

Genetics of panicle-related traits of agronomic importance in rice through triple test cross analysis

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Abstract

A triple test cross analysis was carried out to study the genetics of some panicle related traits of agronomic importance in 'Basmati' rice. Partitioning of total epistasis into i type and $j + l$ type of epistasis revealed that $j + l$ types of interactions were significant for number of panicle per plant and yield per plant. Additive and dominance gene effects were important for panicle length, number of secondary branches per panicle, number of filled grains per panicle, number of sterile grains per panicle and panicle density. However, additive effects were the only source of variation for number of primary branches per plant and fertility percentage. The magnitude of additive variance was higher for all the traits and the degree of dominance was less than unity indicating partial dominance. The non-significant correlation between sums and differences did not show any evidence of directional dominance. Epistatic interactions $j + l$ type can be manipulated to improve number of panicles per plant and yield per plant through recurrent selection. The predominance of additive gene effect suggests the occurrence of selection in late segregating populations however, early selection is proposed for number of primary branches per panicle and fertility percentage to improve rice yield.

Additional key words: additive effects, Basmati rice, dominance effects, epistasis, gene action.

Resumen

Control genético de caracteres de importancia económica relacionados con la panícula de arroz mediante un triple cruzamiento prueba

Se ha llevado a cabo un análisis mediante cruzamientos prueba para estudiar la genética de algunos caracteres de importancia agronómica relacionados con la panícula del arroz tipo 'Basmati'. La separación de la epistasia total en dos tipos, i (aditivo \times aditivo) y $j + l$ (aditivo \times dominancia y dominancia \times dominancia), reveló que las interacciones de tipo $j + l$ eran estadísticamente significativas para el número de panículas por planta y para el rendimiento de la planta. Los efectos génicos aditivos y dominantes fueron importantes para la longitud de la panícula, el n.º de ramas secundarias, el n.º de granos llenos y estériles por panícula, así como para la densidad de panícula. Sin embargo, los efectos aditivos fueron la única fuente de variación para el n.º de ramas primarias por planta y para el porcentaje de fertilidad. La varianza aditiva fue mayor para todos los caracteres y el grado de dominancia fue menor que la unidad, lo que indica una dominancia parcial. La correlación no significativa entre sumas y diferencias no mostró ninguna evidencia de dominancia direccional. Estos resultados indican que las interacciones epistáticas de tipo $j + l$ pueden ser manipuladas para la mejora de los caracteres n.º de panículas por planta y rendimiento por planta mediante selección recurrente. El hecho de que predominen los efectos génicos aditivos sugiere la ocurrencia de selección en poblaciones tardías en segregación. Por ello, para la mejora del rendimiento de arroz se propone una selección temprana para el n.º de ramas primarias por panícula y para el porcentaje de fertilidad.

Palabras clave adicionales: acción génica, arroz Basmati, efectos aditivos, efectos de dominancia, epistasia.

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Introduction

In Pakistan's agrarian economy, rice plays numerous roles. Firstly, it is the second staple food after wheat and contributes more than 2 million tones to food requirements. Secondly, unlike in South Asian countries, rice mostly of «Basmati» type is not considered as a subsistence crop in Pakistan. It is a cash crop grown for export and contributes in the country's foreign exchange exchequer. For instance, during 2003, about 4.5×10^6 tones of rice worth 559 million US\$ was exported (Anonymous, 2003). Thirdly, the rice industry is an important source of employment and income for rural people. Basmati rice predominates in the traditional kalar tract of the Punjab province. The climate is sub-humid and subtropical with 400-700 mm of rainfall mostly in July-August. Among all other rice varieties, none have the distinctive long grains or the subtle aroma for which Basmati rice grain is considered so special and regarded as premium rice all over the world.

Among the 51 accessions in the Basmati group, «Basmati 370» was selected as the potential line and was released for cultivation in 1933. Its release opened the doors to economic revolution in the rice growing areas of Punjab. Later on, efforts were directed towards hybridization and induced mutation programs and as a result, nine Basmati varieties were released for cultivation. However, the yield of Basmati rice could not be substantially increased due to a lack of reliable information on the genetics of yield components including panicle related traits to apply proper breeding methods, though tremendous potential in certain panicle-linked traits was seen in cultivars and mutant lines. In general, increased number of panicles per unit area was the single most important yield component associated with rice yield; number of spikelets per panicle and percent filled grains per panicle being of secondary and tertiary importance (Jones and Synder, 1987; Miller *et al.*, 1991). Another trait directly related to panicle is panicle density, which chiefly affects the yield potential. Other constraints in developing high yielding Basmati cultivars are: narrow genetic base, a scarcity of donors for grain quality and the fact that the Basmati rice genotypes are poor combiners (Akram and Sagar, 1999).

Different biometrical models dealing with the second degree of statistics have been developed to estimate the components of continuous variations

assuming an absence of non-additive gene effects, particularly epistasis (Singh and Singh, 1976). This assumption is rarely true and very few analyses could have proven its validity. To overcome these difficulties, a design which is a simple extension of design III of Comstock and Robinson (1952) has been proposed by Kearsy and Jinks (1968). This design, known as the triple test cross (TTC), provides not only an efficient estimate of additive and dominance genetic components but also an unambiguous test for epistasis.

The present research was carried out to address the main constraints in breeding of high yielding Basmati rice cultivars. The objective was to investigate the genetics of some primary, secondary and tertiary panicle - related yield components along with total yield in Basmati rice, using the TTC model modified by Ketata *et al.* (1976) and Khattak *et al.* (2002) in which the testers L_1 and L_2 were crossed to a number of lines instead of F_2 individuals as suggested by Kearsy and Jinks (1968). The genetic analyses would enable future predictions to be made about the properties of recombinant inbred lines and frame out selection methodologies to develop high yielding Basmati cultivars.

Material and Methods

Plant material, cultural practices and agronomic data recorded

Two Basmati rice genotypes viz: «Basmati-385» and semi-dwarf mutant line «DM-25» (hereafter referred to as testers L_1 and L_2) and their F_1 hybrid (designated as L_3) were crossed to four true breeding genotypes (lines) listed in Table 1. Thus, the experiment included six genotypes (L_1 and L_2 , the testers, plus 4 genotypes), nine single crosses and four three way crosses. The testers were used as females in the entire TTC combinations. The material was planted in randomized complete block design with three replications at the research station of the Nuclear Institute of Agriculture and Biology (NIAB), Faisalabad, Pakistan, during the summer season (May-November 2003). The mean temperature and relative humidity was 29°C and 58%, respectively from May-November. A double row plot of 2-m length was assigned for each replication. The plant-to-plant spacing between and within the rows was 20 cm, respectively. The experimental material was

Table 1. Distinctive characteristics of genotypes used in the studies

Genotype	Origin	Growth type	Yield per plant (g)
Testers:			
L_1 : Basmati 385	TN1 × Basmati 370	Tall	25
L_2 : DM 25	Mutant of Basmati 370	Semi-dwarf	18
L_3 : F_1	Basmati 385 × DM 25	Semi-dwarf	17
Lines:			
DM 107-4	Mutant of Basmati 370	Dwarf	12
DM 25-18-88	Mutant of Basmati 370	Tall	19
NR 1	Mutant of Magnolia × Johna-349	Tall	23
Niab Irri 9	Mutant of IR-6	Dwarf	20

bordered by standard rice variety «Basmati-385». Research field soil was sandy loam. The plots received 72.6 kg ha⁻¹ of N and 23.4 kg ha⁻¹ of P. Half of the N was applied at the time of transplanting while the remaining half in two increments: ¼ after 30 days and the other ¼ after 60 days of transplanting. All the P was applied at the time of transplanting. Weeds were removed by weedicide Machette 60EC [butachlor] and Roanstar [oxadiazon] used at the rate of 2.0 ha⁻¹ and 3.5 ha⁻¹ respectively, after 4 days of transplanting. Rice is a water-loving plant. The water level was kept at 2.5 – 4.0 cm at the time of transplanting and then gradually increased to 8.0 cm for 25 days after transplanting. Irrigation was discontinued for a few days to achieve effective aeration and then re-continued. It was completely stopped more than 15 days before harvesting. The trial was protected from insect pest «leaf roller» and «stem borer» by application of insecticide Talstar 10EC [biphenrin] and Padan 4G [Cartap] at a rate of 500 ml ha⁻¹ and 22 kg ha⁻¹, respectively. The following values were recorded: 1) number of panicles per plant, 2) panicle length (cm), 3) number of primary branches per panicle, 4) number of secondary branches per panicle, 5) number of filled grains per panicle, 6) number of sterile grains per panicle, 7) fertility percentage, 8) panicle density, 9) yield (g) per plant.

Analysis of variance

The analysis of variance was performed following the method described by Singh and Chaudhary (1999) to determine the significance of treatments and to partition the treatment effect to determine the significance

variations among the hybrids, parents, lines, testers, $L_1 + L_2$ vs. F_1 , L_1 vs. L_2 , lines vs. testers and hybrids vs. parents for each trait using the TTC technique.

Test for epistasis

The detection of epistasis was performed according to Singh and Chaudhary (1999). The test to determine significance of the difference ($L_{1j} + L_{2j} - 2L_{3j}$ ($j = \text{genotype}$)), provides information about the presence or absence of epistasis. Therefore, the $L_{1j} + L_{2j} - 2L_{3j}$ for each line (genotype) and each replication was first computed (a replication consisted of four values each for a genotype) and then tested. The total epistasis for 4 degrees of freedom was calculated as the uncorrected genotype (lines) sum of squares $[\sum (L_{1j} + L_{2j} - 2L_{3j})^2]/n$ on the total of replications. Total epistasis was partitioned into two components. The correction factor $cf = [\sum (L_{1j} + L_{2j} - 2L_{3j})^2]/n$ mainly measures the epistasis of additive by additive type (i type) for one degree of freedom and corrected genotypes sums of square $[\sum (L_{1j} + L_{2j} - 2L_{3j})^2/n - cf]$ mainly the $j + l$ type (additive by dominance and dominance by dominance) for 3 degrees of freedom.

The sum of squares due to the interaction of epistasis with blocks (replication) was calculated as the difference between the total sum of squares (ss) and type of epistasis (total $ss - \text{total epistasis}/i$ type epistasis/ $j + l$ type epistasis). Each of three types of epistasis was tested against their respective interactions with blocks. However, before testing individual epistasis the homogeneity of the interaction was tested. As there were only two variances ($i \times \text{block}$ and $j + l \times \text{block}$), homogeneity was tested as under: $F(2, 6) =$

= Mean square of *i* type interaction/Mean square of *j* and *l* type interaction. Where the homogeneity of the interaction variances was not significant, *i* and *j* + *l* type epistasis were also tested against the pooled error, i.e., total epistasis × block interaction.

Individual genotypic epistasis

The individual contribution of each line to the total epistasis was determined and tested for significance according to Ketata *et al.* (1976) for traits in which the total epistasis was significant. The mean value $\Sigma (L_{1j} + L_{2j} - 2L_{3j})/r$ (where *r* is total replications) of each genotype for a trait was tested using a «b» test with 8 degrees of freedom as follows:

$$t = \text{Mean/SE}$$

$$SE = (\text{Error mean square/replication})^{1/2}$$

Additive-dominance model

For the traits where total epistasis effects were not detected by either test, an additive-dominance model was fitted to the data as outlined by Kearsey and Jinks (1968) and Jinks *et al.* (1969).

Estimation of additive variance component (D)

The sum of $L_{1j} + L_{2j}$ for each genotype was calculated replication-wise and subjected to analysis of variance as indicated in Table 2.

The observed mean squares were substituted into the equations as follows:

$$\sigma_s^2 = (MS_s - MS_e)/2r$$

$$\sigma_s^2 = (1/4)D$$

$$D = 4 (MS_s - MS_e)/2r$$

Estimation of dominance component (H)

The difference in $L_{1j} - L_{2j}$ for each genotype was calculated replication-wise and subjected to analysis of variance as indicated in Table 3.

The observed mean squares were substituted into the equations as indicated below:

$$\sigma_d^2 = (MS_d - MS_e)/2r$$

$$\sigma_d^2 = (1/4)H$$

$$H = 4 (MS_d - MS_e)/2r$$

Table 2. Analysis of variance to estimate the additive (D) component

Source of variation	Df	MS	Expected MS
Replication	<i>r</i> - 1	MS_r	
Genotype sum ($L_{ij} + L_{2j}$)	<i>n</i> - 1	MS_s	$\sigma_e^2 + 2r\sigma_s^2$
Error	(<i>n</i> - 1) (<i>r</i> - 1)	MS_e	σ_e^2

r = replication; *n* = genotypes; MS_r, MS_s, MS_e = mean squares of replications, genotypes (sums) and error, respectively; σ_e^2 and σ_s^2 = expected MS of error and genotypes (sums).

Table 3. Analysis of variance to estimate dominance (H) component

Source of variation	Df	MS	Expected MS
Replication	<i>r</i> - 1	MS_r	
Genotype sum ($L_{ij} + L_{2j}$)	<i>n</i> - 1	MS_d	$\sigma_e^2 + 2r\sigma_d^2$
Error	(<i>n</i> - 1) (<i>r</i> - 1)	MS_e	σ_e^2

r = replication; *n* = genotypes; MS_r, MS_d, MS_e = mean squares of replications, genotypes (differences) and error, respectively; σ_e^2 and σ_d^2 = expected MS of error and genotypes (differences).

Average degree of dominance

Average degree of dominance was calculated as $(H/D)^{1/2}$, where H and D are the dominance and additive variance components, respectively.

Direction of dominance (*rs.d*)

Direction of dominance was determined by calculating the linear correlation coefficient *rs.d* between the sum ($L_{1j} + L_{2j}$) and the corresponding differences ($L_{1j} - L_{2j}$) for all genotypes. Significant positive and negative correlations would indicate a predominant direction towards decreasing and increasing values of the trait respectively (Jinks *et al.*, 1969). All the triple test cross calculations were performed using the MSTAT-C package (Michigan State University and Agricultural University of Norway).

Results

Analysis of variance

The analysis of variance for all the characters is shown in Table 4. Highly significant to significant differences were recorded for all the characters among treatments, hybrids, lines, testers and parents, except for number of panicle per plant and number of

sterile grains per panicle in hybrids and lines. Highly significant to significant differences were also found for all the characters between both parentals (L_1 and L_2).

Detection of epistasis

Presence of epistasis (Table 5) was evidenced by the significance of variance ($L_{1j} + L_{2j} - 2L_{3j}$). The total epistasis was found to be significant and highly significant for number of panicles per plant and yield per plant respectively. Further partitioning of total epistasis into *i* type and *j* and *l* type interactions showed that the *i* type interaction was non-significant while *j* and *l* type interactions were important for each of the traits.

The epistatic deviations of individual lines for number of panicles per plant and yield per plant are presented in Table 6 to show the direction, relative magnitudes and to identify the lines, which interacted with L_1 and L_2 to produce significant deviations. Both dwarf mutant genotypes DM-107-4 and DM-25-18-88 were inert and did not contribute to either of the significant portions i.e., of homozygote \times homozygote (*i* type) or homozygote \times heterozygote (*J* and *l* type) types of interaction to the total epistasis. However, another two genotypes NR-1 and Niab-Irri-9 accounted for maximum negative portion to the total epistasis per yield per plant and number of panicle per plant, respectively.

Table 4. Analysis of variance based on mean squares

Source of variation	df	Number of panicles per plant	Panicle length (cm)	Number of primary branches per panicle	Number of secondary branches per panicle	Number of filled grains per panicle	Number of sterile grains per panicle	Fertility (%)	Panicle density	Yield per plant (g)
Replication	2	4.52 *	0.33	0.07	2.86	16.26 **	133.27	14.22	0.05	0.18
Treatments	18	3.14 **	20.01 **	3.56 **	173.99 **	1599.44 **	488.04 **	83.75 **	1.53 **	111.52 **
Hybrids ¹	11	1.26	8.48 **	1.91 **	111.71 **	1,058.68 **	563.16 **	95.07 **	1.31 **	119.00 **
Parents ²	6	6.96 **	32.94 **	5.83 **	163.90 **	1,912.21 **	276.81 **	70.92 **	1.54 **	53.50 **
Lines	3	10.72 **	25.00 **	8.15 **	86.26 **	1,759.53 **	93.57	90.15 **	2.30 **	65.04 **
Testers	2	4.53 *	28.22 **	5.17 **	169.42 **	984.19 **	617.07 **	75.13 **	0.72 **	47.87 **
$L_1 + L_2$ vs L_3	1	3.65	8.27 **	0.72	10.28	706.88 **	214.94 *	23.12 **	0.31 *	15.89 **
L_1 vs L_2	1	5.42 *	48.17 **	9.63 **	328.56 **	1,261.50 **	1,019.21 **	127.14 **	1.14 **	79.86 **
Lines vs Testers	1	0.57	66.24 **	0.16	385.79 **	4,226.29 **	145.98	4.81	0.90 **	30.15 **
Hybrids vs Parents	1	0.84	69.20 **	8.08 **	919.65 **	5,671.15 **	929.05 **	36.32	3.84 **	377.23 **
Error	36	0.90	0.39	0.22	5.77	69.68	46.83	13.13	0.05	1.54

¹ Hybrids: 8 single crosses + 4 three-way crosses. ² Parents: 3 testers + 4 lines. *, ** = Significant at 0.05 and 0.01 levels of probability respectively. df: degrees of freedom

Table 5. Estimates of epistasis based on ANOVA (mean square)

Source	df	Number of panicles per plant	Panicle length (cm)	Number of primary branches	Number of secondary branches	Number of filled grains per panicle	Number of sterile grains per panicle	Fertility (%)	Panicle density	Yield per plant (g)
Total epistasis	4	11.24 *	5.56	5.54	44.93	903.65	855.54	138.42	0.64	133.62 **
<i>i</i> type epistasis	1	0.08	4.20	0.08	73.01	5.60	2380.08	312.94	0.59	0.15
<i>j</i> +/ <i>l</i> type epistasis	3	14.96 *	6.01	7.36	35.56	1203.00	347.36	80.24	0.65	178.11 **
Total epistasis × replicates	8	2.19	1.49	2.05	24.74	730.62	549.20	147.10	0.40	6.98
<i>i</i> type epistasis × replicates	2	1.27	0.51	2.29	52.83	354.91	1075.48	178.97	0.41	10.06
<i>j</i> +/ <i>l</i> type epistasis × replicates	6	2.50	1.81	1.97	15.38	855.86	373.77	136.48	0.39	5.96

*, ** = Significant at 0.05 and 0.01 levels, respectively.

Table 6. Test of epistasis for individual lines

Genotype	No. of panicles per plant	Yield per plant (g)
DM-107-4	1.67	1.29
DM-25-18-88	1.73	2.04
NR-1	-0.03	-3.62 *
Niab-Irri-9	-3.03 *	0.44

* = Significant at 0.05 level.

Additive and dominance components

The estimates of additive and dominance genetic components, degrees of freedom and direction of dominance for these traits, which were not significantly affected by epistasis, are presented in Table 7. Additive and dominance effects were equally important for panicle length and number of filled grains per panicle. The inheritance of number of primary branches per panicle and fertility percentage appeared to be controlled by additive gene effects, since dominance

components for these traits were non-significant. Highly significant to significant additive effects were recorded for number of sterile grains per panicle, panicle density and number of secondary branches. The magnitude of additive variance was higher than that of dominance variance for all these traits. Dominance effect was highly significant for the number of secondary branches per panicle but significant for sterile grains per panicle and panicle density, respectively. The degree of dominance $[(H/D)^{1/2}]$ was less than unity for all these traits. It ranged from 0.28 for fertility percentage to 0.78 for number of secondary branches per panicle. The linear correlation coefficient *rs.d* between the sum $(L_{1j} + L_{2j})$ and the corresponding differences $(L_{1j} - L_{2j})$ for all the traits was non-significant.

Discussion

A considerable amount of genetic variation existed for lines, testers and hybrids (Table 4) on account of

Table 7. Estimates of additive (*D*) and dominance (*H*) variance components, degree of dominance $(H/D)^{1/2}$ and direction of dominance (*rs.d*) for agronomic traits showing non-significant epistasis in rice genotypes

Trait	<i>D</i>	<i>H</i>	$(H/D)^{1/2}$	<i>rs.d</i>
Panicle length (cm)	28.07 **	3.14 **	0.33	0.94
Number of primary branches per panicle	5.29 **	1.31	0.50	0.80
Number of secondary branches per panicle	157.03 *	95.80 **	0.78	0.92
Number of filled grains per panicle	2,984.07 *	566.17 **	0.44	0.92
Number of sterile grains per panicle	2,109.04 **	586.59 *	0.53	0.82
Fertility (%)	504.38 **	38.38	0.28	-0.69
Panicle density	3.88 **	1.01 *	0.51	0.85

*, ** = Significant at 0.05 and 0.01 levels, respectively.

significant to highly significant differences among all the characters except number of panicles per plant and number of sterile grains per panicle for which hybrids and lines were non-significant. Since testers L_1 , L_2 , L_3 , and lines «DM-107-4» and «DM-25-18-88» belong to pure «Basmati» blood while NR-1 and Niab-Irri-9 are from non «Basmati» blood. The significant differences between the two parents clearly disclosed that the L_1 and L_2 testers were the extreme high vs. low selections and would provide an estimate of additive and dominance variation with equal precision, as reported by Kearsley and Jinks (1968). The inadequacy of testers, therefore, cannot be ruled out.

The j and l type epistasis detected for number of panicles per plant and yield per plant (Table 5) are non-directional and unfixable by selection under self-fertilization in rice and would, therefore, not be favorable for developing pure lines for these two traits, although it could be used in the development of hybrids (Subraman and Rangasamy, 1989). The j and l type epistasis has also been found to be less important than i type epistasis in wheat (Singh and Singh, 1976; Dhiman *et al.*, 1999). Although some earlier workers (Perera *et al.*, 1985; Neeraj *et al.*, 1993; Vijayakumar *et al.*, 1996) indicated evidence of epistasis in rice and wheat for all the traits investigated, in the present studies epistasis was only identified in a couple of the traits. The discrepancy in this study might have resulted from environmental influences. Here, only one environment was studied and, genotype-environment interactions could, therefore, have influenced the epistatic effects. These influences have also been reported elsewhere in wheat and mungbean (Jinks and Perkins, 1970; Ketata *et al.*, 1976; Khattak *et al.*, 2001). The presence or absence of epistasis may depend upon the environment in which the plant material has been evaluated and may not always be related to the inherit capacity of a genotype. Similarly, Jinks and Perkins (1970) reported that the components of variance changed to different degrees with changing environments. Environmental influences have also been reported in wheat (Pawar *et al.*, 1994).

The influence of lines on non-allelic interactions for number of panicles per plant and yield per plant indicated that the manifestation of epistasis is determined to some extent by the lines employed for the study (Table 6). The limited number of lines used in these studies might fail to detect non-allelic gene action, which in fact is a part of the genetic system

(Burton, 1968; Ketata *et al.*, 1976). The optimal experimental size required to detect epistasis through TTC depends largely on the gene dispersion in the tester parents (Pooni *et al.*, 1980). Therefore, several lines and extreme high vs. low testers (L_1 and L_2) should be used in studies aimed at the detection of epistasis and to estimate additive and dominance components of variation with equal precision by the TTC technique.

The higher magnitude of additive variance as found in present studies for panicle length, secondary branches per panicle, number of filled grains per panicle, panicle density, number of primary branches per panicle and fertility percentage (Table 7) have also been reported in several papers (Honarnejad and Tarang, 2001; DeLin *et al.*, 2002) following diallel and mean generation analyses of quantitative traits in rice. The higher value of additive genetic variance reflected the presence of common alleles in testers, which increased the magnitude of the additive component; usually the magnitude of the additive component was higher than that of the dominance component for most of the quantitative traits (Singh *et al.*, 1997). Partial dominance can be predicted for panicle length, number of primary branches per panicle, number of secondary branches per panicle, number of filled grains per panicle, number of sterile grains per panicle, fertility percentage and panicle density. The non-significant correlation (Table 7) for all traits indicated that these traits did not supply any evidence for directional dominance in the present studies.

Non-allelic interactions, depicted for number of panicles per plant and yield per plant can be manipulated by a recurrent selection technique to improve these traits. Recurrent selection has also been suggested for non-allelic inherited traits in rice (Subraman and Rangasamy, 1989; Vijayakumar *et al.*, 1996), wheat (Sharma *et al.*, 1995) and mungbean (Khattak *et al.*, 2001). Since both additive and dominance gene effects were important for panicle length, number of filled grains per panicle, sterile grains per panicle, panicle density and number of secondary branches per panicle, a simple selection procedure in the early generations may not contribute significantly to improve these traits. Therefore, selection for the improvement of rice yield through these traits can be successfully exploited following a pedigree method of selection in later generations of segregating populations as suggested by Khattak *et al.* (2002) for improving mungbean seed yield. However,

for the number of primary branches per panicle and fertility percentage, additive gene effects can be exploited in early generations because the dominance effects were also non-significant and lower in magnitude than these additive effects. To exploit all types of gene effects, a bi-parental approach *inter se* crossing and/or recurrent selection may be practical for developing high yielding rice lines in advanced generations as suggested by Khattak *et al.* (2001).

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