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## Generation mean analysis for yield and it's contributing traits in aromatic rice (*Oryza sativa* L.)

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#### Abstract

The present investigation in aromatic rice (*Oryza sativa* L.) was undertaken for studying the magnitude of gene action in four cross combination for grain yield and it's contributing traits deploying generation mean analysis following six parameter model for parents (P<sub>1</sub> and P<sub>2</sub>), F<sub>1</sub>, F<sub>2</sub>, BC<sub>1</sub> and BC<sub>2</sub> generations during three crop season. The results of the scaling tests revealed that the additive-dominance model was inadequate for all of the characters evaluated in all of the four crosses, suggested the existence of epistasis in the inheritance of these characters. Mean values of all the crosses revealed significant. On the basis of six parameters model, main effect viz., mean (m), additive (d) and dominance (h) and all three digenic interactions viz., additive x additive (i), additive x dominance (j) and dominance x dominance (l) were significant for days to flowering in cross-I (GR-104 x IET-26215); for panicle length in all crosses except cross-IV (IET-26215 x GNR-2); for 100 seed weight in cross-I (GR-104 x IET-26215) and cross-II (IET-24617 x NWGR-9081); for grain yield per plant in cross-III (IET-26214 x GAR-1); for straw yield per plant in cross-II (IET-24617 x NWGR-9081); for harvest index in cross-II (IET-24617 x NWGR-9081) and cross-III (IET-26214 x GAR-1); indicated the involvement of additive, dominance as well as epistasis interaction for controlling this trait. The duplicate type epistasis was observed in majority of all traits in all crosses. The present study demonstrates the importance of additive, dominance and epistatic gene effects for the inheritance of almost all the yield as well as quality characters studied.

**Keywords:** Aromatic rice, gene action, scaling test, generation mean

#### Introduction

Rice is one of the most important food crops in the world. As more than 50 per cent of the world population depends on rice for their staple diet. It is cultivated in 114 countries across the globe, but 90 percent of world's rice is grown and consumed in Asia. Nowadays, the quality considerations assume enhanced importance, especially in the countries which are self-sufficient in their production. Aromatic rices constitute a small but special group of rices which are considered best in quality. Among the quality rices, Basmati is the unique aromatic quality rice. It is a nature's gift to Indian sub-continent. As living standards are improving steadily, human demand for high quality rice is continuously on an increase. This entails in incorporation of preferred grain quality features as the most important objective next to yield enhancement. The major concern in rice grain quality for aromatic rice is their unique aroma or flavors. Several chemical constituents are related to the aroma or fragrance of cooked rice (Cordeiro *et al.*, 2002) [11]. Yajima *et al.* (1979) [12] have detected a total of 114 different volatile compounds in rice fragrance. Among them, a "popcorn" like flavor compound, 2-acetyl-1-pyrroline (2AP) stands out as the main aroma compound in basmati-style rice varieties.

Genetic improvement for rice has thoroughly been studied worldwide. To achieve genetic improvement of yield and quality traits, it is imperative to have knowledge about the nature of gene interactions for different characters. The generation mean analysis has been considered to be one of the best methods for estimating the different components of genetic variance and presence or absence of epistasis. Therefore, the study of genetics of yield and quality traits is important to formulate a breeding programme to improve yield while maintaining the quality of rice. Keeping in view the above mentioned facts, present investigation was formulated to study to the gene action for yield and quality traits in aromatic genotypes of rice.

#### Materials and Methods

The material comprising of seven diversified aromatic and non-aromatic elite lines of rice (GR-104, IET-26215, IET-24617, NWGR-9081, IET-26214, GAR-1 and GNR-2). The four

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crosses (GR-104 x IET-26215, IET-24617 x NWGR-9081, IET-26214 x GAR-1 and IET-26215 x GNR-2) obtained by crossing of seven diverse parents during summer 2017 at Main Rice Research Centre, Navsari Agricultural University, Navsari. Backcrossing was done in *khariif*-2017 with its respective parents. Selfing of  $F_1$ s was done in the same season (*khariif*-2017) to get  $F_2$ s. The evaluation trial was conducted in *khariif*-2018 at Main Rice Research Centre, Navsari Agricultural University, Navsari. The experimental material consisting of six generations ( $P_1$ ,  $P_2$ ,  $F_1$ ,  $F_2$ ,  $BC_1$  and  $BC_2$ ) of each of the four crosses were sown during *khariif*-2018 in compact family block design with three replications. Each replication was divided in four compact blocks. Each four crosses consisting of six generations were randomly allotted to each plot within a block. Each plot consisted of one row (10 plants) of parents and  $F_1$ s, two rows of the backcrosses and four rows of the  $F_2$  generations of each cross. The recommended package of practices was followed to raise a good crop. Observations were recorded on yield and its contributing traits *viz.*, days to flowering, plant height (cm), productive tillers per plant, panicle length (cm), grains per panicle, 100 seed weight (g), grain yield per plant (g), straw yield per plant (g), harvest index (%). Generation mean analysis was conducted using six generations *viz.* parental ( $P_1$  and  $P_2$ ),  $F_1$ ,  $F_2$ , and backcrosses ( $BC_1$  and  $BC_2$ ) of four selected crosses involving seven diverse parents. Average values were subjected to scaling test presented in table 1 and table 2. The significance of any one of these scales (A, B, C and D) indicated the presence of non - allelic interaction. Individual simple scaling tests (A, B, C and D) of Hayman and Mather (1955) [7] were employed to detect the presence of epistasis. The joint scaling test as proposed by Cavalli (1952) [1] was also applied to test the adequacy of additive-dominance model because the joint scaling test combines, very effectively, several scaling tests into one and offers a more general and informative approach.

## Results and Discussion

In the present investigation, all the four scaling tests (A, B, C and D) were highly significant for all the characters under study, indicating inadequacy of additive-dominance model to explain the inheritance of yield and its contributing traits characters. The values for individual scaling tests and estimates of mean (m), additive gene effect (d), dominance gene effect (h) and epistatic interactions *viz.*, additive x additive (i), additive x dominance (j) and dominance x dominance (l) interactions are presented in tables 1 and 2 respectively.

On the basis of individual scaling test A, B, C and D the additive-dominance model was found inadequate for description of variation in generation mean for all the traits of all the four crosses, either the entire four or any three, two or one individual scaling test (out of A, B C and D) were found significant which indicated the presence of digenic interaction which implies that the additive-dominance model is inadequate.

When the simple additive-dominance model failed to explain the variation among the generation means, a six parameter model involving three digenic interaction parameters proposed by Hayman (1958) [2] was applied.

The result obtained from six parameter model revealed that in addition to the significance of mean (m), additive (d) and dominance (h) effects and all the three digenic interactions additive x additive (i), additive x dominance (j) and

dominance x dominance (l) were significant for days to flowering in cross-I; for panicle length in all crosses except cross-IV; for 100 seed weight in cross-I and cross-II; for grain yield per plant in cross-III; for straw These results are in agreement with those obtained by Nayak *et al.* (2007) [4], Sultana *et al.* (2016) [6] and Kumar *et al.* (2017) [3].

The additive (d) effect found significant and positive in cross-I for productive tillers per plant, 100 seed weight, grain yield per plant, harvest index; in case of cross-II for productive tillers per plant, 100 seed weight, grain yield per plant, harvest index; in case of cross-III for days to flowering, productive tillers per plant, grain yield per plant, harvest index; in case of cross-IV for productive tillers per plant.

Similarly, the additive (d) effect found significant and negative in cross-I for days to flowering, panicle length, straw yield per plant; in case of cross-II for days to flowering, panicle length, grains per panicle, straw yield per plant, amylose content; in case of cross-III for panicle length, grains per panicle; in case of cross-IV for panicle length.

The additive component of variation can be exploited by simple pedigree selection. Mass selection for several early generation aimed at the improvement of heterozygous population by modifying the frequencies of desirable genes followed by single plant selection in the resulting material would be cheapest and quickest procedure. However, the presence of non-fixable (h, j and l) component together with duplicate type of epistasis may cause delay in the improvement in this trait through selection in early generations. Under this situation, progeny could be achieved and the selection is delayed to later generations. These results are in agreement with those obtained by Nayak *et al.* (2007) [4], Sultana *et al.* (2016) [6] and Kumar *et al.* (2017) [3] for days to flowering, plant height, productive tillers per plant and harvest index.

The dominance (h) effects found positive and significant for plant height, panicle length, harvest index; in case of cross-II for days to flowering, panicle length, straw yield per plant; in case of cross-III for productive tiller per plant, panicle length, straw yield per plant; in case of cross-IV for productive tiller per plant, panicle length, grain yield per plant, harvest index. These results are in agreement with those obtained by Nayak *et al.* (2007) [4] for grains per panicle and 100 seed weight; Patel *et al.* (2015) [5] for productive tillers per plant, grains per panicle, 100 seed weight, grain yield per plant, straw yield per plant, harvest index, Sultana *et al.* (2016) [6] for grains per panicle, 100 seed weight.

Significant and negative dominance (h) effect was observed for grains per panicle, 100 seed weight in cross-I; grains per panicle, 100 seed weight, grain yield per plant, harvest index, in cross-II; days to flowering, plant height, grains per panicle, 100 seed weight, grain yield per plant, harvest index in cross-III; days to flowering, grains per panicle, in cross-IV, respectively.

The sign of dominance x dominance (l) effect was positive in case of cross-I for 100 seed weight and straw yield per plant; in case of cross-II for productive tillers per plant, 100 seed weight, grain yield per plant and harvest index; in case of cross-III for days to flowering, plant height, 100 seed weight, grain yield per plant and harvest index and in case of cross-IV for days to flowering. The sign of dominance x dominance (l) component was positive in these crosses indicating their enhancing effect in the expression of that character in all four crosses of rice. Non fixable gene effect 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.

The sign of dominance x dominance (l) effect was negative for days to flowering, plant height, productive tiller per plant, panicle length and harvest index in cross-I; for plant height, panicle length and straw yield per plant in cross-II; for panicle length and straw yield per plant in cross-III; for days to flowering, plant height, panicle length, 100 seed weight, grain yield per plant, straw yield per plant and harvest index in cross-IV indicating the reducing effect in the expression of these characters, while negative sign of dominance x dominance (l) component for days to flowering in cross-I and cross-IV suggesting the beneficial effect for early flowering of this crop. The sign of dominance x dominance (l) component was positive in the other characters indicating their enhancing effect in the expression of those characters in all four crosses of rice.

The additive x additive (i) interaction had greater effect as compare to additive x dominance (j) and dominance x dominance. The additive x additive (i) effect found significant and positive for days to flowering in cross-I and cross-II; for panicle length in cross-I, cross-II and cross-III, for grain yield per plant in cross-IV, for straw yield per plant in cross-II and cross-III, 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 inter crossed to pool the favourable genes for synthesizing the elite population. Similar results were obtained by Sabesan (2005)<sup>[8]</sup>, Mahalingam and Nadarajan (2010)<sup>[9]</sup> and Chamundeswari *et al.* (2013)<sup>[10]</sup>.

In the present study, the significant additive and additive x additive epistasis was observed in cross-I, cross-II and cross-III for days to flowering; in all crosses except cross-IV for panicle length; in cross-I and II for grains per panicle; in cross-II and cross-III for grain yield per plant; in cross-I and cross-II for straw yield per plant; in cross-II and cross-III for harvest index. These results are in agreement with those obtained by Nayak *et al.* (2007)<sup>[4]</sup> for grains per panicle and 100 seed weight.

The duplicate epistasis was observed in almost all traits except plant height in cross-I and cross-II and for grains per panicle in cross-I and cross-IV, making it difficult to fix genotypes with increased level of character manifestation because the opposite effect of one parameter would be cancelled out by the negative effect of another parameter. The complementary epistasis was observed for plant height in cross-I and cross-II and for grains per panicle in cross-I and

cross-IV, suggestions for selection in early generation might be effective.

**Conclusions**

Generation mean analysis was carried out by evaluating six basic populations (P<sub>1</sub>, P<sub>2</sub>, F<sub>1</sub>, F<sub>2</sub>, B<sub>1</sub> and B<sub>2</sub>) of four cross combinations viz., (GR-104 x IET-26215, IET-24617 x NWGR-9081, IET-26214 x GAR-1 and IET-26215 x GNR-2) for grain yield and it's contributing traits. All the four crosses were subjected to A, B, C and D scaling tests to sort out the model (interacting crosses) for the characters concerned were further subjected to six parameter models to estimate the main gene effects; (m), (d) and (h) and their interactions (i), (j) and (l) involved in the cross for the expression of respective trait under study. Scaling test (A, B, C and D) was applied to test the inadequacy of additive-dominance model. Significant deviation of the scale (s) from zero indicates the presence of epistatic interaction in respective crosses. It is interesting to note that all the four crosses scored significant values for all the six components of gene effect for grain yield and quality traits. The result obtained from six parameter model revealed that in addition to the significance of mean (m), additive (d) and dominance (h) effects and all the three digenic interactions additive x additive (i), additive x dominance (j) and dominance x dominance (l) were significant for days to flowering in cross-I; for panicle length in all crosses except cross-IV; for 100 seed weight in cross-I and cross-II; for grain yield per plant in cross-III; for straw yield per plant in cross-II; for harvest index in cross-II. Since, the sign of dominance (h) and dominance x dominance (l) for majority of traits of these four crosses was opposite therefore, the nature of epistasis was identified as duplicate in these crosses. Duplicate epistasis as observed may postponed single plant selection and biparental mating or diallel selective mating could be followed where in few cycles of crossing of promising segregants in F<sub>2</sub> and onward generations that might help in the incorporation of desirable genes into a single genetic background. In other words, this type of epistasis tends to cancel or weaken the effect of each other in hybrid combination and hinders the progress made under selection and therefore, selection would have to be differed till later generations of segregation where dominance effects are dissipated. However, the crosses showing complementary interactions might be exploited in the form of pedigree methods. Biparental mating, recurrent selection and diallel selective mating system might be profitable in exploiting both additive and non additive gene action to obtain desirable recombinants.

**Table 1:** Scaling test for yield & its contributing characters aromatic in Rice (as per Mather, 1949)

| Days to flowering            |          |   |       |          |   |       |           |   |       |          |   |       |
|------------------------------|----------|---|-------|----------|---|-------|-----------|---|-------|----------|---|-------|
| Scale                        | Cross-I  |   |       | Cross-II |   |       | Cross-III |   |       | Cross-IV |   |       |
| A                            | -7.00**  | ± | 2.06  | -9.20**  | ± | 1.91  | -5.33**   | ± | 1.89  | -9.40**  | ± | 2.07  |
| B                            | 15.80**  | ± | 1.80  | 1.60     | ± | 2.03  | -9.42**   | ± | 2.07  | -5.86**  | ± | 2.13  |
| C                            | -22.06** | ± | 3.13  | -15.80** | ± | 3.00  | -4.40     | ± | 3.18  | 12.38**  | ± | 3.34  |
| D                            | -15.43** | ± | 1.63  | -4.10**  | ± | 1.56  | 5.18**    | ± | 1.57  | 13.82**  | ± | 1.74  |
| Plant height (cm)            |          |   |       |          |   |       |           |   |       |          |   |       |
| A                            | 20.74**  | ± | 6.72  | 28.73**  | ± | 6.68  | -22.01**  | ± | 8.17  | 37.57**  | ± | 6.86  |
| B                            | 38.61**  | ± | 6.79  | 33.09**  | ± | 7.10  | -11.68    | ± | 8.08  | 49.84**  | ± | 6.85  |
| C                            | 60.79**  | ± | 12.48 | 66.56**  | ± | 11.84 | 25.37     | ± | 13.53 | 70.16**  | ± | 11.74 |
| D                            | 0.72     | ± | 6.02  | 2.37     | ± | 5.79  | 29.53**   | ± | 6.06  | -8.63    | ± | 5.66  |
| Productive tillers per plant |          |   |       |          |   |       |           |   |       |          |   |       |
| A                            | 6.13**   | ± | 0.92  | -4.60**  | ± | 1.11  | 0.27      | ± | 1.15  | 0.87     | ± | 1.19  |
| B                            | 2.27*    | ± | 0.95  | -5.60**  | ± | 1.10  | -4.87**   | ± | 1.04  | -5.13**  | ± | 1.10  |

|                           |          |   |       |          |   |       |           |   |       |          |   |       |
|---------------------------|----------|---|-------|----------|---|-------|-----------|---|-------|----------|---|-------|
| C                         | 8.13**   | ± | 1.54  | -6.73**  | ± | 1.85  | -6.73**   | ± | 1.76  | -7.07**  | ± | 1.87  |
| D                         | -0.13    | ± | 0.79  | 1.73*    | ± | 0.81  | -1.07     | ± | 0.86  | -1.40    | ± | 0.85  |
| Panicle length (cm)       |          |   |       |          |   |       |           |   |       |          |   |       |
| A                         | 1.40     | ± | 1.48  | 1.58     | ± | 1.14  | -0.10     | ± | 1.32  | 1.64     | ± | 0.90  |
| B                         | 8.97**   | ± | 1.51  | 8.49**   | ± | 1.69  | 12.19**   | ± | 1.93  | 9.58**   | ± | 1.25  |
| C                         | 1.07     | ± | 2.47  | -7.05**  | ± | 2.58  | -6.70*    | ± | 2.71  | -2.57    | ± | 2.11  |
| D                         | -4.65**  | ± | 1.29  | -8.56**  | ± | 1.21  | -9.40**   | ± | 1.37  | -6.90**  | ± | 1.03  |
| Grains per panicle        |          |   |       |          |   |       |           |   |       |          |   |       |
| A                         | 32.68**  | ± | 8.52  | -5.55    | ± | 6.63  | 0.23      | ± | 7.26  | 40.86**  | ± | 7.16  |
| B                         | 30.39**  | ± | 9.75  | 28.95**  | ± | 6.91  | 22.77**   | ± | 6.51  | 16.09    | ± | 8.55  |
| C                         | 110.84** | ± | 15.04 | 49.09**  | ± | 10.71 | 60.97**   | ± | 11.71 | 97.70**  | ± | 12.99 |
| D                         | 23.88**  | ± | 6.45  | 12.84*   | ± | 5.42  | 18.99**   | ± | 5.14  | 20.37**  | ± | 5.85  |
| 100 seed weight (g)       |          |   |       |          |   |       |           |   |       |          |   |       |
| Scale                     | Cross-I  |   |       | Cross-II |   |       | Cross-III |   |       | Cross-IV |   |       |
| A                         | -0.13    | ± | 0.10  | -0.52**  | ± | 0.11  | -0.23**   | ± | 0.08  | 0.48**   | ± | 0.11  |
| B                         | -1.85**  | ± | 0.06  | -1.75**  | ± | 0.14  | -0.48**   | ± | 0.08  | 0.36**   | ± | 0.08  |
| C                         | -0.32*   | ± | 0.15  | -0.56**  | ± | 0.20  | 1.46**    | ± | 0.15  | 0.83**   | ± | 0.16  |
| D                         | 0.83**   | ± | 0.07  | 0.85**   | ± | 0.10  | 1.09**    | ± | 0.09  | 0.001    | ± | 0.08  |
| Grain yield per plant (g) |          |   |       |          |   |       |           |   |       |          |   |       |
| A                         | 4.52**   | ± | 1.73  | -12.17** | ± | 2.10  | 6.26**    | ± | 1.83  | 0.66     | ± | 1.81  |
| B                         | -11.51** | ± | 1.97  | -12.37** | ± | 1.86  | -10.15**  | ± | 2.22  | 9.06**   | ± | 1.65  |
| C                         | -7.01*   | ± | 3.47  | -9.22*   | ± | 3.68  | 15.69**   | ± | 3.85  | 7.36**   | ± | 2.84  |
| D                         | -0.01    | ± | 1.67  | 7.66**   | ± | 1.76  | 9.79**    | ± | 1.88  | -1.18*   | ± | 1.45  |
| Straw yield per plant (g) |          |   |       |          |   |       |           |   |       |          |   |       |
| A                         | -35.40** | ± | 2.32  | 1.89     | ± | 2.16  | 6.10**    | ± | 2.07  | -3.37    | ± | 1.78  |
| B                         | -11.56** | ± | 2.43  | 13.77**  | ± | 2.02  | 2.18      | ± | 1.97  | -10.82** | ± | 1.76  |
| C                         | -35.62** | ± | 4.27  | 3.63     | ± | 3.38  | -2.52     | ± | 3.04  | -12.21** | ± | 2.91  |
| D                         | 5.67**   | ± | 2.10  | -6.02**  | ± | 1.54  | -5.39**   | ± | 1.64  | 0.99     | ± | 1.40  |
| Harvest index             |          |   |       |          |   |       |           |   |       |          |   |       |
| A                         | 30.93**  | ± | 2.50  | -14.91** | ± | 2.93  | 1.11      | ± | 2.57  | 3.38     | ± | 2.42  |
| B                         | -3.25    | ± | 2.79  | -23.06** | ± | 2.35  | -11.80**  | ± | 2.92  | 18.66**  | ± | 2.16  |
| C                         | 17.81**  | ± | 4.64  | -12.79** | ± | 4.17  | 14.95**   | ± | 4.35  | 18.03**  | ± | 3.43  |
| D                         | -4.93    | ± | 2.53  | 12.59**  | ± | 2.05  | 12.82**   | ± | 2.15  | -2.00    | ± | 1.83  |

**Table 2:** Estimation of gene effects for yield & its contributing characters using six parameter model in aromatic rice

| Six parameter model (Hayman, 1958) [2] |               |   |       |               |   |       |           |   |       |           |   |       |
|--|---------------|---|-------|---------------|---|-------|-----------|---|-------|-----------|---|-------|
| Days to flowering                      |               |   |       |               |   |       |           |   |       |           |   |       |
| m                                      | 86.15**       | ± | 0.61  | 85.47**       | ± | 0.56  | 91.73**   | ± | 0.58  | 94.60**   | ± | 0.64  |
| d                                      | -10.14**      | ± | 1.08  | -4.30**       | ± | 1.09  | 2.38*     | ± | 1.06  | -1.33     | ± | 1.18  |
| h                                      | 31.80**       | ± | 3.41  | 8.43*         | ± | 3.28  | -10.55**  | ± | 3.33  | -27.48**  | ± | 3.64  |
| i                                      | 30.87**       | ± | 3.26  | 8.20**        | ± | 3.12  | -10.36**  | ± | 3.15  | -27.65**  | ± | 3.48  |
| j                                      | -11.40**      | ± | 1.27  | -5.40**       | ± | 1.30  | 2.04      | ± | 1.27  | -1.77     | ± | 1.36  |
| l                                      | -39.67**      | ± | 5.35  | -0.60         | ± | 5.30  | 25.11**   | ± | 5.31  | 42.91**   | ± | 5.77  |
| Types of epistasis                     | Duplicate     |   |       | Duplicate     |   |       | Duplicate |   |       | Duplicate |   |       |
| Plant height (cm)                      |               |   |       |               |   |       |           |   |       |           |   |       |
| m                                      | 110.90**      | ± | 2.39  | 112.19**      | ± | 2.18  | 113.99**  | ± | 2.32  | 115.36**  | ± | 2.15  |
| d                                      | -3.81         | ± | 3.66  | 3.92          | ± | 3.80  | 4.05      | ± | 3.90  | -3.06     | ± | 3.69  |
| h                                      | -2.21         | ± | 12.69 | -6.29         | ± | 12.25 | -71.20**  | ± | 13.09 | 22.54     | ± | 12.01 |
| i                                      | -1.43         | ± | 12.04 | -4.74         | ± | 11.58 | -59.06**  | ± | 12.13 | 17.2-     | ± | 11.32 |
| j                                      | -8.94*        | ± | 4.02  | -2.18         | ± | 4.13  | -5.17     | ± | 5.17  | -6.13     | ± | 4.17  |
| l                                      | -57.92**      | ± | 19.23 | -57.08**      | ± | 19.28 | 92.75**   | ± | 20.65 | -104.67** | ± | 18.86 |
| Types of epistasis                     | Complementary |   |       | Complementary |   |       | Duplicate |   |       | Duplicate |   |       |
| Productive tillers per plant           |               |   |       |               |   |       |           |   |       |           |   |       |
| m                                      | 12.57**       | ± | 0.29  | 12.02**       | ± | 0.30  | 11.37**   | ± | 0.31  | 11.50**   | ± | 0.31  |
| d                                      | 2.13**        | ± | 0.54  | 1.10*         | ± | 0.54  | 1.93**    | ± | 0.61  | 2.27**    | ± | 0.59  |
| h                                      | 2.00          | ± | 1.66  | -0.60         | ± | 1.76  | 4.57*     | ± | 1.84  | 6.40**    | ± | 1.85  |
| i                                      | 0.27          | ± | 1.59  | -3.47         | ± | 1.62  | 2.13      | ± | 1.73  | 2.80      | ± | 1.71  |
| j                                      | 1.93**        | ± | 0.58  | 0.50          | ± | 0.67  | 2.57**    | ± | 0.66  | 3.00**    | ± | 0.69  |
| l                                      | -8.67**       | ± | 2.65  | 13.67**       | ± | 2.83  | 2.47      | ± | 3.00  | 1.47      | ± | 3.01  |
| Types of epistasis                     | Duplicate     |   |       | Duplicate     |   |       | Duplicate |   |       | Duplicate |   |       |

**Table 2:** Cont.....

| Panicle length (cm) |         |   |      |         |   |      |         |   |      |         |   |      |
|---------------------|---------|---|------|---------|---|------|---------|---|------|---------|---|------|
| m                   | 21.32** | ± | 0.49 | 20.43** | ± | 0.49 | 19.95** | ± | 0.51 | 20.94** | ± | 0.42 |
| d                   | -3.98** | ± | 0.84 | -4.46** | ± | 0.71 | -5.28** | ± | 0.92 | -3.60** | ± | 0.60 |
| h                   | 10.07** | ± | 2.68 | 17.13** | ± | 2.56 | 20.34** | ± | 2.89 | 13.49** | ± | 2.16 |
| i                   | 9.30**  | ± | 2.57 | 17.11** | ± | 2.43 | 18.80** | ± | 2.74 | 13.79   | ± | 2.07 |
| j                   | -3.79** | ± | 0.98 | -3.45** | ± | 0.94 | -6.14** | ± | 1.05 | -3.97** | ± | 0.66 |

|                            |               |   |       |           |   |       |           |   |       |               |   |       |
|----------------------------|---------------|---|-------|-----------|---|-------|-----------|---|-------|---------------|---|-------|
| l                          | -19.68**      | ± | 4.17  | -27.18**  | ± | 3.83  | -30.89**  | ± | 4.57  | -25.01**      | ± | 3.19  |
| Types of epistasis         | Duplicate     |   |       | Duplicate |   |       | Duplicate |   |       | Duplicate     |   |       |
| <b>Grains per panicle</b>  |               |   |       |           |   |       |           |   |       |               |   |       |
| m                          | 143.58**      | ± | 2.39  | 128.21**  | ± | 1.98  | 130.91**  | ± | 1.95  | 140.62**      | ± | 2.16  |
| d                          | -0.94         | ± | 4.33  | -15.63**  | ± | 3.70  | -14.36**  | ± | 3.35  | 6.60          | ± | 3.93  |
| h                          | -47.71**      | ± | 14.15 | -34.44**  | ± | 11.42 | -33.05**  | ± | 11.17 | -44.68**      | ± | 12.66 |
| i                          | -47.77**      | ± | 12.91 | -25.69*   | ± | 10.84 | -37.97**  | ± | 10.29 | -40.75**      | ± | 11.70 |
| j                          | 1.15          | ± | 5.61  | -17.25**  | ± | 4.39  | -11.27**  | ± | 4.16  | 12.38*        | ± | 4.82  |
| l                          | -15.31        | ± | 22.93 | 2.28      | ± | 18.25 | 14.98     | ± | 17.78 | -16.20        | ± | 20.41 |
| Types of epistasis         | Complementary |   |       | Duplicate |   |       | Duplicate |   |       | Complementary |   |       |
| <b>100 seed weight (g)</b> |               |   |       |           |   |       |           |   |       |               |   |       |
| m                          | 2.78**        | ± | 0.03  | 2.82**    | ± | 0.04  | 2.76**    | ± | 0.04  | 2.32**        | ± | 0.03  |
| d                          | 0.93**        | ± | 0.04  | 0.73**    | ± | 0.07  | -0.05     | ± | 0.05  | 0.04          | ± | 0.05  |
| h                          | -1.39**       | ± | 0.15  | -1.27**   | ± | 0.21  | -2.04**   | ± | 0.18  | 0.11          | ± | 0.17  |
| i                          | -1.66**       | ± | 0.14  | -1.71**   | ± | 0.20  | -2.17**   | ± | 0.17  | 0.001         | ± | 0.16  |
| j                          | 0.86**        | ± | 0.06  | 0.62**    | ± | 0.08  | 0.13*     | ± | 0.05  | 0.06          | ± | 0.06  |
| l                          | 3.64**        | ± | 0.22  | 3.97**    | ± | 0.34  | 2.88**    | ± | 0.26  | -0.83**       | ± | 0.27  |
| Types of epistasis         | Duplicate     |   |       | Duplicate |   |       | Duplicate |   |       | Duplicate     |   |       |

Table 2: Cont.....

|                                  |           |   |      |           |   |      |           |   |      |           |   |      |
|----------------------------------|-----------|---|------|-----------|---|------|-----------|---|------|-----------|---|------|
| <b>Grain yield per plant (g)</b> |           |   |      |           |   |      |           |   |      |           |   |      |
| m                                | 25.05**   | ± | 0.67 | 26.50**   | ± | 0.69 | 28.76**   | ± | 0.77 | 25.98**   | ± | 0.16 |
| d                                | 5.10**    | ± | 0.98 | 2.69*     | ± | 1.09 | 6.26**    | ± | 1.09 | -0.64     | ± | 0.44 |
| h                                | 5.90      | ± | 3.50 | -8.83*    | ± | 3.72 | -14.37**  | ± | 3.93 | 10.93**   | ± | 1.13 |
| i                                | 0.02      | ± | 3.33 | -15.32**  | ± | 3.52 | -19.59**  | ± | 3.76 | 2.37*     | ± | 1.08 |
| j                                | 8.01**    | ± | 1.14 | 0.10      | ± | 1.13 | 8.20**    | ± | 1.26 | -4.20**   | ± | 0.49 |
| l                                | 6.97      | ± | 5.23 | 39.85**   | ± | 5.69 | 23.48**   | ± | 5.81 | -12.09**  | ± | 1.98 |
| Types of epistasis               | -         |   |      | Duplicate |   |      | Duplicate |   |      | Duplicate |   |      |
| <b>Straw yield per plant (g)</b> |           |   |      |           |   |      |           |   |      |           |   |      |
| m                                | 33.21**   | ± | 0.82 | 28.98**   | ± | 0.60 | 31.61**   | ± | 0.59 | 29.72**   | ± | 0.54 |
| d                                | -8.53**   | ± | 1.31 | -7.09**   | ± | 0.96 | -1.83     | ± | 1.13 | 0.53      | ± | 0.90 |
| h                                | -6.86     | ± | 4.42 | 12.73**   | ± | 3.31 | 14.06**   | ± | 3.42 | 0.74      | ± | 2.97 |
| i                                | -11.34**  | ± | 4.21 | 12.03**   | ± | 3.09 | 10.79**   | ± | 3.28 | -1.99     | ± | 2.81 |
| j                                | -11.92**  | ± | 1.44 | -5.94**   | ± | 1.43 | 1.96      | ± | 1.38 | 3.73**    | ± | 1.17 |
| l                                | 58.30**   | ± | 6.76 | -27.69**  | ± | 5.13 | -19.06**  | ± | 5.46 | 16.18**   | ± | 4.63 |
| Types of epistasis               | Duplicate |   |      | Duplicate |   |      | Duplicate |   |      | Duplicate |   |      |
| <b>Harvest index</b>             |           |   |      |           |   |      |           |   |      |           |   |      |
| m                                | 43.25**   | ± | 0.99 | 47.54**   | ± | 0.74 | 47.11**   | ± | 0.78 | 46.54**   | ± | 0.66 |
| d                                | 12.37**   | ± | 1.59 | 7.98**    | ± | 1.43 | 7.86**    | ± | 1.48 | -0.96     | ± | 1.28 |
| h                                | 12.74*    | ± | 5.21 | -21.41**  | ± | 4.36 | -23.49**  | ± | 4.56 | 10.64**   | ± | 3.83 |
| i                                | 9.87      | ± | 5.06 | -25.18**  | ± | 4.10 | -25.64**  | ± | 4.30 | 4.00      | ± | 3.67 |
| j                                | 17.09**   | ± | 1.74 | 4.08*     | ± | 1.69 | 6.46**    | ± | 1.76 | -7.64**   | ± | 1.55 |
| l                                | -37.55**  | ± | 7.86 | 63.15**   | ± | 7.07 | 36.32**   | ± | 7.35 | -26.03**  | ± | 6.16 |
| Types of epistasis               | Duplicate |   |      | Duplicate |   |      | Duplicate |   |      | Duplicate |   |      |

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

Cross-I: GR-104 x IET-26215, Cross-II: IET-24617 x NWGR-9081,

Cross-III: IET 26214- x GAR-1, Cross-IV: IET-26215 x GNR-2

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