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Research Article

Generation mean analysis and inbreeding depression in pearl millet [*Pennisetum glaucum* (L.) R. Br.]

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Abstract
In the present investigation, nature and magnitude of gene action was analyzed in six generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) for grain yield and its attributing characters in four crosses of pearl millet. On the basis of individual scaling test A, B and C and joint scaling test, the additive-dominance model was found to be adequate for description of variation in generation means for number of nodes per plant, number of effective tillers per plant, grain yield per plant and biological yield per plant in all the four crosses, days to flowering in ICMB-04999 x J-2454; days to maturity and earhead length in crosses ICMB-20071 x J-2480 and ICMB-04999 x J-2454; while, test weight in crosses ICMB-20071 x J-2500 and ICMB-20071 x J-2480. For remaining cases, significance of either all or the three or any of the individual scaling tests A, B or C and significant Chi-square values confirming the involvement of digenic interaction parameters in the inheritance of these characters. Looking to the interaction components, all the three or any one or any two interaction parameters were found significant for most of the traits in most of the crosses indicating interaction parameters also played important role in the inheritance of these characters. Study indicated that grain yield per plant and its component characters were mostly governed by additive and non-additive gene effects but the magnitude of dominance effect was higher for almost all the characters. Duplicate type of epistasis played a greater role then complementary epistasis was observed for most of cases. The highest estimate of heterobeltiosis was observed for grain yield per plant in cross 1 (76.45%) followed by biological yield in cross 1 (73.76%), number of effective tillers per plant in cross 1 (40.00%), plant height in cross 1 (26.84%), earhead length in cross 4 (11.43%), test weight in cross 1 (11.23%), days to flowering in cross 2 (-8.37%), earhead girth in cross 4 (8.06%) and days to maturity in cross 2 (-3.42%). Highly significant heterobeltiosis with low inbreeding depression was observed for number of effective tillers per plant, earhead length, grain yield and biological yield in the cross ICMB-94555 x J-2290; ICMB-20071 x J-2500 for grain yield and biological yield; ICMB-20071 x J-2480 for test weight and in ICMB-04999 x J-2454 for earhead girth and biological yield.

Key words
Pearl millet, generation mean, gene action, heterosis, inbreeding depression

Introduction

Pearl millet is the most important cereal crop of arid and semi-arid tropics of India, having great yield potential. Therefore, the major objective of pearl millet breeding is to improve the genetic potential for grain yield. In pearl millet, practically all plant characters of economic importance are quantitatively inherited and therefore, improvement in grain yield through its contributing traits depends on the nature and magnitude of heritable variation. Grain yield is a complex character, which final product is resulting from the interaction of yield attributing characters. The understanding of relationship of component traits with grain yield is essential, which aid to ensure effective selection for simultaneous improvement of more characters. The assessment of the magnitude of gene action for various yield attributing characters is useful in deciding the appropriate breeding procedure. The knowledge on nature and magnitude of fixable and non-fixable type of gene effects in the control of components of yield is highly essential in order to achieve the genetic improvement in this crop. Hence, the present objective was taken up to study the nature and magnitude of gene actions involved in the inheritance of grain yield and its component traits, heterosis and inbreeding depression in pearl millet. Considering the importance of the crop, there is a need to generate more information on nature of gene action, heterosis and inbreeding depression for grain yield and its attributing characters.

Materials and methods

The present investigation was carried-out at the Instructional Farm, Department of Agronomy, Junagadh Agricultural University, Junagadh during *kharif* 2013-14. Six generations namely, P_1, P_2, F_1, F_2, BC_1 and BC_2 of four crosses of pearl millet *viz.,* ICMB-94555 x J-2290 (cross 1), ICMB-20071 x J-2500 (cross 2), ICMB-20071 x J-2480 (cross 3) and ICMB-04999 x J-2454 (cross 4) were grown to study the nature and magnitude of gene effect. Each block was comprised of total ten rows consisting of a single row each of P_1, P_2 and F_1, four rows of F_2 and two rows each of BC_1 and BC_2 generations. Each row was 5 m long, spaced 60 cm apart and plant to plant distance within the each row was 15 cm. All the recommended packages of practices were adopted time to time to raise a healthy crop. Experiment was laid-out in Compact Family Block Design (CFBD) with three replications. The observations were recorded on five randomly selected plants from P_1, P_2 and F_1, twenty plants from F_2 and ten plants from BC_1 and BC_2 generations in each replication for ten characters *viz*., days to flowering, plant height, number of nodes per plant, days to maturity, number of effective tillers per plant, ear head length, ear head girth, grain yield per plant, biological yield per plant and test weight. The scaling test (A, B and C) were calculated for each trait to detect adequacy of additive-dominance model or presence of non-allelic interaction according to Hayman and Mather (1955). The adequacy of additive-dominance model was tested by joint scaling test of Cavalli (1952). The six parameter genetic model (m, d, h, i, j and l) was computed according to Hayman (1958). Re-analysis of data was performed using best fitting model after the removal of non-significant effects one-by-one starting with that of lowest magnitude until the remaining inter-allelic interaction became significant. The heterotic effect in terms of superiority of F_1 over better parent (heterobeltiosis) was worked out as per Fonseca and Patterson (1968) and the inbreeding depression (ID) in F_2 generation was worked out as per cent decrease in the performance of F_1 to the F_2.

Results and discussion

The analysis of variance between families (crosses) revealed that the mean squares due to crosses were significant for all the characters under study. The analysis of variance among progenies within each family indicated significant differences among six generation means for all the characters studied in all the four crosses (Table 1).

*Components of generation means based on additive-dominance model (Mather, 1949:*The application of individual scaling test *viz*., A, B and C of Mather (1949) and joint scaling test of Cavalli (1952) showed that the additive-dominance model was found adequate for description of variation in generation means for characters *viz.,* number of nodes per plant, number of effective tillers per plant, grain yield per plant, biological yield per plant in all the four crosses; for days to flowering in cross 4; for days to maturity in crosses 3 and 4; for earhead length in crosses 3 and 4 and for test weight in the crosses 2 and 3. Singh *et al.* (1999) reported that the three parameter model was satisfactory to detect genetic differences in characters *viz.,* diameter of spike and number of effective tillers per plant.

On the other side, this model was found inadequate for description of variation in generation means for the remaining crosses (Table 2 and 3) as on the basis of individual scaling tests, it was observed that all the three or two or any of the individual scaling tests A, B or C were significant for these characters in all the four crosses indicating the presence of epistasis. The application of joint scaling test expressed significant chi-square values for these traits further confirming involvement of digenic interaction parameters in the inheritance of all these characters. The failure of additive-dominance model was attributed mainly to the epistasis. Cockerham (1959) postulated that the epistatic gene action is common in the inheritance of quantitative traits and there is no sound biological reason as to why this type of gene action should be less common for quantitative traits.

*Components of generation means based on three parameter model (Cavalli, 1952):*The results obtained from three parameter model of additive-dominance by Cavalli (1952) revealed that parameter ‘m’ was found significant in all the crosses in which three parameter model was satisfied for various traits. The significant ‘m’ suggested that all the generations differed significantly from one another for their performance (Table 2).

The crosses showing three parameter model, had significant additive (d) and dominance (h) effects for days to flowering in cross 4; number of nodes per plant in all the four crosses; days to maturity in crosses 3 and 4; number of effective tillers per plant on crosses 2, 3 and 4; earhead length in crosses 3 and 4; grain yield per plant and biological yield per plant in all the four crosses and test weight in crosses 2 and 3. Here, the magnitude of dominance (h) effect was higher than that of additive (d) effect, suggesting greater influence of dominance effect in expression of these characters. For the exploitation of dominance effect non-conventional breeding procedure might be adopted. Dangaria *et al.* (2004) and Davda (2004) reported the preponderance of dominance effect for grain yield per plant and related traits. Chaudhary *et al.* (2012) also reported preponderance of non-additive gene action in the inheritance of grain yield per plant and other related traits.

Components of generation means based on six parameter model (Hayman, 1958): When the simple additive-dominance model failed to explain the variation among generation means, a six parameter perfect fit model involving three digenic interaction parameters proposed by Hayman (1958) was applied. The results obtained from six parameter model revealed that in addition to the significance of main gene effects m, (d) and (h); all the three digenic interactions *viz*., additive x additive (i), additive x dominance (j) and dominance x dominance (l) were significant for plant height in cross 1; earhead length in cross 2; earhead girth in cross 2 and test weight in cross 4 except earhead length in cross 2 in which additive (d) gene effect was found non-significant. The goodness of fit for six parameter model could not be tested in the present study owing to no degrees of freedom left for testing chi-square estimates for

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various characters. The perfect fit solution of Hayman (1958), therefore, does not provide a general method for testing the adequacy of digenic interaction model. Such a method would require experiment with more number of family means than the minimum number necessary for fitting a full digenic interaction model.

The magnitude of dominance (h) component was higher than that of additive (d) effects suggesting greater importance of dominance effect in the expression of characters *viz.*, plant height, earhead length and earhead girth suggesting greater importance of dominance effect in the expression of these characters.

Epistasis gene effects are known to contribute a sizable part of variation in the genetic makeup of character which shows higher estimate of dominance effects (Gamble, 1962). In the present investigation also, high estimate of dominance (h) effect for plant height, earhead length, earhead girth and test weight were associated with significant epistasis interaction in the respective crosses. Considering the contribution of epistasis gene effect for any character in relation to magnitude, dominance x dominance (l) interaction had considerable effect as compare to additive x additive (i) and additive x dominance (j) in the expression of plant height in cross 1, earhead length and earhead girth in cross 2 and test weight in cross 4. Non fixable gene effects were important in the expression of these traits in these crosses could be exploited by bi-parental mating of recurrent selection or the use of population improvement concept as an alternative to conventional method. Bhanderi *et al.* (2007) also reported non-additive gene action for days to 50% flowering, days to maturity, number of effective tillers per plant, fodder yield per plant, harvest index and grain yield per plant. Ghodasara *et al.* (2010) reported presence of epistasis for days to flowering, plant height, number of nodes per plant, earhead length and earhead girth. Vagadiya *et al.* (2010a) revealed the preponderance of non-additive gene action in the inheritance of grain yield per plant, days to flowering, number of nodes per plant, earhead length, earhead girth, days to maturity, 1000-grain weight.
The (h) and (l) components had opposite sign for plant height in cross 1 and for earhead length and earhead girth in cross 2, presuming largely duplicate type of epistasis. Singh *et al.* (2000) observed duplicate gene interaction for grain yield and other related traits.

Components of generation means based on best fitting model (Mather and Jinks, 1980): As explained earlier, the goodness of fit for six parameter model could not be tested in the present study owing to no degree of freedom available for chi-square-test. The six parameter models for different characters were scrutinized to detect if non-significant interaction parameter had occurred. Whenever such case was found, the omission of non-significant interaction parameters of a perfect fit solution and re-analysis based on the remaining four or five parameter(s) was practiced in all such cases. This exercise resulted into increased precision of the estimated parameters (i), (j) and (l) to provide the test for goodness of fit of the model. This could be seen by a considerable change in the magnitude of different parameters, reduction in standard errors associated with a change in significance of the parameters for several traits in comparison to the six parameter model. The estimates of (h) parameter observed to be non-significant in perfect fit solution became significant in best fitting model. The change in significance might be attributed to the relative change of C_{ii} (error component) in terms of the inverse matrix (Table 4). The parameter m, (d) and (i) were least affected by the re-analysis of the data.

Individual digenic epistasis effect *viz*., additive x additive (i) type of interaction, additive x dominance (j) effect and dominance x dominance (l) component as well as joint influence of different interaction parameters like both (i) and (l), (i) and (j) and (j) and (l) also played important role in the expression of various traits.

Results obtained through best fitting model showed that both additive (d) and dominance (h) components were significant for days to flowering in crosses 1, 2 and 3; plant height in crosses 2, 3 and 4; days to maturity in cross 1 and 2; earhead girth in cross 1, 3 and 4; test weight in cross 1. Davda (2004) reported the importance of additive and non-additive gene action for various traits. Bhanderi *et al.* (2007) observed that additive and non-additive gene actions are equally important for number of nodes per plant, earhead weight and threshing index. Chotaliya *et al.* (2010) also reported the role of both additive and non-additive gene action in the inheritance of traits *viz.*, days to 50% flowering, days to maturity, number of effective tillers per plant and number of nodes per plant.

Estimates of additive (d) and dominance (h) components varied from cross to cross and character to character. The variable expression of gene effects in different crosses might be due to the genetic makeup of a particular cross and the effect of variable environmental conditions on the expression of different traits.

Dominance (h) component was negative for days to flowering in cross 1; days to maturity in crosses 1 and 2, indicating dominance of earliness over late flowering and maturity. Dominance (h) effect was higher than additive (d) effect for days to flowering in crosses 1, 2 and 3; days to maturity in crosses 1 and 2; earhead girth in crosses 1 and 4; test weight in cross 1 indicating greater effect of dominance effect on expression of these characters.

Considering individual digenic epistatic effect, additive x additive (i) type of interaction appeared to be significant and positive for days to maturity, earhead girth and test weight in cross 1. While, it was negative for days to flowering in crosses 2 and 3; plant height in crosses 2, 3 and 4; earhead length in cross 1. Additive × dominance (j) was significant and positive for plant height in crosses 2, 3 and 4; days to maturity in crosses 1 and 2; earhead girth in cross 4. While, it was significant and negative for days to flowering in cross 3; earhead length in cross 1; earhead girth in cross 3. Dominance × dominance (l) gene interaction was significant and negative for days to flowering and test weight in cross 1; but significant and positive estimates were observed for days to maturity and earhead girth in cross 2 and cross 3 respectively.

Estimates of dominance × dominance (l) interaction was higher than additive × additive (i) interaction for days to flowering, days to maturity, earhead girth and test weight in cross 1, cross 2, cross 3 and cross 1 respectively. Non-fixable gene effect was important in the expression of these traits, could be exploited by bi-parental mating of recurrent selection or the use of population improvement concept as an alternative to conventional method. Dangaria *et al*. (2004) reported the predominant role of non-additive genetic variance for days to 50% flowering, days to maturity, plant height, earhead length, earhead girth, 1000-grain weight, dry fodder yield and grain yield per plant. Davda (2004) also reported the predominance of non-additive gene action with respect to yield and yield related traits.

Estimates of additive (d) effect was higher than dominance (h) effect and additive x additive (i) interaction also significant and higher for plant height in crosses 2, 3 and 4; for earhead length in cross 1 indicating more importance of additive gene action for plant height and earhead length in these crosses. Fixable gene effect was important for these traits which could be improved through simple selection method. Davda (2004) reported the importance of additive gene action for grain yield and its component traits in pearl millet.

The additive × additive (i) interaction had greater effect than additive × dominance (j) interaction for days to flowering in crosses 2 and 3; plant height in crosses 2, 3 and 4; and earhead girth in cross 1. This indicated better response to selection pressure in population for these characters. In these crosses, improvement could be made by cyclic method of breeding in which desirable recombinants are selected and intercrossed to pool the favorable genes for synthesizing the elite population.

The dominance (h) and dominance x dominance (l) components had opposite sign for days to flowering and test weight in cross 1 and for days to maturity in cross 2, presuming largely duplicate type of epistasis. While, similar sign observed for earhead girth in cross 3, indicating largely complementary type of epistasis.

The biometrical approaches followed in the present investigation revealed that both additive and non-additive components of genetic variance were important. All the characters for remaining crosses under study were under the control of both additive and dominance gene effects for most of the crosses. All the three epistatic effect *viz*., additive x additive (i), additive x dominance (j) and dominance x dominance (l) type of epistasis, their combination or even one of them were important for the crosses in which four, five or six parameter model was found adequate. Hence, bi-parental mating or few cycles of recurrent selection followed by heterosis breeding may give fruitful results for improvement of these traits in respective crosses in pearl millet.

Heterosis and inbreeding depression: The results of heterobeltiosis as well as inbreeding depression for different traits are summarized in Table 5. The magnitude of heterosis varied from cross to cross for all the characters under study. It was high in grain yield per plant and biological yield per plant; moderate for days to flowering, plant height, number of effective tillers, earhead length, earhead girth and test weight; and low for days to maturity and number of nodes per plant. Chotaliya *et al*. (2009) and Vagadiya *et al.* (2010b) reported the high magnitude of heterosis for grain yield and other component characters.

In the present study, either low or moderate amount of inbreeding depression (ID) in desirable direction was found in most of the traits. With few expectations the higher magnitude of inbreeding depression was noted in grain yield per plant in cross 3 (22.00%). The inbreeding depression in remaining crosses was within the range of -1.62 to 21.64 per cent. The character which manifested low heterosis in F_1 also showed low inbreeding depression in F_2. All the four crosses exhibited significant and positive inbreeding depression for plant height, earhead girth, grain yield per plant and biological yield per plant suggesting that F_2s had lower estimates than their respective F_1s for these characters.

It is desirable to have highly significant and positive heterosis with low inbreeding depression. Cross 1 exhibited highly significant heterosis with low inbreeding depression for number of effective tillers per plant, earhead length, grain yield and biological yield; in cross 2 for grain yield and biological yield; in cross 3 for test weight and in cross 4 for earhead girth and biological yield. The magnitude of inbreeding varied from cross to cross indicating influence of genetic constitution of cross. Rai *et al.* (1985) reported the average inbreeding depression was highest for grain yield followed by 1000-grain weight. In present investigation for grain yield, the highest heterobeltiosis was observed in ICMB-94555 x J-2290. This cross also exhibited higher heterobeltiosis for other yield attributing characters. So, among all the four crosses, ICMB-94555 x J-2290 had performed the best for grain yield and its attributing characters. It is desirable to have highly significant and positive heterosis with low inbreeding depression for grain yield and its attributing characters.

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Table 1. Analysis of variance (mean squares) between crosses and between generations within cross of six generations for different characters in pearl millet

Source of variation	d. f.	Days to flowering	Plant height (cm)	No. of nodes per plant	Days to maturity	No. of effective tillers per plant	Ear head length (cm)	Ear head girth (cm)	Grain yield per plant (g)	Biological yield (g)	Test weight (g)
Analysis of variance between crosses											
Replications	2	0.27	0.09	0.02*	0.02	0.01	0.01	0.00	1.73	3.61	0.00
Crosses	3	9.26**	59.86**	0.05**	12.22**	0.53**	14.77**	2.09**	451.91**	940.05**	1.38**
Error	6	0.09	0.12	0.00	0.02	0.00	0.01	0.00	1.13	3.86	0.00
χ^2 test	3	S	S	NS	NS	NS	NS	NS	S	S	S
Analysis of variance between generations within cross											
ICMB-94555 x J-2290											
Replications	2	1.10	0.01	0.03	0.08	0.03	0.03	0.00	20.41	53.80*	0.01
Generations	5	30.35**	1479.88**	2.03**	13.34**	0.53**	12.48**	0.77**	1066.48**	4268.14**	1.21**
Error	10	2.52	0.11	0.02	0.05	0.02	0.05	0.01	5.13	10.19	0.01
ICMB-20071 x J-2500											
Replications	2	0.28	1.35	0.13	0.08	0.02	0.06	0.00	8.82	28.76	0.00
Generations	5	22.34**	588.78**	1.88**	23.01**	0.21**	9.18**	0.72**	721.05**	2612.24**	1.32**
Error	10	0.18	0.51	0.04	0.08	0.01	0.05	0.00	8.19	26.52	0.03
ICMB-20071 x J-2480											
Replications	2	0.08	1.06	0.00	0.17	0.03	0.07	0.00	1.22	7.42	0.00
Generations	5	31.77**	410.86**	1.23**	6.74**	0.95**	5.20**	0.47**	241.45**	1544.80**	0.13**
Error	10	0.09	0.68	0.04	0.10	0.02	0.07	0.01	2.62	11.46	0.00
ICMB-04999 x J-2454											
Replications	2	0.25	0.28	0.03	0.13	0.01	0.01	0.00	0.31	1.27	0.01
Generations	5	12.31**	881.48**	0.52**	14.16*	0.50**	7.16**	0.40**	152.87**	967.90**	0.78**
Error	10	0.27	0.17	0.03	0.13	0.02	0.04	0.01	0.70	2.44	0.01

*, ** = Significant at 5% and 1% levels, respectively

Table 2. Estimates of scaling tests and gene effects for various characters of four crosses in pearl millet based on Cavalli's (1952) three parameters model

Character	Cross	Scaling test			Gene effects			χ^2
		A	B	C	m	d	h	
Days to flowering	I	5.53	7.67**	16.33**	56.66**	-2.59**	-1.83**	**
	II	0.47	2.93**	9.53**	54.60**	-1.79**	-5.82**	**
	III	0.07	3.20**	7.73**	56.55**	-3.49**	-5.15**	**
	IV	0.67	0.07	1.00	58.69**	1.07**	-4.98**	NS
Plant height (cm)	I	24.67**	10.27**	26.73**	104.70**	-14.65**	50.95**	**
	II	13.60**	1.33	29.33**	108.78**	-14.87**	24.16**	**
	III	14.93**	3.33**	29.73**	102.96**	-8.03**	25.54**	**
	IV	-17.07**	4.53**	40.87**	107.14**	-15.92**	30.77**	**
No. of nodes / plant	I	0.40	-0.13	0.00	5.54**	-0.89**	1.45**	NS
	II	0.67	-0.13	1.07	5.74**	-0.93**	1.13**	NS
	III	0.13	0.00	1.47	5.48**	-0.64**	1.10**	NS
	IV	0.53	0.07	0.33	5.81**	-0.33**	0.80**	NS
Days to maturity	I	0.27	-1.53**	-2.80**	88.86**	-1.93**	-4.05**	**
	II	-0.67	-3.60**	-2.00	87.89**	-2.18**	-5.98**	**
	III	-0.07	-0.67	0.87	86.82**	-1.70**	2.32**	NS
	IV	0.00	0.27	2.93	83.65**	-2.56**	-3.07**	NS
No. of effective tillers/plant	I	0.13	0.20	-0.47	2.20**	0.13	1.07**	NS
	II	-0.33	-0.13	-0.27	2.17**	-0.28**	0.43**	NS
	III	0.20	-0.33	0.13	2.59**	-0.55**	1.07**	NS
	IV	0.40	0.00	-0.13	2.97**	-0.35**	0.80**	NS
Ear head length (cm)	I	0.02	2.79**	5.34**	14.99**	1.99**	3.56**	**
	II	-0.45	1.95**	-1.97	18.76**	1.49**	3.47**	**
	III	-0.59	-0.87	-1.81	19.44**	1.08**	2.83**	NS
	IV	-0.63	-0.97	-0.13	15.20**	-1.36**	3.21**	NS

Table 2. (*Contd*.)

Character	Cross	Scaling test			Gene effects			χ^2
		A	B	C	m	d	h	
Ear head girth (cm)	I	0.03	-0.18	-1.11**	8.93**	-0.48**	0.98**	*
	II	0.30*	-0.14	-0.94**	7.63**	-0.49**	0.88**	**
	III	-0.54**	0.07	-0.26	7.36**	-0.36**	0.71**	**
	IV	0.30**	-0.01	0.15	7.12**	-0.23**	0.88**	*
Grain yield / plant (g)	I	15.95	-0.04	15.15	43.94**	-7.46**	49.17**	NS
	II	12.97	8.99	20.89	39.44**	-7.77**	38.60**	NS
	III	-3.37	3.33	-7.40	35.68**	-5.17**	21.35**	NS
	IV	3.02	4.16	1.58	30.23**	-2.87**	17.88**	NS
Biological yield/plant (g)	I	33.82	18.89	28.38	88.91**	-16.06**	94.91**	NS
	II	24.14	9.89	32.89	74.42**	-17.18**	72.29**	NS
	III	21.83	7.00	7.48	76.17**	-16.59**	51.96**	NS
	IV	-7.53	9.17	20.90	72.38**	-9.56**	42.84**	NS
Test weight (g)	I	0.34	0.00	-0.94*	8.12**	-0.46**	1.44**	*
	II	0.32	-0.14	-1.14	7.67**	-0.57**	1.42**	NS
	III	0.01	0.03	0.24	6.92**	0.20**	0.39**	NS
	IV	-0.30**	0.40*	-0.90**	7.61**	0.57**	0.86**	**

**Significant at 5% and 1% levels, respectively

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Table 3. Estimation of gene effects for various characters from a set of six basic generations for four crosses in pearl millet based on Hayman's (1958) six parameter model

Character	Cross	Gene effects					
		m	d	h	i	j	l
Days to flowering	I	57.25**	-3.60*	-8.67*	-3.13	-1.07	-10.07
	II	53.65**	-2.97**	-12.27**	29.47	20.67**	-21.47
	III	55.53**	-4.83**	-9.80**	-4.47**	-1.57*	1.20
	IV	58.69**	1.07**	-4.98**	-	-	-
Plant height (cm)	I	132.47**	-8.90**	55.97**	8.20**	7.20**	-43.13**
	II	127.45**	-8.83**	9.10*	-14.40**	6.13**	-0.53**
	III	121.65**	-2.63**	12.90**	-11.47**	5.80**	-6.80
	IV	130.62**	-10.60**	11.00**	-19.27**	6.27**	-2.33
No. of nodes / plant	I	5.54**	-0.89**	1.45**	-	-	-
	II	5.74**	-0.93**	1.13**	-	-	-
	III	5.48**	-0.64**	1.10**	-	-	-
	IV	5.81**	0.33**	0.80**	-	-	-
Days to maturity	I	86.38**	-1.27**	-2.37*	1.53	0.90**	-0.27
	II	84.97**	-1.07**	-7.73**	-2.27	1.47**	6.53**
	III	86.82**	-1.70**	2.32**	-	-	-
	IV	83.65**	-2.56**	-3.07**	-	-	-
No. of effective tillers/plant	I	2.20**	0.13	1.07**	-	-	-
	II	2.17**	-0.28**	0.43**	-	-	-
	III	2.59**	-0.55**	1.07**	-	-	-
	IV	2.97**	-0.35**	0.80**	-	-	-

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Table 3. Contd.,

Character	Cross	Gene effects					
		m	d	h	i	j	l
Ear head length (cm)	I	10.21**	0.13	1.42**	-	-	-
	II	9.76**	-0.36**	1.92**	-	-	-
	III	9.41**	0.00	2.39**	-	-	-
	IV	10.45**	0.03	3.60 **	1.50**	-0.18	-2.06**
Ear head girth (cm)	I	2.02**	-0.25**	1.73**	0.62*	0.04	-0.56
	II	2.03**	-0.34**	1.96**	0.63*	0.04	-0.53
	III	1.97**	-0.11	1.10**	0.03	0.12	-0.32
	IV	2.00**	0.05	1.19**	0.37	-0.06	-0.29
Grain yield / plant (g)	I	43.94**	-7.46**	49.17**	-	-	-
	II	39.44**	-7.77**	38.60**	-	-	-
	III	35.68**	-5.17**	21.35**	-	-	-
	IV	30.23**	-2.87**	17.88**	-	-	-
Biological yield/plant (g)	I	88.91**	-16.06**	94.91**	-	-	-
	II	74.42**	-17.18**	72.29**	-	-	-
	III	76.17**	-16.59**	51.96**	-	-	-
	IV	72.38**	-9.56**	42.84**	-	-	-
Test weight (g)	I	8.60**	-0.30*	2.72**	1.28*	0.17	-1.62*
	II	7.67**	-0.57**	1.42**	-	-	-
	III	6.92**	0.20**	0.39**	-	-	-
	IV	7.84**	0.24*	1.89**	1.00**	-0.35**	-1.09*

*, ** = Significant at 5% and 1% levels, respectively

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Table 4. Estimates of gene effects for various characters from a set of six basic generations of four crosses in pearl millet based on best fitting model (Mather and Jinks, 1980)

Character	Cross	Gene effects (Based on best fitting model)						χ^2	Type of epistasis
		m	d	h	i	j	l		
Days to flowering	I	55.94**	-2.52**	10.24**	-	-	-15.78**	NS	D
	II	58.77**	-1.84**	-10.61**	-4.48**	-	-	NS	-
	III	59.96**	-3.26**	-9.04**	-3.70**	-3.18**	-	NS	-
	IV	-	-	-	-	-	-	-	-
Plant height (cm)	I	-	-	-	-	-	-	-	D
	II	123.11**	-14.97**	8.76**	-14.76**	12.22**	-	NS	-
	III	118.42**	-8.44**	8.08**	-16.34**	11.38**	-	NS	-
	IV	126.15**	-16.87**	9.41**	-20.86**	12.56**	-	NS	-
No. of nodes/plant	I	-	-	-	-	-	-	-	-
	II	-	-	-	-	-	-	-	-
	III	-	-	-	-	-	-	-	-
	IV	-	-	-	-	-	-	-	-
Days to maturity	I	87.66**	-2.17**	-2.51**	1.38**	1.81**	-	NS	-
	II	88.20**	-2.53**	-9.08**	-	2.96**	3.61**	NS	D
	III	-	-	-	-	-	-	-	-
	IV	-	-	-	-	-	-	-	-
No. of effective tillers/plant	I	-	-	-	-	-	-	-	-
	II	-	-	-	-	-	-	-	-
	III	-	-	-	-	-	-	-	-
	IV	-	-	-	-	-	-	-	-
Earhead length (cm)	I	17.50**	2.15**	0.70	-2.71**	-2.80**	-	NS	-
	II	-	-	-	-	-	-	-	-
	III	-	-	-	-	-	-	-	-
	IV	-	-	-	-	-	-	-	-

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Table 4. Contd.,

Character	Cross	Gene effects (Based on best fitting model)						χ^2	Type of epistasis
		m	d	h	i	j	l		
Earhead girth (cm)	I	8.51**	-0.48**	1.48**	0.46**	-	-	NS	-
	II	-	-	-	-	-	-	-	-
	III	7.38**	-0.32**	0.32*	-	-0.60**	0.43**	NS	C
	IV	7.12**	-0.25**	0.88**	-	0.31**	--	NS	-
Grain yield per plant (g)	I	-	-	-	-	-	-	-	-
	II	-	-	-	-	-	-	-	-
	III	-	-	-	-	-	-	-	-
	IV	-	-	-	-	-	-	-	-
Biological yield/plant (g)	I	-	-	-	-	-	-	-	-
	II	-	-	-	-	-	-	-	-
	III	-	-	-	-	-	-	-	-
	IV	-	-	-	-	-	-	-	-
Test weight (g)	I	6.82**	-0.46**	4.40**	1.30**	-	-1.66**	NS	D
	II	-	-	-	-	-	-	-	-
	III	-	-	-	-	-	-	-	-
	IV	-	-	-	-	-	-	-	-

*, ** = Significant at 5% and 1% levels, respectively, - = Non-significant differences among the generations
C= Complementary type of epistasis gene effect and D= Duplicate type of epistasis gene effect

Table 5. Heterobeltiosis (BP) and inbreeding depression (ID) for ten characters of four crosses in pearl millet

Characters	ICMB-94555 × J-2290 (cross 1)		ICMB-20071 × J-2500 (cross 2)		ICMB-20071 × J-2480 (cross 3)		ICMB-04999 × J-2454 (cross 4)	
	BP (%)	ID (%)	BP (%)	ID (%)	BP (%)	ID (%)	BP (%)	ID (%)
Days to flowering	-5.62**	-13.59**	-8.37**	-11.31**	-3.90**	-9.03**	-6.94**	-5.16**
No. of nodes per plant	7.22	10.10**	1.00	3.96	6.59	2.58	6.52	4.85
No. of effective tillers per plant	40.00**	19.90**	8.11	11.25	14.58*	13.64*	12.00*	11.61*
Ear head girth (cm)	5.58**	7.89**	4.24**	7.92**	5.54**	5.41**	8.06**	4.84**
Biological yield per plant (g)	73.76**	21.53**	56.96**	18.38**	34.76**	18.35**	45.48**	14.27**
Plant height (cm)	26.84**	11.49**	6.92**	3.35**	14.42**	3.76**	10.97*	3.63**
Days to maturity	-2.00**	-1.47**	-3.42**	-2.70**	-0.63	-1.62**	-0.82	-2.90**
Ear head length (cm)	7.44**	2.02	8.08**	9.92**	9.01**	8.49**	11.43**	9.02**
Grain yield per plant (g)	76.45**	21.64**	62.33**	17.25**	41.79**	22.00**	46.54**	17.83**
Test weight (g)	11.23**	9.99**	10.27**	10.96**	2.50**	1.80	3.65**	7.86**

*, ** Significant at 5% and 1% levels, respectively