
	C4	21.40* ± 3.79	18.20* ± 4.38	-17.36* ± 7.39	28.48* ± 3.52	62.63* ± 0.64	-3.53 ± 0.64	11.52* ± 1.74	76.50**
	C5	28.40* ± 3.29	20.80* ± 2.16	1.12 ± 8.85	24.04* ± 4.68	5.70* ± 0.65	3.23* ± 0.64	28.56* ± 0.93	160.41**
	C6	-33.20* ± 8.28	47.00* ± 29.34	-34.68* ± 10.32	24.24 ± 15.38	71.22* ± 1.97	1.03 ± 2.05	16.06* ± 3.55	22.95**
Cob length	C1	15.40* ± 3.72	39.20* ± 3.22	33.16* ± 13.80	10.72 ± 6.49	13.22* ± 0.07	-0.70* ± 0.07	2.95* ± 0.12	223.2**
	C2	4.20* ± 0.41	5.46* ± 0.47	-3.21 ± 2.12	6.44* ± 1.06	10.79* ± 0.11	-0.23* ± 0.11	3.44* ± 0.22	210.38**
	C3	4.74* ± 0.38	4.56* ± 0.52	0.12 ± 1.75	4.59* ± 0.90	10.50* ± 0.06	0.32* ± 0.06	4.60* ± 0.17	202.08**
	C4	5.22* ± 0.43	4.68* ± 0.43	-6.62* ± 1.61	8.26* ± 0.75	9.63* ± 0.10	-0.00 ± 0.08	2.52* ± 0.22	261.06**
	C5	6.04* ± 0.22	6.08* ± 0.18	-1.85 ± 1.58	6.98* ± 0.80	9.11* ± 0.05	-0.27* ± 0.05	5.98* ± 0.09	1706.9**
	C6	2.14* ± 0.26	2.62* ± 0.19	3.32* ± 0.51	0.72* ± 0.23	13.01* ± 0.05	-0.09 ± 0.05	1.94* ± 0.12	190.43**
Cob Diameter	C1	1.06* ± 0.25	0.22 ± 0.25	0.50 ± 0.38	0.39* ± 0.16	3.85* ± 0.06	-0.18* ± 0.06	0.30* ± 0.13	17.86**
	C2	1.16* ± 0.27	0.50 ± 0.35	0.68 ± 0.74	0.49 ± 0.36	3.60* ± 0.06	-0.20* ± 0.06	0.45* ± 0.15	18.78**
	C3	0.82* ± 0.21	0.60* ± 0.21	0.80 ± 0.47	0.30 ± 0.22	3.35* ± 0.05	0.06 ± 0.05	0.93* ± 0.12	18.08**
	C4	1.16* ± 0.20	0.68* ± 0.18	1.84* ± 0.52	-0.004 ± 0.27	4.19* ± 0.05	-0.09 ± 0.05	0.85* ± 0.08	50.73**
	C5	0.76* ± 0.18	0.72* ± 0.13	0.61* ± 0.26	0.43* ± 0.13	3.89* ± 0.04	0.14* ± 0.04	0.30* ± 0.08	41.41**
	C6	0.96* ± 0.14	0.84* ± 0.13	1.41* ± 0.37	0.19 ± 0.19	3.49* ± 0.03	-0.12* ± 0.03	0.75* ± 0.07	75.55**
Number of grains per cob	C1	130.60* ± 18.22	188.60* ± 16.91	-175.10* ± 75.26	247.20* ± 37.69	195.26* ± 5.11	-8.92 ± 4.97	161.74* ± 8.83	174.94**
	C2	219.00* ± 14.08	248.30* ± 10.30	-122.50* ± 23.63	294.90* ± 12.61	179.52* ± 3.22	-11.16* ± 3.20	217.47* ± 5.57	916.75**
	C3	192.20* ± 9.96	215.00* ± 7.54	-7.76 ± 79.27	207.40* ± 39.72	180.96* ± 2.02	-12.18* ± 1.97	161.36* ± 4.08	108.89**
	C4	173.60* ± 6.44	173.80* ± 4.26	-43.08 ± 80.07	195.20* ± 40.10	205.84* ± 1.12	-14.34* ± 1.17	135.26* ± 2.35	2088.1**
	C5	184.60* ± 4.57	179.60* ± 4.47	-50.36 ± 45.89	207.30* ± 22.97	210.59* ± 1.05	-7.33* ± 1.02	134.54* ± 2.17	2707.6**
	C6	40.40 ± 32.50	240.80* ± 114.2	-244.80* ± 60.40	263.00 ± 64.59	243.21* ± 10.26	-6.20 ± 10.60	197.98* ± 10.91	24.14**
100 grain weight	C1	4.21* ± 0.54	4.94* ± 0.64	6.69* ± 1.81	1.23 ± 0.82	19.23* ± 0.22	-929* ± 0.16	5.17* ± 0.42	97.58**
	C2	12.44* ± 1.57	2.46 ± 2.25	5.40 ± 2.78	4.75* ± 1.79	18.34* ± 0.41	-1.65* ± 0.42	6.56* ± 0.57	64.43**
	C3	7.14* ± 1.63	6.72* ± 1.16	0.76 ± 3.10	6.55* ± 1.76	17.10* ± 0.27	-1.72* ± 0.27	7.43* ± 0.38	51.41**
	C4	2.98* ± 0.61	5.90* ± 0.42	0.66 ± 1.96	4.11* ± 1.01	19.07* ± 0.15	-1.52* ± 0.15	5.33* ± 0.18	220.40**
	C5	3.21* ± 0.36	5.80* ± 0.47	-1.19 ± 1.34	5.10* ± 0.68	19.42* ± 0.12	-2.05* ± 0.12	5.42* ± 0.21	216.00**
	C6	6.91* ± 1.87	8.44 ± 8.78	-6.21* ± 3.05	9.57* ± 4.55	19.84* ± 0.67	-0.02 ± 0.75	2.84* ± 0.91	20.50**

Cond.

Table 1 (*Concluded*)

Trait	Cross	Scaling Test				Joint Scaling Test (Three Parameter Model)			
		A	B	C	D	m	d	h	χ^2 (df = 3)
Grain yield per plant	C1	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**
	C2	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**
	C3	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**
	C4	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**
	C5	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**
	C6	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**
Shelling percentage	C1	5.41* ± 2.55	6.27* ± 1.23	2.76 ± 4.29	4.46* ± 2.13	74.60* ± 0.58	-1.28* ± 0.55	2.84* ± 0.96	28.51**
	C2	7.10 ± 7.09	1.53 ± 2.10	-0.39 ± 5.03	4.51 ± 3.93	73.84* ± 1.00	2.96* ± 1.02	6.27* ± 1.51	1.66
	C3	5.11* ± 0.57	3.10* ± 0.72	7.38* ± 2.73	0.41 ± 1.36	75.54* ± 0.19	1.17* ± 0.18	3.90* ± 0.36	86.91**
	C4	5.40* ± 0.54	7.27* ± 0.58	13.25* ± 1.51	-0.47 ± 0.60	60.75* ± 0.30	-5.41* ± 0.30	30.80* ± 0.54	1149.5**
	C5	6.74* ± 0.48	7.70* ± 0.29	2.70 ± 1.53	5.87* ± 0.77	76.81* ± 0.09	-1.50* ± 0.09	2.16* ± 0.18	783.77**
	C6	2.86* ± 0.92	2.92* ± 0.64	0.33 ± 2.00	2.72* ± 1.30	77.33* ± 0.22	-0.55* ± 0.21	4.22* ± 0.38	27.68**

C1- HKI 209 × HKI 1128; C2- HKI 209 × HKI 163; C3- HKI 1332 × HKI 1128; C4- HKI 1332 × HKI 163, C5- HKI 325-17AN × HKI 1128; C6- HKI 325-17AN × HKI 163.

Table 2 Estimates of genetic effects for some quantitative traits in six maize crosses

Trait	Cross	Component						χ^2 (df = 3)	Type of Epistasis
		m	d	h	i	j	l		
Days to 50% tasselling	C1	54.36* ± 0.52	3.00* ± 0.63	2.06 ± 2.46	4.56 ± 2.43	6.00 ± 1.37	-9.56* ± 3.37	23.42**	-
	C2	54.50* ± 0.50	-4.00* ± 0.47	1.00 ± 2.24	4.66* ± 2.21	6.00* ± 1.05	-13.33* ± 2.86	62.7**	-
	C3	53.44* ± 0.31	-3.20* ± 0.45	3.14* ± 1.54	7.04* ± 1.52	-2.10* ± 0.96	-13.64* ± 2.25	47.16**	Duplicate
	C4	53.16* ± 0.27	2.80* ± 0.45	0.66 ± 1.42	2.56* ± 1.40	1.30* ± 0.97	-4.36* ± 2.15	62.42**	-
	C5	53.76* ± 0.28	-2.40* ± 0.35	2.76* ± 1.37	6.56* ± 1.33	-3.00* ± 0.86	-13.36* ± 1.92	29.46**	Duplicate
	C6	53.52* ± 0.33	2.80* ± 0.32	2.82 ± 1.50	5.92* ± 1.46	1.10 ± 0.82	-9.32* ± 1.96	14.91**	-
Days to 50 % silking	C1	57.24* ± 0.50	-1.20* ± 0.44	-5.36* ± 2.23	-4.16 ± 2.18	6.33* ± 1.14	9.76* ± 2.84	18.99**	Duplicate
	C2	56.70* ± 0.52	4.00* ± 0.57	1.86 ± 2.41	5.20* ± 2.37	6.33* ± 1.33	-13.20* ± 3.24	59.51**	-
	C3	55.52* ± 0.32	-3.60* ± 0.55	4.72* ± 1.76	8.32* ± 1.69	-2.00* ± 1.32	-15.52* ± 2.72	39.12**	Duplicate
	C4	56.12* ± 0.30	2.40* ± 0.63	5.62* ± 1.77	9.12* ± 1.75	2.90* ± 1.33	-16.52* ± 2.86	47.11**	Duplicate
	C5	56.64* ± 0.30	2.80* ± 0.34	2.74 ± 1.45	5.44* ± 1.38	1.30 ± 0.82	-8.84* ± 2.03	29.10**	-
	C6	57.08* ± 0.34	3.00* ± 0.42	-3.22** ± 1.62	-1.52 ± 1.59	1.90* ± 0.96	0.52 ± 2.26	26.63**	Duplicate

Cond.

Table 2 (*Continued*)

Trait	Cross	m	d	h	i	j	l	χ^2 (df = 3)	Type of Epistasis
		Component							
Days to maturity	C1	82.72* ± 0.52	-1.40* ± 0.31	5.02* ± 2.21	8.72* ± 2.17	3.30* ± 0.82	-10.52 ± 2.54	50.88	Duplicate
	C2	85.30* ± 0.53	1.80* ± 0.39	-4.7* ± 2.29	-3.20 ± 3.61	3.30* ± 3.25	1.80* ± 1.22	46.82	Duplicate
	C3	83.40* ± 0.43	-4.60* ± 1.25	15.20* ± 4.93	19.60* ± 6.45	-2.40* ± 1.21	-25.60* ± 4.75	101.07	Duplicate
	C4	83.96* ± 0.49	3.60* ± 1.24	12.86* ± 3.23	15.36* ± 3.19	4.10 ± 2.59	-20.76* ± 5.47	131.93	Duplicate
	C5	85.28* ± 0.36	3.80* ± 0.34	8.98* ± 1.66	12.88* ± 1.62	2.10* ± 0.86	-17.48* ± 2.14	94.26	Duplicate
	C6	85.72* ± 0.28	6.66* ± 0.34	-6.38* ± 1.37	18.44* ± 1.33	4.49* ± 0.77	-28.78* ± 1.89	24.25	Complementary
Plant height	C1	165.68* ± 7.35	21.80* ± 2.21	-16.82 ± 30.05	-81.52* ± 29.74	6.50 ± 5.81	208.12* ± 31.90	201.64	-
	C2	191.70* ± 3.48	13.60* ± 3.43	-143.9* ± 16.05	-226.0* ± 15.33	6.50 ± 8.48	382.6* ± 21.16	517.22	Duplicate
	C3	173.64* ± 2.54	-13.00* ± 0.63	-102.96* ± 10.26	-180.56* ± 10.25	-19.60* ± 1.35	339.36* ± 10.51	135.31	Duplicate
	C4	176.64* ± 2.98	-12.95* ± 2.29	-131.3* ± 13.58	-203.65* ± 12.80	-7.04 ± 6.312	340.90* ± 17.58	307.572	Duplicate
	C5	174.88* ± 3.99	-5.40* ± 2.38	-91.72* ± 16.74	-148.72* ± 16.65	-2.2 ± 5.19	258.30* ± 18.90	593.57	Duplicate
	C6	180.08* ± 4.70	-18.66* ± 1.568	-110.3* ± 19.18	-215.0* ± 19.07	-29.10* ± 3.78	401.60* ± 20.24	1179.37	Duplicate
Ear height	C1	73.76* ± 3.18	26.00* ± 1.31	2.46 ± 13.25	-21.44 ± 12.97	8.67* ± 3.54	76.04* ± 14.76	153.49**	-
	C2	88.30* ± 1.12	29.00* ± 3.42	-33.53* ± 8.58	-59.20* ± 8.16	8.67 ± 7.58	93.86* ± 15.32	117.58**	Duplicate
	C3	75.76* ± 1.31	0.00 ± 2.59	-22.34* ± 7.39	-44.64* ± 7.37	-1.90 ± 5.22	88.84* ± 11.66	73.09**	Duplicate
	C4	75.64* ± 1.36	2.00 ± 2.24	-39.96* ± 7.47	-56.96* ± 7.04	-1.60 ± 4.68	96.56* ± 11.62	76.50**	Duplicate
	C5	72.72* ± 2.16	-9.00* ± 1.78	-20.88* ± 9.40	-48.08* ± 9.35	-3.80 ± 3.85	97.28* ± 11.32	160.41**	Duplicate
	C6	82.12* ± 1.85	33.20* ± 14.93	-31.38 ± 30.98	-48.48* ± 23.77	40.10 ± 30.26	62.28 ± 60.62	22.95**	-
Cob length	C1	14.40* ± 0.19	0.88* ± 0.15	1.18 ± 0.85	-2.17* ± 0.84	0.92* ± 0.34	8.14* ± 1.03	223.2**	-
	C2	14.42* ± 0.52	0.16 ± 0.24	0.42* ± 0.21	-2.88 ± 2.13	0.08 ± 0.56	7.64* ± 2.35	210.38**	Complementary
	C3	13.55* ± 0.43	-0.28 ± 0.29	-3.35 ± 1.81	-9.18* ± 1.80	-0.47 ± 0.59	18.48* ± 2.10	202.08**	-
	C4	14.38* ± 0.36	-0.18 ± 0.17	-10.89* ± 1.54	-16.52* ± 1.50	-0.27 ± 0.39	26.42* ± 1.75	261.06**	Duplicate
	C5	13.63* ± 0.39	0.36* ± 0.12	-7.59* ± 1.60	-13.97* ± 1.59	0.02 ± 0.27	26.08* ± 1.66	1706.9**	Duplicate
	C6	14.06* ± 0.10	1.07* ± 0.11	-7.02* ± 0.48	-11.46* ± 0.46	0.63* ± 0.25	21.13* ± 0.68	190.43**	Duplicate

Cond.

Table 2 (*Continued*)

Trait	Cross	m	d	h	i	j	l	χ^2 (df = 3)	Type of Epistasis
Cob Diameter	C1	4.02* ± 0.05	-0.20 ± 0.13	-0.18 ± 0.36	-0.78* ± 0.33	-0.34 ± 0.29	2.06* ± 0.64	17.86**	-
	C2	3.93* ± 0.16	-0.03 ± 0.18	-0.20 ± 0.75	-0.99 ± 0.73	-0.34 ± 0.38	2.65* ± 1.02	18.78**	-
	C3	3.84* ± 0.10	-0.02 ± 0.11	0.45 ± 0.47	-0.62 ± 0.45	-0.11 ± 0.26	2.04* ± 0.64	18.08**	-
	C4	4.33* ± 0.13	-0.14 ± 0.11	0.87 ± 0.56	0.008 ± 0.55	-0.52* ± 0.25	1.83* ± 0.69	50.73**	-
	C5	4.06* ± 0.05	-0.16 ± 0.09	-0.40 ± 0.28	-0.86* ± 0.27	-0.02 ± 0.20	2.34* ± 0.44	41.41**	-
	C6	3.76* ± 0.09	0.08 ± 0.07	0.79* ± 0.38	-0.38 ± 0.37	-0.06 ± 0.16	2.18* ± 0.47	75.55**	Complementary
Number of grains per cob	C1	352.68* ± 18.24	53.80* ± 9.48	-324.92* ± 75.94	-494.32* ± 75.37	-2.50 ± 23.10	813.52* ± 84.28	174.94**	Duplicate
	C2	352.30* ± 5.15	8.00 ± 7.26	-345.86* ± 25.87	-502.00* ± 25.21	-2.50 ± 16.25	866.00* ± 37.45	916.75**	Duplicate
	C3	309.04* ± 19.70	23.00* ± 5.18	-199.16* ± 79.58	-414.96* ± 79.45	11.40 ± 11.21	822.16* ± 81.94	108.89**	Duplicate
	C4	320.72* ± 19.98	27.56* ± 3.32	-219.18* ± 80.23	-463.36* ± 80.19	14.56* ± 7.10	930.48* ± 81.16	2088.1**	Duplicate
	C5	330.44* ± 11.41	7.00* ± 2.62	-258.06* ± 46.01	-429.36* ± 45.95	0.10 ± 5.69	776.76* ± 47.07	2707.6**	Duplicate
	C6	397.12* ± 13.92	116.40* ± 58.27	-317.08* ± 129.70	-526.08* ± 129.18	100.20 ± 118.6	807.28* ± 240.80	24.14**	Duplicate
100 grain weight	C1	22.06* ± 0.40	0.76* ± 0.18	2.40 ± 1.69	-2.46 ± 1.642	-4.99* ± 0.73	11.60* ± 1.96	174.94**	-
	C2	21.05* ± 0.63	-2.94* ± 1.27	-2.97 ± 3.37	-9.50* ± 3.59	-4.99* ± 2.70	24.40* ± 5.80	916.75**	-
	C3	22.12* ± 0.75	0.97 ± 0.94	-5.93 ± 3.56	-13.10* ± 3.54	-0.21 ± 1.96	26.96* ± 4.87	108.89**	-
	C4	22.14* ± 0.48	2.74* ± 0.32	-3.37 ± 2.04	-8.22* ± 2.03	1.46* ± 0.73	17.11* ± 2.35	2088.1**	-
	C5	23.39* ± 0.31	2.64* ± 0.24	-4.66* ± 1.37	-10.20* ± 1.36	1.30* ± 0.55	19.20* ± 1.64	2707.6**	Duplicate
	C6	22.44* ± 0.59	2.25 ± 4.40	-16.39* ± 7.15	-19.14* ± 9.10	0.76 ± 8.95	34.49* ± 17.84	24.14**	Duplicate
Grain yield per plant	C1	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
	C2	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
	C3	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
	C4	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
	C5	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
	C6	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

Cond.

Table 2 (*Concluded*)

	Cross	Component						χ^2 (df = 3)	Type of Epistasis
		m	d	h	i	j	l		
Shelling percentage	C1	77.26* ± 0.92	1.26 ± 1.08	-3.41 ± 4.40	-8.92* ± 4.26	-0.84 ± 2.54	20.60* ± 6.10	28.51**	-
	C2	77.37* ± 0.97	-5.72 ± 3.42	-2.54 ± 8.03	-9.00 ± 7.87	-8.64 ± 7.24	17.67 ± 14.59	1.66	-
	C3	76.85* ± 0.66	-1.95* ± 0.34	4.07 ± 2.74	-0.83 ± 2.71	-2.89* ± 0.81	9.03* ± 3.05	86.91**	-
	C4	75.94* ± 0.29	1.95* ± 0.14	6.00* ± 1.30	0.95 ± 1.21	1.12 ± 0.54	11.36* ± 1.61	1149.5**	Comple-mentary
	C5	79.31* ± 0.37	1.53* ± 0.23	-7.09* ± 1.55	-11.73* ± 1.54	0.48 ± 0.50	26.17* ± 1.78	783.77**	Duplicate
	C6	79.98* ± 0.46	0.53 ± 0.45	-0.85 ± 2.09	-5.44* ± 2.05	0.03 ± 1.04	11.23* ± 2.71	27.68**	-

C1- HKI 209 × HKI 1128; C2- HKI 209 × HKI 163; C3- HKI 1332 × HKI 1128; C4- HKI 1332 × HKI 163, C5- HKI 325-17AN × HKI 1128; C6- HKI 325-17AN × HKI 163.

all types of epistatic components were also observed in all the crosses that corroborates to Shahrokhi *et al*. (2013). Dominance and duplicate type of epistatic effects were found to contribute more than additive effects alone and results were in conformity with Irshad-ul-haq *et al.* (2010). The important portion of inheritance for shelling percentage was controlled by additive effects in C3, and epistatic effects also contributed to some extent in all the crosses. Duplicate type of epistasis in C5 and complementary type in C4 was observed with conclusions reached by Noor *et al*. (2018). Preponderance of dominance gene effects thus suggests that conventional selection procedure may not be rewarding for improvement of maize traits rather positively significant and predominant nature of dominant gene actions observed in all crosses can be effectively utilized in hybrid breeding programs. Thus, it appears that selections may be practiced in later generations or intermitting among the selected segregants followed by one or two generations of selfing could be useful to break the undesirable linkage and allow accumulation of favourable alleles for improvement of these traits.

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