Estimation of combining ability, heterosis, heritability, and generation mean in basmati rice (Oryza sativa L.) by line x tester design

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Article Info
ABSTRACT

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Genetic parameters help to identify the breeding behavior of plants and aids in the selection of elite genotypes for hybridization programs. To determine the nature and type of gene action, to select superior genotypes and best cross combinations, combining ability, heterosis, heritability and five generation mean were estimated based on three susceptible varieties as lines and three resistant genotypes as testers in 2016. The three lines and testers were Pant Basmati-1, Pant Basmati-2, and Pant Basmati-17 and, BBL-180-5-1-4-1, Oryza perennis and improved Pusa Basmati-1 respectively. They were crossed in line x tester mating fashion. The plant progenies were grown up to three seasons to get P1, P2, F1, F2, and F3 to find out five generation mean. The experimental trial showed that all genotypes were significant and showed maximum variations among the traits. The general and specific combining ability values of lines and testers were also significant which prerequisite need for selection of superior genotypes. Maximum heterosis was reported in Pant Basmati-2 x Oryza perennis followed by Pant Basmati-2 x BBL-180-5-1-4-1 and Pant Basmati-1 x Oryza perennis respectively. The Highest heritability was recorded for 100-grain weight and lowest for days to flowering in all crosses. Five generation mean analysis showed epistatic non-allelic gene interactions like dominance and additive x additive gene interactions respectively. The overall results suggested that the selected lines, testers and cross Pant Basmati-2 x Oryza perennis were most appropriate for creating maximum heterosis which showed non-allelic gene interactions.

Keywords: Combining ability, Five generation Mean, Genetic parameters, Heritability, Heterosis

INTRODUCTION

Crops are good gift of nature, ultimately utilized by human being for the benefit of mankind. Mendel’s discovery revealed the facts that crop traits are determined by certain phenomena known as heredity. The study of heredity and its mechanism thus help to understand and develop crops of interest. Scientists are able to predict genetic parameters of edible food crops and hence hundreds of improved varieties and hybrid are now available globally (Yang and Hwa 2008).

Genetic parameters like combining ability, generation mean, heterosis and heritability are the fundamental biometrical tools used mostly for forecasting the breeding behavior of plants. Their estimation is prerequisite pre-breeding statistical procedure to select superior genotypes as parents and develop them as a variety. To predict the suitable genotypes as a parents, combining ability and heritability could help as a wonderful tools if the crossing materials are novel (Singh et al. 2019, Bagheri et al. 2008). Heterosis is the superiority of first generation (F1) over its parents that compares the novel hybrid with their competitors. It is popularly used for comparing different hybrids. Heritability determines the heritable nature of traits and number of genes transferred from parents to its offspring. It depicts the percent of traits transfer from parents to next generations. Combining ability like general and specific combining ability determine the degree and direction of cross among
the germplasm which help in selection of superior parents for developing best performing hybrid (Singh et al. 2019). Generation mean analysis determines type of gene interaction that guide to find out the basis of heterosis from mean values of parents and its offspring. The joint scaling test which was proposed by Mather and Jinks (1982) is used to calculate the mean (m), additive effect (d), dominance effect (h), additive x additive (i), additive x dominance (j) and dominance x dominance (l) values (Tiwari et al. 2011).

Combining ability is a key way to identify superior and desirable parents with respect to expected performance of the hybrids and their progenies (Dhillon 1975). It has already been reported that gca critically analyze the parents for their ability to transmit superior performance to their progenies. The general combining ability (gca) is a value derived from the general mean of hybrid involving all parents. Simmonds (1979) told that the gca values were relative and dependent upon the mean of the chosen material. Thus it is better to choose parents possessing significant gca effects or merely based on mean performance (Tiwari et al. 2011). This assumption is based on the principle that the gca effect reflects additive gene action. Sometimes, though the parents possess high gca effects for a trait, the immediate hybrid may not perform well due to interaction of the parental gca effects which may cause distortions on expectation. The reverse trend may also happen with low performing parents showing high hybrid values than expected. This interaction is measured by the sca effects of the hybrids where interaction effects are not fixable. The sca and gca is estimated to identify the hybrids which could be forwarded further for selection in the segregating generation and hybrids suitable for heterosis breeding. The specific combining ability is the deviation from the performance predicted on the basis of gca (Allard, 1960) whereas Sprague and Tatum (1942) suggested that the specific combining ability is controlled by non-additive gene action. The sca effect is an important criterion for the evaluation of hybrids.

Basmati rice is a fine aromatic rice, known for its excellent cooking quality. They are low yielding, have longer maturity days and susceptible to diseases like Bacterial leaf blight (Xanthomonas Orzya pv. Orzyae). Some new basmati varieties Pant Basmati-1, Pant Basmati-2, and Pant Basmati Dhan-17 are popular among farmers in plain region of Uttrakhand, India because of its medium maturity days, non-lodging nature, and have higher productivity than the local basmati landraces. But these varieties became susceptible to Bacterial leaf blight with few years of its cultivation. Thus, to develop BLB resistant basmati variety of the same quality, extensive research is needed to determine the genetic parameters of cross materials that would help to predict the possibility of success of a variety. Uttrakhand state has mandate to cultivate basmati rice, hence a large number of germplasm need to be tested to utilize them in crossing program as a parents to develop a desired variety.

MATERIALS AND METHODS
To estimate genetic parameters like combining ability, generation mean, heterosis and heritability, three susceptible varieties were chosen as lines and three resistant genotypes as testers for developing Bacterial leaf blight (Xanthomonas oryzae pv. Orzyae) resistant basmati rice variety in 2016. The three lines and testers were Pant Basmati-1, Pant Basmati-2, and Pant Basmati-17 and, BBL-180-5-1-4-1, Orzya perennis and Improved Pusa Basmati-1 respectively. They were crossed in line x tester mating fashion (Kempthorne 1957), produced 9 F1 hybrids, and subsequent selfing was done to generate F2 and F3 lines in the following year. The F1 and its pedigree were transplanted in randomized complete block design with an area of 2 meter square and plant to plant spacing of 20 x 20 cm. Forty plants per plot were selected for traits analysis. The traits data were taken following Standard Evaluation System for Rice IRRI Protocol (www.irri.org). The line x tester analysis was based on traits like days to flowering, days to maturity, plant height, effective tiller per plant, panicle length, fertile and sterile grain number and 100 grain weight. The genetic parameters like heterosis, heritability, general and specific combining ability and, five generation mean analysis were estimated by OPSTAT software program, can be assessed online on Hariyana Agricultural University portal, India.

Heterosis was estimated with the formula given by Fonseca and Patterson (1968). Heritability was calculated from generation mean analysis where variance of F2 was subtracted from F1 multiplied by 100 upon F2. General and specific combining ability was calculated using formula given by Kempthorne (1957) and five generation mean analysis was calculated using Hayman (1958) formula. The research trial was carried out in Norman E. Borlaug Crop Research Center, College farm of G. B. Pant University of Agriculture and Technology, Pantnagar, Uttrakhand, India.

RESULTS AND DISCUSSION
Selection of parents based on combining ability
The randomized complete block design experimental trial revealed that all traits were highly significant at 5% level of significance (Table 1). The analysis of variance for combining ability in fixed effect model depicted that the traits mean square values for male were significant except panicle length and 100 grain weight whereas
Table 1. Analysis of variance of rice genotypes in randomized complete block design

| Source of variation | DF  | Mean square |
|---------------------|-----|-------------|
|                     |     | DTF  | DTM  | PHT  | TILN | PANL | FGN  | SGN  | 100 GRWT |
| Block               | 1   | 3.33* | 32.03* | 8.74* | 31.62* | 2.73* | 73.00* | 478.40* | 0.11* |
| Genotypes           | 14  | 65.77* | 68.58* | 300.25* | 39.79* | 6.10* | 110.24* | 1181.76* | 0.48* |
| Error               | 14  | 5.54  | 6.17  | 72.19 | 6.02  | 2.14  | 215.79 | 581.46  | 0.20  |

Table 2. Combining ability analysis of variance table for fixed effect model

| Source of variation | DF  | Mean square |
|---------------------|-----|-------------|
|                     |     | DTF  | DTM  | PHT  | TILN | PANL | FGN  | SGN  | 100 GRWT |
| Blocks              | 1   | 14.22* | 1.38* | 22.22* | 22.22* | 0.13* | 206.72* | 2307.45* | 0.32* |
| Due to males        | 2   | 174.05* | 48.22* | 423.16* | 29.16* | 0.62* | 1389.55* | 1956.33* | 0.11* |
| Due to females      | 2   | 57.05* | 59.55* | 24.00* | 140.66* | 7.61* | 287.05* | 350.93* | 1.17* |
| Male X Female       | 4   | 70.63* | 36.30* | 164.16* | 16.08* | 5.07* | 633.22* | 570.47* | 0.51* |
| Error               | 8   | 4.59  | 3.01  | 116.34 | 9.22  | 2.82  | 339.59 | 682.17  | 0.26  |

values for female were also significant except plant height and sterile grain per panicle (Table 2). The line x tester combined analysis of variance reported that all the crosses were significant except sterile grain per panicle but the parents versus crosses were non-significant. Similarly, the variant male was significant except effective tillers and sterile grain per panicle and, 100 grain weight whereas female were also significant except days to flowering, and 100 grain weight (Table 3).

Most traits like effective tillers, panicle length and 100 grain weight for all lines and testers were non-significant (p<0.05). Days to flowering and maturity for all lines, and plant height and fertile grain per panicle for all testers had high gca. Lowest gca for lines and testers were found in 100 grain weight. Highest gca was observed in Pant Basmati-1 (19.44) for days to maturity followed by Pant Sugandh Dhan-17 (17.01) for sterile grain per panicle respectively. The result revealed that the traits having high gca were most suitable for further crossing. Similarly, sca values for days to maturity and 100 grain weight were non-significant for all the crosses. Best cross was observed as Pant Basmati-1 x Oryza perennis followed by Pant Basmati-2 x BBL-180-5-1-4-1 respectively based on sca value (Table 4).

The values for general and specific combining ability were positive except panicle length and sterile grain per panicle respectively. Similarly, the additive and dominant genetic variance value were positive except panicle length and sterile grain per panicle respectively. The value of standard error of GCA effects for lines and testers were same and positive. Similarly, the standard error of SCA effects for crosses were also positive. The value of standard error of difference between GCA effects of two lines and testers were same. In the same way, the standard error of difference between SCA effects of any two crosses having a common line and tester was also the same (Table 5).

The GCA/SCA ratio ranged from positive to negative. Pant Basmati-1 had 6.88, the highest value for fertile grain per panicle. Similarly, the

Table 3. Combined analysis of variance of rice traits in line x tester design

| Source of variation | DF  | Mean square |
|---------------------|-----|-------------|
|                     |     | DTF  | DTM  | PHT  | TILN | PANL | FGN  | SGN  | 100 GRWT |
| Blocks              | 1   | 3.33* | 32.03* | 8.74* | 31.62* | 2.73* | 73.00* | 478.40* | 0.11* |
| Parents             | 5   | 29.13* | 22.53* | 430.12* | 10.20* | 9.08* | 709.20* | 934.95* | 0.04* |
| Males               | 2   | 47.16* | 35.16* | 761.33* | 7.14* | 11.94* | 896.72* | 733.76* | 0.06* |
| Females             | 2   | 9.50* | 15.16* | 313.93* | 17.24* | 7.56* | 605.60* | 1591.28* | 0.04* |
| Male vs. Female     | 4   | 30.43* | 12.00* | 0.08* | 2.25* | 6.42* | 541.35* | 24.65* | 0.01* |
| Crosses             | 8   | 30.42* | 486.75* | 502.00* | 102.15* | 3.18* | 6001.95* | 2973.54* | 1.89* |
| Parent vs. crosses  | 14  | 5.54  | 6.17  | 72.19 | 6.02  | 2.14  | 215.79 | 581.46  | 0.20  |

(nons: Non-significant at 0.05%, *: Significant at 0.05% probability level, DTF: days to flowering, DTM: days to maturity, PHT: plant height, TILN: mean of tillers number per five plant, PANL: mean of five panicle length, FGN: mean of fertile grain number per five panicle, SGN: mean of sterile grain number per five panicle, 100 GRWT: mean of 100 grain weight per five plants)
The analysis of variance for line x tester design showed that almost all sources of variation were highly significant indicating high variations among the traits which resembles with the results of Murtadha et al. (2018) who reported highly significant variance (P<0.01) among almost all sources of variation. The GCA and SCA value for line and testers were also found significant that revealed the importance of both additive and non-additive gene actions, while low GCA/SCA value of each traits implied importance of dominant gene effects (Machado et al., 2009; Abdel-Moneam et al. 2009). The standard errors of GCA and SCA value of lines and testers were same for different traits which showed the equal contribution of both additive and non-additive effects to the traits.

Our results reported that sca values were higher than gca values but Bahari et al. (2012) observed that mean squares were higher in general combining ability than that of specific combining ability for majority of traits which suggested that the additive gene effects are more important than the non-additive gene effects. Zhang (2015) reported that GCA was significantly different among parents and SCA was also significantly different among crosses.

The GCA/SCA ratio ranged from positive to negative which indicated that additive effects played a more important role than non-additive effects for all the traits. Therefore, it is necessary to select parents with high GCA, which would benefit the offspring. Parents with high GCA can be crossed to select superior combinations (Zhang et al. 2015). Dominance variance was greater than additive variance for all the characters which indicated the predominance of non-additive gene action (Table 4). Similar result was observed by Pawan et al. (2011).

**Comparison of crosses**

Crosses of different genotypes with their traits were calculated based on mid and better parent value. Best cross combination was reported as Pant Basmati-1 x Pant Basmati-2 with mid parent value

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### Table 4. The GCA and SCA value of lines, tester, and its crosses

| SN | Parents and their crosses | DTF | DTM | PHT | TILN | PANL | FGN | SGN | 100 GRWT |
|----|---------------------------|-----|-----|-----|------|------|-----|-----|---------|
| 1  | Pant Basmati-1            | 3.39*| 19.44**| 2.11| 0.34 | 0.78 | 6.89*| -5.66| 0.5     |
| 2  | Pant Basmati-2            | 3.05*| 2.45 | 2.06| 5    | 1.36 | -6.94| -11.35| -0.31   |
| 3  | Pant Sugandh Dhan-17      | -3.31| 3.56*| 0.06| -4.67| 0.61 | 0.053| 17.01**| -0.17   |
| 4  | BBL-180-5-1-4-1           | -1.39| -1.11| 5.56*| 2.49 | 0.33 | 10.55**| -10.85| -0.02   |
| 5  | Oryza perennis            | -4.56| -2.11| 4.22*| -1.67| -0.39| -17.44| 20.84**| -0.14   |
| 6  | Pusa Improved Basmati-1   | 5.94*| 3.22 | -9.77| -0.83| 0.061| 6.89*| -9.99| 0.13    |
| 7  | Pant Basmati-1X BBL-180-5-1-4-1 | 2.96*| 2.11 | -7.38| -0.83| -50.13| -8.23| -10.21| -0.13   |
| 8  | Pant Basmati-1X Oryza perennis | -4.27| -4.39| 4.95*| 0.34 | 48.91**| 8.27*| -12.18| 0.49    |
| 9  | Pant Basmati-1X           |      |      |      |      |      |      |      |         |
| 10 | Improved Pusa Basmati-1   | 1.23 | 2.18 | 2.45| 0.51 | -46.86| 49.94**| 52.88**| -0.37   |
| 11 | Pant Basmati-2X BBL-180-5-1-4-1 | -5.93| -4.05| 11.45**| 3.33*| 1.37 | 12.11**| -4.24| 0.2     |
| 12 | Pant Basmati-2X           | 1.23 | 2.95 | -4.22| -0.5 | -0.28| -22.89| 21.06**| -0.63   |
| 13 | Improved Pusa Basmati-1   | 4.73*| 1.12 | -7.21| -2.83| -1.13| 45.26**| -17.11| 0.41    |
| 14 | Pant Sugandh Dhan-17X     | 2.89 | 1.95 | -4.05| -2.49 | 0.09 | -3.89 | 2.36 | -0.09   |
| 15 | Pant Sugandh Dhan-17 X    | 3.06*| 1.45 | -0.71| 0.17 | 0.52 | 14.61**| -8.84| 0.13    |
| 16 | Improved Pusa Basmati-1   | -5.94| -3.38| 4.79*| 2.34 | -0.64| -10.72| 6.49*| -0.03   |

(*=significant at 5% significance level, F value 2.96 at 14 df)
61.67 and better parent value 58.20 followed by Pant Basmati-1 x Pant Basmati-1 with mid parent value 36.49 and better parent value 32.29, and Pant Basmati-1 x Pant Sugandh Dhan-17 with mid parent value 28.85 and better parent value 25.18, based on 100 grain weight (Table 7). The values over mid and better parents was negative for days to maturity whereas 100 grain weight values were positive except in Pant Basmati-2 x Pant Basmati-2. Effective tiller per plant was maximum in Pant Basmati-2 x Pant Basmati-1 with mid parents value 151.18 and better parents 145.37. The overall mid and better parents value were negative for fertile tillers per plant except Pant Basmati-1 x Pant Sugandh Dhan-17 with mid parents value 1.42. Similarly, mid and better parents value for panicle length was also negative except in Pant Basmati-1 x Pant Sugandh Dhan-17, and Pant Sugandh Dhan-17 x Pant Sugandh Dhan-17 (Table 7).

Most values of mid and better parents for different traits and crosses were positive except days to maturity. It indicates positive heterosis and provide maximum chance of selection of best hybrids. The negative value of days to maturity predicts that these crosses would have shorter days to maturity compared to their parents which will be beneficial to farmers.

**Selection of super hybrid based on heterosis**

Among different cross combinations, only three crosses Pant Basmati-1 x *Oryza perennis*, Pant Basmati-2 x *Oryza perennis* and Pant Basmati-2 x BBL-180-5-1-4-1 were chosen for heterosis study. Maximum heterosis was observed in Pant Basmati-1 x *Oryza perennis* (75.9) followed by Pant Basmati-2 x *Oryza perennis* (60.4) and Pant Basmati-2 x BBL-180-5-1-4-1 (59.4) based on days to maturity. Inbreeding depression was also high in Pant Basmati-1 x *Oryza perennis* (76.28) followed by Pant Basmati-2 x *Oryza perennis* (76.28) and Pant Basmati-2 x BBL-180-5-1-4-1 (65.95) based on days to maturity. The heterosis value was only positive in Pant Basmati-2 x BBL-180-5-1-4-1 for panicle length whereas Pant Basmati-2 x *Oryza perennis* (58.17) had highest heterosis followed by Pant Basmati-1 x *Oryza perennis* (52.84) for fertile grain per panicle.

Similarly, inbreeding depression was also highest in Pant Basmati-2 x BBL-180-5-1-4-1 (64.65) followed by Pant Basmati-1 x *Oryza perennis* (63) and Pant Basmati-2 x *Oryza perennis* (62.93) (Table 7). Days to maturity showed highest heterosis followed by highest inbreeding depression. This result implies that the maturity days for the hybrids might fluctuates maximum from the parents and there would be maximum effect of environment for deciding the date of maturation of the variety. Based on above interpretations, Pant Basmati-2 x *Oryza perennis* can be considered as best cross combinations followed by Pant Basmati-2 x BBL-180-5-1-4-1 and Pant Basmati-1 x *Oryza perennis* respectively.

Standard error of heterosis of Pant Basmati-1 x *Oryza perennis*, Pant Basmati-2 x *Oryza perennis* and Pant Basmati-2 x BBL-180-5-1-4-1 were non-significant. Highest value of standard error of heterosis was 240.20 for sterile grain in Pant Basmati-1 x *Oryza perennis*, 225.61 for 100 grain weight in Pant Basmati-2 x *Oryza perennis* and, 233.28 for 100 grain weight in Pant Basmati-2 x BBL-180-5-1-4-1(Table 8).

The different component values were significant and varies over traits. Similar is the finding of Zhou et al. (2012) who reported that the relative contributions of the genetic components varied with a particular trait. The heterosis for yield, number of grains per panicle, and grain weight are mostly contributed by over-dominance whereas the heterosis for tillers per plant and grain weight are determined by dominance x dominance interaction which has roles in yield and grain numbers. This results suggested that cumulative effects of these components may adequately
explain the genetic basis of heterosis in the hybrid. Luo et al. (2009) over-dominant effects also explained 50.1% and 27.1% phenotypic variations in 93-11BC population and DT713BC population respectively, revealing that over-dominance played an important role in heterosis of rice. This result suggested that additive and over-dominance resulting from epistatic loci might be the primary genetic basis of heterosis in rice. Similarly, Li et al. (2001) investigated a Lemont/Teqing RIL population and found that there was 22.1–43.9% reduction of the RIL from the mid-parental values of Lemont/Teqing. In the same way, Luo (2009) observed the 7.0–16.8% reduction of the 93-11/DT713RI population from the mid-parental values for five yield-related trait.

Virmani et al. (1982) conducted a study at IRRI during 1980 and 1981, have shown up to 73% heterosis, 59% heterobeltiosis and 34% standard heterosis for yield in rice compared with IR36 and IR42 (yield 4–5 t/ha in wet season trials and 7–8 t/ha in dry season trials). Yields up to 5.9 t/ha (22% standard heterosis) in the wet season and 10.4 t/ha (34% standard heterosis) in the dry season were obtained. Most of the hybrids performed better in both seasons while some performed well in both seasons. Yield advantage in hybrids was primarily due to increase in number of spikelets per unit area even though tiller number was less. High yielding hybrids also showed significant heterosis and hetero-beltiosis for total dry matter and harvest index.

**Estimation of heritability**

Maximum heritability was observed in effective tillers per plant (89.69) followed by 100 grain weight (88.76) and fertile grain (86.76) in Pant Basmati-1 x *Oryza perennis*. Similarly, heritability was at peak for 100 grain weight (88.96) followed by fertile grain (86.96) and effective tiller (83.99) in Pant Basmati-2 x *Oryza perennis*. In the same way, highest heritability was observed for effective tiller (91.49) followed by 100 grain weight (89.03) and days to maturity (88.64) in Pant Basmati-2 x BBL-180-5-1-4-1. Highest heritability was found for 100 grain weight and lowest heritability was recorded for days to flowering among all crosses (Table 8).

The heritability value of fertile grain number per plant (86) was nearly same for all the crosses whereas negative value was found for plant height. The heritability of yield contributing traits like effective tillers per plant, fertile grain per panicle and 100 grain weight were high in all cross combinations which showed these traits were highly heritable and suitable for hybridization. Generally high heritable trait is selected during crossing program. Anbessa et al. (2006) reported high heritability estimates (39–48%) for days to flowering, days to first pod maturity, percent pod maturity at four months after planting in chickpea which suggested that early generation selection is effective for days to flowering and maturity. High heritability shows presence of reasonably high additive genetic variance component for this trait. According to Tefera et al. (2003) accumulation of heritability information for traits from different

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**Table 6. The GCA/SCA value of rice genotypes and its crosses in line x tester design**

| Genotype             | DTF  | DTM  | PHT  | TILN | PANL | FGN  | SGN  | 100 GRWT |
|----------------------|------|------|------|------|------|------|------|----------|
| Pant Basmati-1       | -0.05| -1.11| -2.00| -0.33| -0.68| 6.88 | -5.65| 0.50     |
| Pant Basmati-2       | -3.05| -2.44| 2.00 | 5.00 | 1.30 | -6.94| -11.35| -0.32    |
| Pant Sugandh Dhan-17 | 3.11 | 3.55 | 0.00 | -4.66| -0.62| 0.05 | 17.01| -0.17    |
| BBL-180-5-1-4-1      | -1.38| -1.11| 5.50 | 2.50 | 0.28 | 10.55| -10.85| 0.02     |
| *Oryza perennis*     | -4.55| -2.11| 4.16 | -1.66| -0.35| -17.44| 20.84| -0.14    |
| Pusa Improved Basmati | 5.94 | 3.22 | -9.66| -0.83| 0.07 | 6.88 | -9.98 | 0.12     |
| Pant Basmati-1 X BBL-180-5-1-4-1 | 3.05 | 2.11 | -7.50| -0.83| -1.60| -8.22| 1.52 | -0.12    |
| Pant Basmati-1 X *Oryza perennis* | -4.27| -4.38| 4.83 | 0.33 | -0.20| 8.27 | -12.17| 0.49     |
| Pant Basmati-1 X Improved Pusa Basmati-1 | 1.22 | 2.27 | 2.66 | 0.50 | 1.80 | -0.05| 10.65| -0.37    |
| Pant Basmati-2 X BBL-180-5-1-4-1 | -5.94| -4.05| 11.50| 3.33 | 1.46 | 12.11| -3.87| 0.21     |
| Pant Basmati-2 X *Oryza perennis* | 1.22 | 2.94 | -4.16 | -0.50 | -0.32 | -22.88| 21.02| -0.62    |
| Pant Basmati-2 X Improved Pusa Basmati-1 | 4.72 | 1.11 | -7.33| -2.83| -1.14| 10.77| -17.14| 0.40     |
| Pant Sugandh Dhan-17 X BBL-180-5-1-4-1 | 2.88 | 1.94 | -4.00| -2.50| 0.13 | -3.88| 2.35 | -0.09    |
| Pant Sugandh Dhan-17 X *Oryza perennis* | 3.05 | 1.44 | -0.66| 0.16 | 0.52 | 14.61| -8.84 | 0.12     |
| Pant Sugandh Dhan-17 X Improved Pusa Basmati-1 | -5.94| -3.38| 4.66 | 2.33 | -0.65| -10.72| 6.48 | -0.03    |
genetic populations is useful to ascertain its true magnitude.

Our findings resembles the result of Akinwale et al. (2011) who estimated high to medium broad sense heritability on days to heading and maturity, plant height, grain yield, number of grains per panicle, panicle weight, number of panicles per meter square and panicle length which suggested high component of heritable portion of variation that can be selected directly based on their phenotypic performance. The low broad sense heritability observed for the number of tillers per plant and 1000 grain weight was indicative of the influence of the environment on these traits which indicated the ineffectiveness of direct selection for these traits. High to medium heritability and genetic advance were recorded for the number of grains per panicle, grain yield, panicle weight and the number of panicles per plant. This suggests that these traits are primarily under genetic control and selection for them can be achieved through their

| Crosses                        | DTF  | DTM  | PHT  | TILN | PANL | FGN  | SGN  | 100 RWT |
|--------------------------------|------|------|------|------|------|------|------|--------|
|                                | Over | Over | Over | Over | Over | Over | Over | Over   | Over | Over | Over | Over |
|                                | mid  | better | mid | better | mid | better | mid | better | mid | better | mid | better |
| Dhan 17 X Pant Basmati 1       | 2.38 | 0.467 | -8.85 | -7.01 | -19.21 | -25.09 | 20.30 | 8.28 | -11.97 | -18.14 | -22.82 | -34.29 | 38.19 | 10.26 | 36.49 | 32.59 |
| Pant Sugandh 1 X Pant Basmati 1| -8.70 | -1.141 | -11.97 | -11.97 | 1.42 | -2.97 | -4.43 | -10.82 | -7.97 | -13.56 | -36.62 | -46.75 | 101.34 | 78.21 | 61.67 | 58.20 |
| Dhan 17 X Pant Sugandh 1       | 11.05 | 9.70 | -1.08 | -3.52 | -10.29 | -16.59 | 16.73 | -4.45 | 9.71 | 8.44 | 1.42 | -0.53 | 28.72 | -7.34 | 28.85 | 23.43 |
| Pant Basmati 2 X Pant Basmati 1| -9.26 | -1.074 | -12.89 | -13.49 | -4.65 | -8.36 | 151.18 | 145.37 | 1.53 | -0.17 | -26.91 | -28.23 | -4.17 | -6.73 | 14.41 | 14.10 |
| Pant Basmati 2 X Pant Sugandh 1| -6.57 | -0.138 | -8.55 | -9.34 | -6.87 | -14.03 | 54.81 | 36.02 | -6.20 | -6.80 | -86.92 | -87.36 | 109.26 | 90.12 | -18.91 | -23.07 |
| Dhan 17 X Pant Sugandh 1       | 11.27 | 9.66 | -3.75 | -6.92 | -19.22 | -27.44 | 67.48 | 65.04 | -8.57 | -7.07 | -18.13 | -30.36 | -35.46 | -45.19 | 23.07 | 21.64 |
| Pant Basmati 2 X Pant Basmati 1| 7.02 | 3.27 | -2.66 | -3.86 | -9.39 | -21.09 | 9.19 | 0.00 | -3.87 | -11.74 | -23.93 | -36.62 | 19.15 | 0.52 | 6.02 | 3.50 |
| Pant Basmati 2 X Pant Sugandh 1| 2.87 | -1.82 | -3.55 | -4.57 | 5.59 | 2.98 | -22.76 | -30.14 | -3.72 | -10.72 | -35.82 | -47.20 | 59.45 | 22.10 | 13.20 | 5.26 |
| Dhan 17 X Pant Sugandh 1       | 9.00 | 8.45 | -0.73 | -2.15 | 0.49 | 0.00 | 19.04 | 13.63 | 1.06 | 0.84 | -20.13 | -20.69 | 9.53 | 5.78 | 9.83 | 8.77 |

Table 7. Comparison of different cross combinations for different traits over mid and better parent’s value.
Table 8. Comparison of cross combinations and their traits based on heterosis, inbreeding depression and heritability

| Components | Pant Basmati-1 X Oryza perennis | Pant Basmati-2 X Oryza perennis | Pant Basmati-2 X BBL-180-5-1-4-1 |
|------------|---------------------------------|---------------------------------|---------------------------------|
| DTF        | 167.86                          | -16.82                          | 1.62                            |
| DTM        | 162.39                          | 75.97                           | 76.28                           |
| PHT        | 169.78                          | 8.70                            | 19.00                           |
| TILN       | 176.58                          | 64.22                           | 60.66                           |
| PANL       | 221.69                          | -10.55                          | -17.68                          |
| FGN        | 217.66                          | 52.84                           | 63.00                           |
| SGN        | 240.20                          | -12.62                          | -23.02                          |

(Standard error are non-significant)

phenotypic performance. Therefore, the results suggest that the number of panicles per plant, panicle weight, and the number of grains per panicle are important yield contributing traits and selection based on these traits would be most effective. Similar findings was reported by Fahliani et al. (2011).

Analysis of gene interaction based on five generation mean

The scaling value of A, B, C and D for rice traits were significant in Pant Basmati-1 x Oryza perennis, A and B were significant in Pant Basmati-2 x Oryza perennis and Pant Basmati-2 X BBL-180-5-1-4-1 respectively. Scale C had highest value (121.06) in Pant Basmati-1 x Oryza perennis for sterile grain, 112.16 in Pant Basmati-2 x Oryza perennis and 109.79 in Pant Basmati-2 x BBL-180-5-1-4-1 for 100 grain weight (Table 9).

If any of the four parameters A, B, C and D were found significant then it indicates the presence of epistasis. The significance of A and B scale indicate presence of all the three types of non allelic gene interaction viz. additive x additive, additive x dominance and dominance x dominance. The significance of C scale indicates dominance x dominance type non allelic gene interaction and significance of D scale indicates additive x additive type gene interaction respectively. The significance of both C and D scale indicates additive x additive and dominance x dominance type of gene interaction (Anonymous). Our results show all type of gene interactions present in the crosses.

Five generation parameters like m, h, and i were significant and d, l were non-significant for different traits in Pant Basmati-1 x Oryza perennis, Pant Basmati-2 x Oryza perennis and Pant Basmati-2 x BBL-180-5-1-4-1. Highest value of m was observed in sterile grain (26.91), d in 100 grain weight (23.1), h in sterile grain (55.45), i in sterile grain (71.02) and I in sterile grain (221.83) in Pant Basmati-1 x Oryza perennis (Table 10).

The mean and variance value for F3 generation and its traits were found zero. The mean value for days to maturity of P1 were 49.75, 65.27 and 65.27; P2 were 20.73, 32.26 and 32.26; F1 were 125.75, 125.75 and 124.75, F2 were 49.46, 49.46 and 58.80, and F3 were zero in Pant Basmati-1 x Oryza perennis, Pant Basmati-2 x Oryza perennis and Pant Basmati-2 x BBL-180-5-1-4-1 respectively. Similarly, the mean value for fertile grain per panicle in P1 was 60.75, 64.57 and 50.75; P2 was 67.15, 43.30 and 38.59; F1 was 120, 122.75 and 121.50; F2 was 57.00, 59.81 and 56.81; and F3 was zero in Pant Basmati-1 x Oryza perennis, Pant Basmati-2 x Oryza perennis and Pant Basmati-2 x BBL-180-5-1-4-1.

Table 9. Standard error of rice traits and its cross combinations calculated through scaling test

| Rice Traits and its cross combinations | Pant Basmati-1 X Oryza perennis | Pant Basmati-2 X Oryza perennis | Pant Basmati-2 X BBL-180-5-1-4-1 |
|---------------------------------------|---------------------------------|---------------------------------|---------------------------------|
| A                                     | 18.64*                          | 32.92*                          | 86.27*                          |
| B                                     | 17.63*                          | 14.47*                          | 78.40*                          |
| C                                     | 25.87*                          | 36.20*                          | 90.81*                          |
| D                                     | 12.93*                          | 26.43*                          | 86.72*                          |
| A                                     | 21.89*                          | 40.96*                          | 112.65*                         |
| B                                     | 22.56*                          | 41.90*                          | 121.06*                         |
| C                                     | 22.56*                          | 42.94*                          | 113.23*                         |
| D                                     | 18.64*                          | 32.92*                          | 86.27*                          |
| A                                     | 17.63*                          | 14.47*                          | 78.40*                          |
| B                                     | 25.87*                          | 36.20*                          | 90.81*                          |
| C                                     | 12.93*                          | 26.43*                          | 86.72*                          |
| D                                     | 21.89*                          | 40.96*                          | 112.65*                         |

(*) = indicates 5% level of significance
Our crosses showed epistatic non allelic gene interactions. The variance h and i were significant in all crosses which indicated dominance and additive x additive gene interactions respectively. The variance d and I were non-significant which showed absence of additive effects and dominance x dominance gene interactions in all above crosses. Since several important characters are influenced by dominance and non-allelic gene interaction, it is better to delay selection to later generation with increased homozygosity.

Our results is similar with the result of Said (2014) who reported A, B, C and D scaling test for two wheat crosses which revealed that significance of any of these tests indicates the presence of non-allelic gene interactions or epistasis on the scale of measurement used. Scaling test results showed that additive–dominance model is inadequate for explaining the inheritance of all studied characters, indicated the presence of non-allelic gene interaction in two crosses under the two environments. Additive gene effect (d) was significant, indicating potentiality of improving the performance of these characters using the pedigree selection program may be more effective, on the other hand, the estimated of dominance gene action (h) was significant for the rest characters, indicating the important gene effects in inheritance of these characters. The significant [d] and [h] in the inheritance revealed that both types of additive and dominance effects are involved in the genetics cross (Said, 2014). Uzokwe et al. (2017) also reported similar results where generation mean analysis of soybean phenotypic data showed that phosphorus use efficiency was heritable, with complex inheritance patterns and the presence of additive, dominance and epistatic gene effects. Seed P, shoot P, root P, P-incorporation efficiency and PUE were largely quantitatively inherited traits. There were dominance, additive x additive and dominance x dominance gene effects on PUE, grain yield, shoot dry weight, 100-seed weight, root dry weight and shoot dry matter per unit P for populations grown under low-P conditions. Dominance effects were generally greater than additive effects on PUE-related indices.

CONCLUSIONS

The general and specific combining ability analysis of selected lines and testers showed maximum variations among the genotypes that could be further used for developing high yielding varieties. The gca and sca values of different traits were both significant which reveals presence of both additive and non-additive gene interactions. The gca value suggested that Pant Basmati-1 and Pant Sugandh Dhan-17 was best line whereas BBL-180-5-1-4-1 and Pusa Improved Basmati-1 was best tester respectively. Based on sca value, best cross was Pant Basmati-1 x Oryza perennis followed by Pant Basmati-2 x BBL-180-5-1-4-1. Maximum heterosis was recorded in Pant Basmati-2 x Oryza perennis followed by Pant Basmati-2 x BBL-180-5-1-4-1 and Pant Basmati-1 x Oryza perennis respectively. Heritability was also found highest for 100 grain weight and lowest for days to flowering for all the crosses. Five generation mean analysis showed non epistatic allelic gene interactions like dominance and additive x additive gene interactions respectively.

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CONFLICT OF INTEREST
The authors declare that there are no conflicts of interest regarding the publication of this manuscript.

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