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## Detection of Epistasis by Generation Means Analysis in Maize Hybrids

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**Abstract:** The success of any breeding strategy aiming at crop improvement relies heavily on action, interaction and linkage relationships of genes governing quantitative traits. The relative importance of additive, dominance and epistasis on grain yield and its component traits was studied in two promising maize hybrids viz.,  $W_3 \times W_5$  and  $W_3 \times W_8$  by generation means analysis by developing six generations viz.,  $P_1$ ,  $P_2$ ,  $F_1$ ,  $F_2$ ,  $BC$  and  $BC_2$ . Both additive and dominance components were significant with predominance of latter indicating non-additive gene action for the expression of the traits studied, except for days to 75% husk browning and 100 seed weight in the cross  $W_3 \times W_8$  where only additive effects were significant. Among digenic interactions, additive x additive (i), additive x dominance (j) and dominance x dominance (l), types were significant for most of the traits in both crosses. Additive x additive and dominance x dominance interactions were greater than their corresponding additive and dominance components for most of the traits in both the crosses indicating thereby that epistasis was a significant contributor to genetic variances in both the crosses. However, additive x dominance type interaction was lesser than additive, dominance and other digenic interaction. The present study indicated presence of favorable epistatic gene combinations in both the hybrids i.e.,  $W_3 \times W_5$  and  $W_3 \times W_8$  and as such both have exhibited consistently better performance in evaluation trails. Gene action was found to be duplicate, for most of the traits in both crosses with notable exception of grains yield in  $W_3 \times W_5$ . Thus it is suggested that reciprocal recurrent selection can be a viable breeding strategy in such situation as duplicate gene action is usually undesirable for hybrid breeding. However, continuous directional selection can lead to evolution of complementary gene action in genetically diverse inbred lines.

**Key words:** Maize, epistasis, generation means analysis, gene action

### INTRODUCTION

The inheritance of quantitative traits is a moving target. The expression of these traits is affected not only by large number of genes governing them but also by environmental effects. Frequently, these genes interact with each other causing distortions in Mendelian ratios and leading to novel phenotypes (Phillips, 1998). The term epistasis was coined by Bateson (1909) to describe a situation wherein action of one gene masks the effect of other much like the phenomenon of complete dominance in which one allele at a locus masks the effect of other.

Studies on detection of epistasis in maize have been reviewed by Hallaur and Miranda (1988). The general conclusions from earlier studies of Eberhart *et al.* (1966), Chi *et al.* (1969) and Silva and Hallaur (1975) have been that epistasis is unimportant and that additive component accounts for major portion of genetic variance followed by dominance component. However, there are large number of reports which suggest that epistasis plays a major role in the expression of quantitative traits (Lamkey *et al.*, 1995; Wolf and Hallaur, 1997; Eta-Ndu and Openshaw, 1999; Yu and Bernardo, 2004;

Mihaljevic *et al.*, 2005). The estimation of epistasis assumes more significance in view of the fact that in its presence, variance component estimates are likely to be biased hence inferences drawn from such estimates are more likely to be misleading. The magnitude of the bias depends upon the relative magnitude of epistatic effects comparatively to the deviations of 'd' and 'h', type of prevailing epistasis and direction of dominance. The existence of large array of interactions in a polygenic system causes over-estimation or under-estimation of heritability estimates (narrow sense) thereby causing additional bias in predicted gains. Generation means analysis is a powerful statistical procedure for detection of epistasis using several basic generations from a cross between two inbred lines. Therefore the present study was undertaken to detect epistatic variance in two maize hybrids using generation means analysis.

### MATERIALS AND METHODS

The inbreds used in present study were white maize inbred lines  $W_3$ ,  $W_5$  and  $W_8$  developed at High Altitude Maize Research Station (SKUAST-K). Six generations of

progeny were developed from these lines. The first set consisted of  $P_1(W_3)$ ,  $P_2(W_5)$ ,  $F_1(W_3 \times W_5)$ ,  $F_2((W_3 \times W_5) F_2)$   $BC_1((W_3 \times W_5) \times W_3)$  and  $BC_2((W_3 \times W_5) \times W_5)$ . The second set consisted of  $P_1(W_5)$ ,  $P_2(W_8)$ ,  $F_1(W_5 \times W_8)$ ,  $F_2(W_5 \times W_8 F_2)$   $BC_1((W_5 \times W_8) \times W_5)$  and  $BC_2(W_5 \times W_8 \times W_8)$ . The test cross progenies were developed in 2004 in winter maize nursery, Amberpet, Hyderabad (ICAR). The progenies were evaluated at two locations in Kashmir valley namely High Altitude Rice Research Station, Larnoo and Regional Research Station, Wadura representing distinct environments. Each generation was represented by two rows of 2 m length with inter-row spacing of 60 cm and intra-row spacing of 25 cm. Observations were recorded on 10 randomly selected competitive plants for grain yield/plant, plant height, days to pollen shed, days to 75% husk browning, ear length, ear diameter, number of rows/ear and 100 seed weight. The data was subjected to scaling test (Mather, 1949) and joint scaling test (Cavalli, 1952). For estimation of gene effects and interactions procedure given by Hayman (1958) was followed.

## RESULTS

The results of joint scaling test of both the crosses  $W_3 \times W_5$  and  $W_3 \times W_8$  are presented in Table 1 and 2, respectively. Perusal of the tables reveals that the estimates of mean (m) was significant for all traits studied in both crosses except for 100 seed weight in  $W_3 \times W_8$ . Both additive (d) and dominance (h) were significant for days to pollen shed, days to 75% husk browning, plant height, ear diameter and grain yield in the crosses  $W_3 \times W_5$ , while as for ear length, 100 seed weight and number of rows/ear only dominance component (h) was

significant. In the crosses  $W_3 \times W_8$ , both (d) and (h) were significant for most of the traits. However, in case of days to 75% husk browning and 100 seed weight only additive component (d) was significant and for number of rows/ear only (h) was significant. Strikingly, for most of the traits studied, (h) component was greater in magnitude than its corresponding (d) component.

As far as the interaction components i.e., (i), (j) and (l) are concerned, the additive x additive type interaction (i) was significant for all traits in both crosses except for days to 75% husk browning in  $W_3 \times W_5$  and 100 seed weight in  $W_3 \times W_8$ . Additive x dominance type interaction (j) was significant only for days to pollen shed, days to 75% husk browning, plant height, 100 seed weight and grain yield/plant for the cross  $W_3 \times W_5$  while as for the cross  $W_3 \times W_8$ , (j) type of digenic interaction was significant for plant height, ear length, ear diameter and grain yield/plant. The dominance interaction (l) was significant for traits viz., days to pollen shed, plant height, ear diameter and grain yield/plant in the cross  $W_3 \times W_5$  while as for the cross  $W_3 \times W_8$ , dominance by dominance interaction (l) was significant for all the traits studied except in case of number of rows/ear.

Comparative analysis of additive (d), dominance (h) and digenic interactions (i, j and l) revealed that additive x additive (i) type interactions was greater than the additive component (d) in both crosses. The dominance x dominance interaction (l) was greater than dominance component (h) for plant height, ear length and 100 seed weight only in the cross  $W_3 \times W_5$  while as for the cross  $W_3 \times W_8$ . Similar results were found in case of days to 75% husk browning, ear length and 100 seed weight. For rest of the traits dominance component was greater in

Table 1: Result of joint scaling test and genetic components in the cross  $W_3 \times W_5$  across environments

Genetic component	Day of pollen shed	Days of 75% husk browning	Plant height (cm)	Ear length (cm)	Ear diameter (cm)	100 seed weight (g)	Number of rows/ear	Grain yield/plant (g)
(m)	70.38±0.49**	105.45±0.76**	116.21±0.96**	14.79±6.13	6.43±2.72*	21.93±0.40	210.09±5.40**	80.79±0.70**
(d)	5.91±0.74**	10.76±0.60**	-7.79±0.86	-0.95±0.94	0.27±0.10	-3.31±2.10	0.70±0.40	2.59±0.94
(h)	-15.55±3.59**	-16.47±2.17**	18.90±1.37**	8.37±1.66**	60.18±11.75**	5.42±1.42**	5.63±1.49**	156.12±0.93**
(i)	-9.49±0.94**	-93.46±10.21	77.12±8.13**	8.42±1.48**	2.04±0.85	-7.10±2.2	2.84±0.35**	64.80±10.84
(j)	-5.63±1.09**	-11.37±2.34**	2.04±0.48**	-0.24±0.40	0.15±0.43	6.37±1.30**	0.42±4.85	8.41±4.13*
(l)	12.05±1.90**	4.30±2.70	-77.72±8.12**	-17.38±12.57	-2.45±0.40	28.12±14.38	-0.28±4.03	136.80±11.25*

\*, \*\* Significant at 5% and 1% level, respectively

Table 2: Result of joint scaling test and genetic components in the cross  $W_3 \times W_8$  across environments

Genetic component	Day of pollen shed	Days of 75% husk browning	Plant height (cm)	Ear length (cm)	Ear diameter (cm)	100 seed weight (g)	Number of rows/ear	Grain yield/plant (g)
(m)	72.83±0.50**	77.72±8.12**	119.70±1.05**	13.24±0.79**	6.92±0.17**	23.12±0.48	12.30±0.2**	86.30±0.70**
(d)	-2.43±0.77**	5.95±0.70**	-20.26±0.72**	0.76±0.25**	-0.52±0.10**	-2.06±0.7*	-0.53±0.40	10.25±4.8*
(h)	-5.01±1.32**	-3.90±2.49	48.90±8.9**	2.30±0.78*	6.92±0.30**	-0.90±1.23	7.79±0.86**	263.23±9.80**
(i)	3.33±1.37*	-8.19±3.12*	26.22±1.27**	4.02±0.53*	-0.78±0.20**	4.68±10.48	3.74±1.16**	74.34±3.95**
(j)	0.14±0.46	0.65±1.17	-0.47±0.14**	0.77±0.15**	0.81±0.26**	0.34±0.49	-0.48±0.88	6.99±3.29*
(l)	1.89±0.39**	5.63±2.29*	-25.23±5.47*	-6.52±0.12**	-2.73±0.40**	17.70±4.63**	-4.09±2.40	127.45±18.89**

\*, \*\* Significant at 5% and 1% level, respectively

magnitude than dominance x dominance interaction. The additive x dominance interaction was less than additive, dominance and other digenic interactions for most of the traits in both crosses. The components (h), (j) and (l) were negative for days to pollen shed and days to 75% husk browning in the cross  $W_3 \times W_5$ , while as only (h) was negative for these traits in the cross  $W_3 \times W_8$ . The gene action was duplicate in most of the traits for both the crosses in pooled analysis.

## DISCUSSION

Most of the traits of economic worth such as yield are quantitative in nature and given that it is hard to imagine a situation where gene interaction (epistasis) can be thought to be absent. In presence of epistasis, the estimation of various genetic parameters gets biased and as such expectations of response to selection can be misleading. The present study was undertaken to assess genetic components of variance and detect epistasis using generation means analysis owing to its greater statistical power. Besides the crosses used in the study i.e.,  $W_3 \times W_5$  and  $W_3 \times W_8$  were identified as promising high yielding hybrids and have been recommended for release for general cultivation.

In the present study, both additive and dominance components were significant for most of the traits studied but latter was greater in magnitude for most of the cases in both the crosses indicating preponderance of dominance effects in the expression of these traits. Similar results in maize have been reported by Gamble (1962), Kalla *et al.* (2001) and Atanaw-Alamnie *et al.* (2003). It is thus quite obvious that hybrid breeding can be a better strategy for maize improvement. Recurrent selection can also be useful in the sense that it will exploit both additive and non-additive components for bringing about improvement in grain yield and its attributes. Such a strategy will help in increasing the frequency of favorable alleles while maintaining the genetic variation in breeding population (Doerksen *et al.*, 2003).

Significant digenic interactions of all three types i.e. additive x additive, additive x dominance and dominance x dominance were detected in present study indicating thereby that epistasis is important for the hybrids  $W_3 \times W_5$  and  $W_3 \times W_8$ . Hybrid maize breeding as suggested by Hallauer (1990) is effective in selecting favorable epistatic gene combinations. Lamkey *et al.* (1995) also found epistasis to be of greater importance in an elite maize hybrid B73 x B84. They proposed that since inbreeding and hybrid evaluations are done simultaneously, favorable epistatic gene combinations can ultimately be fixed in the inbred lines. Melchinger *et al.* (1998) proposed that epistasis, was one of the reason for the fact that why

it was not possible to recover high yielding hybrids from some seemingly good inbred lines.

The presence of positive epistatic effects may significantly contribute to expression of heterosis. In fact the recent evidences suggest that dispersion of favorable alleles coupled with complementary epistasis are major components of heterosis in maize, while as duplicate epistasis is not desirable. In the present study complementary epistasis was found for grain yield in  $W_3 \times W_5$  that is why  $W_3 \times W_5$  has been consistently high yielding than  $W_3 \times W_8$ . The type of gene action is the intrinsic property of genes and no simple breeding methodology developed so far can convert duplicate epistasis into complementary epistasis (Chahal *et al.*, 1991). However, Mather (1974) was of the view that complementary type of gene action evolves under continuous directional selection whereas duplicate type evolves under stabilizing selection. Given this, inbred lines developed from genetically diverse populations are likely to yield successful hybrids under continuous directional selection. Comstock *et al.* (1949) proposed that in a situation as evidenced in present study, reciprocal recurrent selection could be a viable approach for effective utilization of both additive and non-additive types of gene actions simultaneously.

The presence of epistasis indicates that the estimation of genetic components by procedures assuming absence of epistasis would have been biased. However, as of now, no sound theoretical principles have been established to actually quantify the nature of epistatic bias on estimation of genetic components and the effect of epistasis on expression of polygenic traits. Thus future research should focus on the development of experimental designs and statistical procedures for quantifying epistasis and partition it into fixable and non-fixable components in order to exclude the epistatic bias from the estimates of additive and dominance components and frame a sound theoretical and applied breeding principles for exploiting epistasis.

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