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Study on combining ability, heterosis and genetic parameters of yield traits in rice

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A study was conducted on heterosis, combining ability and genetic parameters of yield and yield components in rice. Five lines were crossed with two testers in line × tester manner to produce ten F₁ hybrids. Results show that general combining ability (GCA) effect was only significant for total number of kernels per panicle, number of filled kernels and grain yield per plant, and specific combining ability (SCA) effect was significant for yield and all of its studied components (except for 100-kernel weight). Lines IR42 and Pouya showed a significant GCA for grain yield in opposite direction (20.9 and -13.7 g/plant, respectively). The two lines also showed highest significant GCA for number of filled kernels (22.7 and 23.3, respectively). In the total number of kernels, lines IR8 and IR42 and tester Usen showed the highest significant GCA (34.79, 27.97 and 12.56). In tiller number, only line IR36 and tester IR68897 had the highest significant GCA (3.51 and 0.84). Combination of IR68897×IR8 showed highest significant SCA for grain yield (9.7 g/plant), while in the case of number of filled kernels and tiller number, combinations IR68897×IR8 and Usen/IR36 showed a significant positive SCA (18.9 and 2.1, respectively), indicating that hybridization can be a choice for improving hybrids with better quantity of these traits. The highest general heritability (h_b^2) was obtained for tiller number (96.1%), indicating slight effects of the environment on the trait, while for other traits, a mild general heritability (~70%) was obtained, indicating considerable effect of environment on phenotypic expression of most yield traits. A low specific heritability (h_n^2) was obtained for all traits (18.2 to 26.3%), indicating that non-additive effects play an important role in genetic control of yield traits. Therefore, it seems that hybridization must be a choice for utilizing the putative heterosis in special crosses, and such a condition was observed for tiller number and grain yield in combinations of IR42×IR68897 and IR42×Usen.

Key words: Rice, line × tester, combining ability, heritability, heterosis.

INTRODUCTION

Rice is one of the most important crop plants in the world and is the main nutritional staple food for approximately 40% of the world's population. Therefore, increasing its productivity is of high importance in breeding programs. Reduced plant height, moderate tillering, large and compact panicles, increased kernel number per panicle, increased thousand kernel weight and higher yield are the most important rice characters to be improved in breeding programs (Mackill and Lei, 1997; Miller et al.,

1993; Nemoto et al., 1995; Paterson et al., 2005; Wayne and Dilday, 2003). Since some rice hybrids show heterosis, it subsequently result to production yields which is 15 to 30% higher than inbred varieties (Yuan, 1994; Fujimura et al., 1996), and finding a better cross combination is of high importance. Line × tester analysis is used to evaluate the general and specific combining ability of various lines and to estimate gene effects and it is useful in deciding the relative ability of female and male lines to produce desirable hybrid combinations (Kempthorne, 1957). It also provides information on genetic components and enables the breeders to choose appropriate breeding methods for hybrid variety or

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Table 1. Analysis of variance (ANOVA) of yield traits in line × tester experiment.

SOV	d.f	Mean square				
		Tiller number	Number of total kernel	Number of filled kernel	100-kernel weight (g)	Yield (g/plant)
Replication	2	0.093	32.72	4.53	0.0007	0.79435
Genotype	16	122.5**	4686**	1796.84**	0.285**	532.506**
Parents	6	232.4**	5065**	1051.64**	0.618**	368.957**
Parents vs. crosses	1	392.9**	0.826	4044.61**	0.03	1045.42**
Crosses	9	19.18**	4955**	2043.89**	0.092*	584.549**
Lines	4	28.67	8434	3447.73	0.084	983.009
Testers	1	21.17	4735	1059.69	0.259	370.868
Lines x Testers	4	9.189**	1530*	886.10**	0.058	239.508*
Error	32	1.639	563.3	210.21	0.031	63.6824
Mean		22.6	187.5	125.0	2.86	46.5
C.V(%)		5.7	12.7	11.6	6.2	17.2

* and ** Indicate significance at 5 and 1% level of probability, respectively.

cultivar development programs.

The nature and magnitude of gene action involved in expression of quantitative traits is important for successful development of crop varieties (Pradhan et al., 2006). Several workers reported the predominance of dominant gene action for a majority of the yield traits (Peng and Virmani, 1999, Ramalingan et al., 1993, Satyanarayana et al., 2000; Kumar et al., 2004), while Vijay Kumar et al. (1994) reported the predominance of additive gene action. Preponderance of non-additive gene action in the expression of yield and yield-related traits was reported by Pradhan et al. (2006), Ganesan et al. (1997), Ramalingam et al. (1997), Ganesan and Rangaswamy (1998) and Thirumeni et al. (2000).

Wu et al. (1986) reported a low specific heritability for tiller number and grain yield. Ahmadikhah (2008) reported highest specific heritability (~42%) for 1000-kernel weight and obtained a low specific heritability (~26%) for grain yield. Swati and Ramesh (2004) reported high heritability for grain yield and moderate heritability for flag leaf area and plant height. Saleem et al. (2008) noted high specific heritability and high genetic advance in response to selection in next generation for all the studied traits. Marilia et al. (2001) stated that specific combining ability (SCA) effects of hybrids alone had limited power for parental selection in breeding programs, and must be used in combination with other parameters such as hybrid means and GCA of the respective parents. The hybrid combinations with high mean performance, desirable SCA estimates and involving at least one of the parents with high GCA would likely enhance the concentration of favorable alleles (Gnanasekaran et al., 2006; Kenga et al., 2004; Manivannan and Ganesan, 2001; Thirumeni et al., 2000).

The objectives of this research were to study the important genetic parameters and estimate the GCA and SCA for yield and its components in rice.

MATERIALS AND METHODS

Two testers and five lines were grown, and at flowering stage, they were crossed with each other in a line × tester manner to produce 10 F₁ hybrids in 2009. The five lines were Pouya (L1), IR42 (L2), IR36 (L3), IR8 (L4) and Neda-A/IR36 (L5), and the two testers were Usen (T1) and IR68897 (T2). F₁s together with parental lines and testers were grown in the second year in a randomized complete blocks design with three replications. Four-week seedlings were transplanted in each experimental plot with 25 × 25 cm spacing.

Yield and yield-related traits (viz. tiller number, total number of kernels per panicle, number of filled kernels per panicle and 100-kernel weight) were recorded at suitable times. Genotype means were used for the analysis of variance as described by Singh and Chaudhary, (1985). Line × tester analysis was conducted as described for by Kempthorne (1957). Combining ability analysis was also performed according to Singh and Chaudhary (1985). Mid-parent based heterosis (MP) and better-parent based heterosis (BP) were estimated as outlined by Falconar and Mackey (1996). General combining ability (GCA) and specific combining ability (SCA) values were estimated as described for by Kempthorne (1957). Some important genetic parameters such as additive variance, non-additive variance, degree of dominance (d), broad-sense heritability (h_b^2) and narrow-sense heritability (h_n^2) were also estimated according to Falconar and Mackey (1996).

RESULTS AND DISCUSSION

Analysis of variance (ANOVA)

Analysis of variance showed that effects of genotype, parents and crosses were significant for all the studied traits (Table 1). However, effects of lines and testers were not significant. The non-significance of the mean squares due to lines and testers indicates the prevalence of non-additive variance (Singh and Kumar, 2004). Line × tester effect was significant for all studied traits, except for 100-kernel weight. Therefore, line × tester analysis was done only for tiller number, number of total kernels,

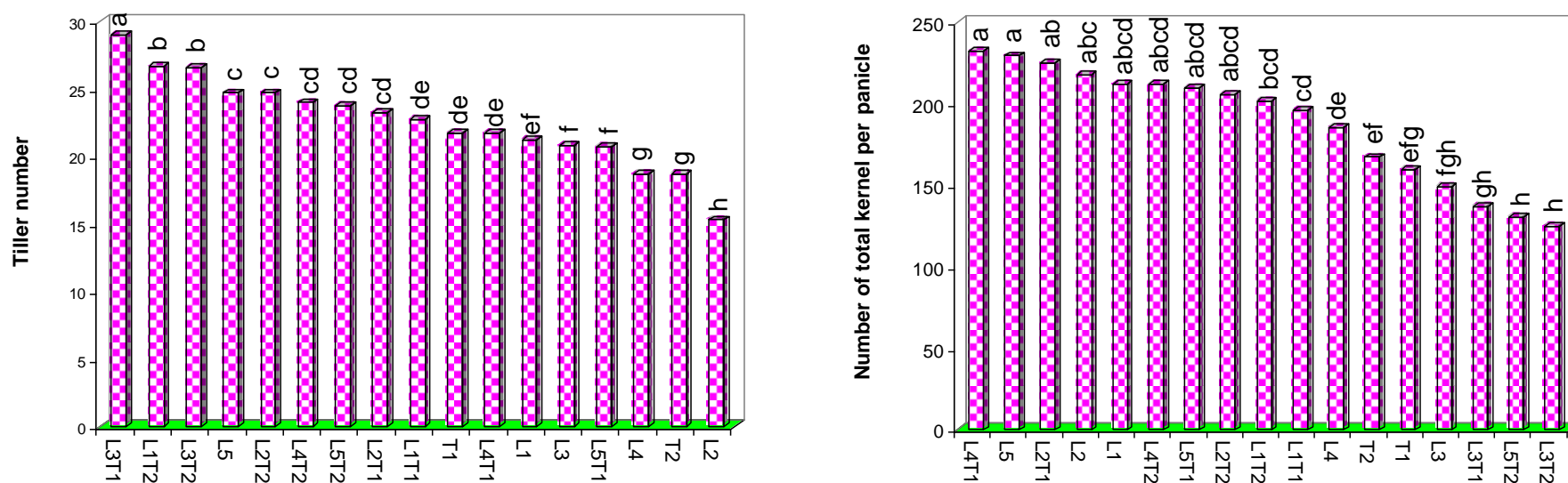


Figure 1. Mean performance of lines, testers and their hybrids for different yield traits in the study. Means with common letters have no significant difference at 5% level of probability.

number of filled kernels and plant yield. Significant mean square of parents vs. crosses for tiller number, number of filled kernels and yield indicated that crosses differed from the parents significantly; therefore, it is inferred that variations in the cases of the earlier mentioned traits were transmitted to progeny (Saleem et al., 2010).

Mean performance of studied genotypes are shown in Figure 1. Among parents, in the case of tiller number, lines L5 and L2 showed highest and lowest values, respectively (24.7 and 15.3 tillers/plant). For total number of kernels per panicle, again line L5 showed the highest value (229.1 kernels) and line L3 showed the lowest value (148.5 kernels). In the case of filled kernels per panicle, line L2 showed the highest value (168 filled kernels) and line L3 showed the lowest value (104.3 filled kernels). For 100-kernel weight, line L4 showed the highest value (3.54 g) and tester

T2 showed the lowest value (2.2 g). Finally, in the case of yield per plant, line L4 showed the highest yield (77.5 g/plant) and tester T2 showed the lowest value (34.4 g). Among hybrids, combination L3T1 showed the highest value for tiller number (29.1 tillers/plant) and L5T1 showed the lowest value (20.7 tillers/plant). For total number of kernels per panicle, combination L4T1 showed the highest value (232 kernels/panicle) and L3T2 showed the lowest value (124.3 kernels/panicle). In the case of filled kernels per panicle, hybrid L1T2 showed the highest value (3.1 g) and L5T1 showed the lowest value (2.49 g). Finally, in the case of yield, hybrids L2T2 and L4T1 showed the highest and the lowest yield per plant, respectively (68.2 and 24 g/plant) (Figure 1).

Heterosis study

In tiller number, the highest significant MP-based heterosis was estimated for L3T1 and L2T2 (7.8 and 7.7, respectively), and the highest significant BP-based heterosis was estimated for L3T2 and L3T1 (7.9 and 7.3, respectively) (Table 2). In total number of kernels, the highest significant MP-based heterosis was estimated for L4T1 and L2T1 (59.7 and 36.2, respectively), and the highest significant BP-based heterosis was estimated for L4T1 (46.8). For filled kernels per panicle, no hybrid showed positive significant MP and BP-based heterosis. For 100-kernel weight, the highest significant MP-based heterosis was estimated for L1T2 and L5T2 (0.62 and 0.52 g, respectively) and the highest significant BP-based heterosis was estimated for the same hybrids (0.35 and 0.26 g, respectively). In the case of

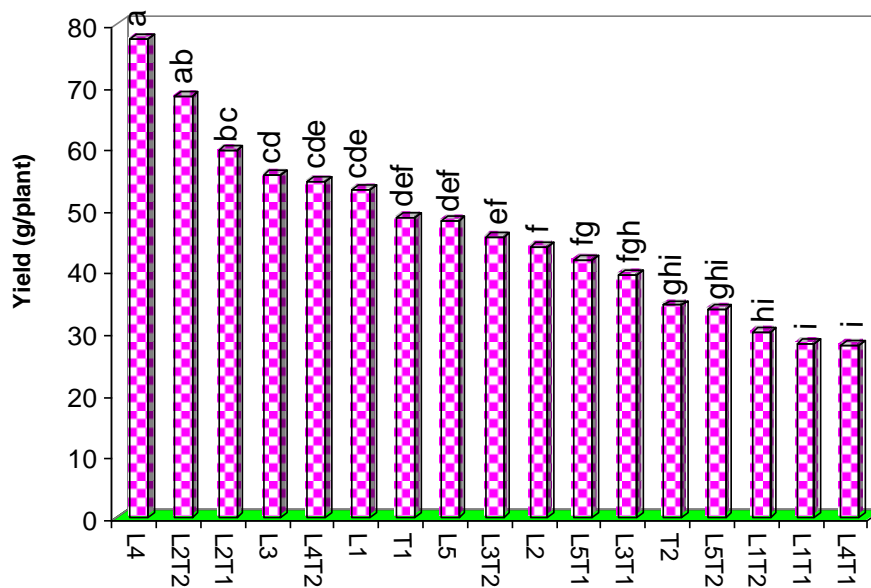
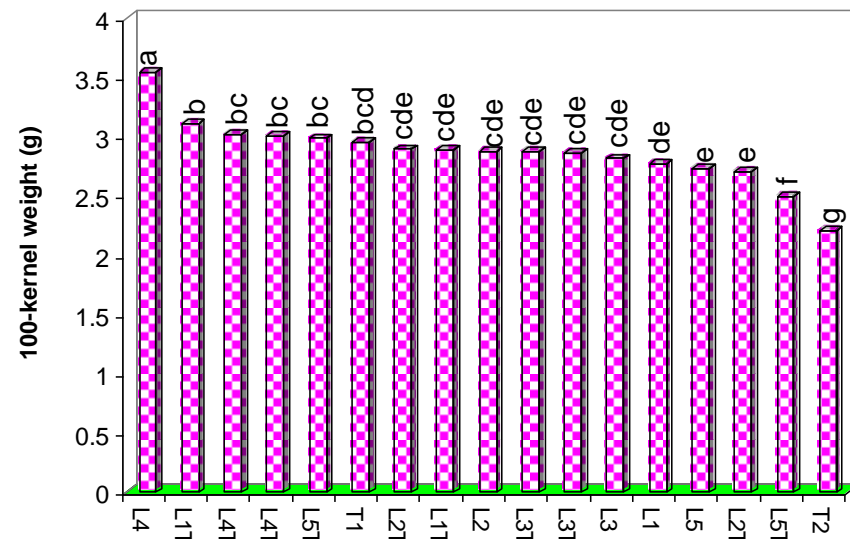
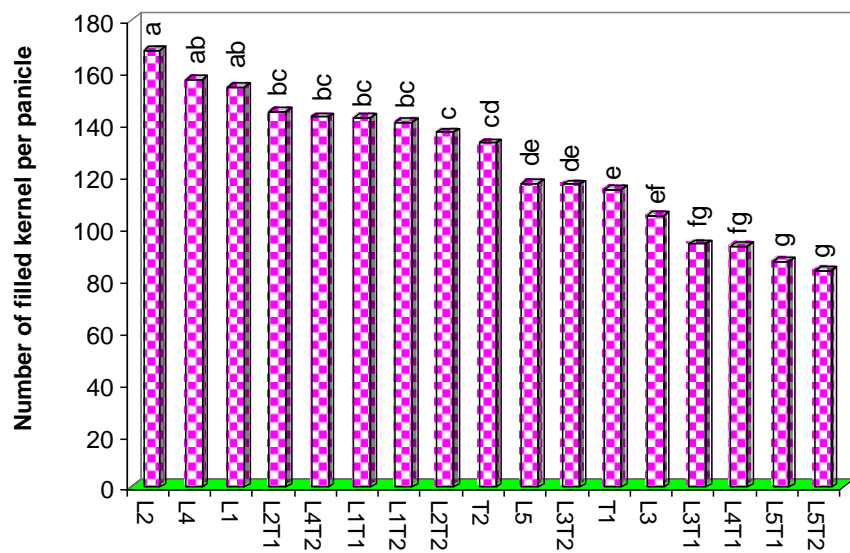


Figure 1. Contd.

Table 2. Values of mid-parent (MP) and better parent (BP) heterosis for yield and its components.

Parameter	Tiller number		Total kernel		Number of filled kernel		100-kernel weight (g)		Yield (g/plant)	
	MP	BP	MP	BP	MP	BP	MP	BP	MP	BP
L1T1	1.3	1.0	9.9	-16.2	8.1	-11.5	0.03	-0.07	-22.8**	-25.1**
L1T2	6.8**	5.5**	11.7	-10.6	-2.7	-13.3	0.62**	0.35**	-13.7**	-23.1**
L2T1	4.7**	1.5*	36.2*	7.3	3.3	-23.4**	-0.21*	-0.25*	13.23**	10.8*
L2T2	7.7**	6.0**	13.2	-12.1	-13.6	-31.4**	0.35**	0.01	29.03**	24.3**
L3T1	7.8**	7.3**	-17.6	-23.1	-15.8	-20.9*	-0.02	-0.08	-12.8**	-16.2**
L3T2	6.8**	7.9**	-26.7	-24.2	-1.8	12.2	0.36**	0.06	0.49	-10.0*
L4T1	1.5	3.0**	59.7**	46.8**	-42.8**	-64.0**	-0.25*	-0.55**	-35.04**	-49.5**
L4T2	5.3**	5.3**	35.4*	26.2	-2.2	-14.3	0.14	-0.53**	-1.45	-23.0**
L5T1	-2.5**	-4.1**	14.9	-19.9	-28.9**	-30.2**	-0.35**	-0.24*	-6.58	-6.4
L5T2	2.0*	-1.07	-68.0**	-99.1**	-41.2**	-33.5**	0.52**	0.26*	-7.66	-14.6**
S.E	0.739		13.7		8.37		0.102		4.607	

* and ** indicate significance at 5 and 1% level of probability, respectively.

Table 3. Analysis of combining ability effects of yield traits in the experiment.

S.O.V	Mean square			
	Tiller number	Total number of kernel	Number of filled kernels	Yield
GCA	0.46	158.1**	53.44**	15.92**
SCA	2.52**	322.2**	225.30**	58.61**
Error	0.331	6.13	3.744	2.06
$\delta_{GCA}^2 / \delta_{SCA}^2$	0.183	0.491	0.237	0.272

* and ** indicate significance at 5 and 1% level of probability, respectively.

yield, the highest significant MP-based heterosis was estimated for L2T2 and L2T1 (29 and 13.2 g/plant, respectively), and the highest significant BP-based heterosis was estimated for the same hybrids (24.3 and 10.8 g/plant, respectively).

GCA and SCA values

Analysis of combining ability effects is shown in Table 3. GCA effect was significant for total number of kernels, number of filled kernels and yield per plant, and SCA effect was significant for all mentioned traits. This shows the contribution of both additive and non-additive effects in genetic control of total number of kernels, number of filled kernels and yield per plant, and highly preponderance of non-additive effects in control of tiller number. $\delta_{GCA}^2 / \delta_{SCA}^2$ ratio in all cases was less than 0.5, showing that non-additive effects are preponderant in the control of all studied traits. Importance of non-additive gene action in the expression of yield-related traits was reported by Pradhan et al. (2006) who stated that $\delta_{GCA}^2 / \delta_{SCA}^2$ ratio was less than unity. Similar results

were also reported by Ganesan et al. (1997), Ramalingam et al. (1997), Ganesan and Rangaswamy (1998) and Thirumeni et al. (2000).

GCA values of parents are shown in Table 4. As shown, in tiller number, only line L3 (IR36) and tester T2 had highest significant GCA (3.51 and 0.84, respectively); that is, these two parents were better general combiners for tiller number. In contrast, lines L5 and L4 and tester T1 had significant negative GCA; that is, the use of these parents in breeding programs reduces tiller number. Lines L4 and L2 and tester T1 showed the highest significant GCA for total number of kernels per panicle (34.8, 27.97 and 12.6, respectively), while line L3 and tester T2 showed the highest significant negative GCA for the trait (-56.6 and -12.6, respectively). These results indicate that two lines, L4 and L2, and tester T1 are good general combiners for improving total number of kernels per panicle and the use of these parents in breeding programs increases the trait value. In the case of number of filled kernels per panicle, lines L1 and L2 showed the highest significant GCA (23.3 and 22.7, respectively), indicating that these lines are good general combiners for improving the trait value. In yield performance, only line L2 showed the highest significant GCA (20.9 g/plant).

Table 4. Estimated GCA values of parents for yield traits in the experiment.

Parents	Tiller number	Total number of kernel	Number of filled kernel	Yield (g/plant)
Lines				
L1	0.393	11.2	23.31**	-13.71**
L2	-0.357	27.97**	22.66**	20.94**
L3	3.51**	-56.6**	-12.9*	-0.512
L4	-1.44**	34.79**	-0.29	-1.604
L5	-2.107**	-17.4	-32.8**	-5.112
S.E (gi)	0.523	9.69	5.919	3.258
Testers				
T1	-0.84*	12.56*	-5.94	-3.516
T2	0.84*	-12.56*	5.943	3.516
S.E(gi)	0.331	6.13	3.744	2.06

* and ** indicate significance at 5 and 1% level of probability, respectively.

Table 5. Estimated SCA values in different hybrid combinations for yield traits.

Combination	Tiller number	Total number of kernel	Number of filled kernel	Yield (g/plant)
L1T1	-1.16	-15.33	6.9	2.52
L1T2	1.16	15.33	-6.9	-2.52
L2T1	0.09	-2.9	9.9	-0.83
L2T2	-0.09	2.9	-9.9	0.83
L3T1	2.057**	-6.5	-5.5	0.42
L3T2	-2.057**	6.5	5.5	-0.42
L4T1	-0.327	-2.28	-18.9*	-9.72*
L4T2	0.327	2.28	18.9*	9.72*
L5T1	-0.66	27.0	7.6	7.61
L5T2	0.66	-27.0	-7.6	-7.61
S.E(sca)	0.739	13.7	8.37	4.61

* and ** indicate significance at 5 and 1% level of probability, respectively.

Since the other two traits (total number of kernels and number of filled kernels) also showed significant GCA in this line, it can be concluded that these traits are most important yield components in this line. SCA values of the hybrids are shown in Table 5. As shown, in the case of tiller number, only L3T1 and L3T2 showed significant SCA at 1% level in opposite directions (2.06 and -2.06, respectively). In the case of number of filled kernels, combinations L4T1 and L4T2 showed significant SCA at 5% level in opposite directions (-18.9 and 18.9, respectively) and in the case of yield, combinations L4T1 and L4T2 showed significant SCA at 5% level in opposite directions (-9.7 and 9.7 g/plant, respectively). The SCA values of these hybrids were high enough, so hybridization can be a choice for improving hybrids with higher yield. In the case of total number of kernels, no significant SCA was observed. However, Marilia et al. (2001) noted that SCA effects of hybrids alone had limited power for parental selection in breeding programs, such as hybrid means and GCA of the respective

parents.

Genetic parameters

Important estimated genetic parameters are shown in Table 6. Additive and non-additive variances were significant for all studied traits. However, non-additive effects played more important role as confirmed by value of degree of dominance (d). This parameter in all cases was estimated to be >1, indicating that over-dominance is preponderant in controlling the studied traits. Several workers also reported the predominance of dominant gene action for a majority of the yield traits (Peng and Virmani, 1999; Ramalingan et al., 1993; Satyanarayana et al., 2000; Kumar et al., 2004), while Vijay Kumar et al. (1994) reported the predominance of additive gene and must be used in combination with other parameters action. Preponderance of non-additive gene action in the expression of yield and yield-related traits, was also

Table 6. Genetic parameters estimated for yield traits.

Parameter	Tiller number	Total number of kernel	Number of filled kernels	Yield (g/plant)
σ^2_A	0.922**	316.1**	106.9**	31.85**
S.E(σ^2_A)	0.331	6.13	3.74	2.06
σ^2_D	2.517**	322.2**	225.3**	58.61**
S.E(σ^2_D)	0.739	13.7	8.37	4.61
σ^2_P	41.93	1937.6	739.1	219.96
σ^2_G	40.29	1374.3	528.9	156.27
σ^2_E	1.639	563.27	210.2	63.68
d	2.336	1.43	2.05	1.92
h_b^2 (%)	96.1	70.9	71.6	71.0
h_n^2 (%)	18.2	26.3	19.7	20.7

* and ** indicate significance at 5 and 1% level of probability, respectively.

reported by Pradhan et al. (2006), Ganesan et al. (1997), Ramalingam et al. (1997), Ganesan and Rangaswamy (1998) and Thirumeni et al. (2000).

The highest general heritability (h_b^2) was obtained for tiller number (96.1%), indicating slight effects of environment on the trait. However, a mild h_b^2 (~71%) was obtained for the remaining traits, indicating that the environment had relatively large effects on these traits (Pradhan et al., 2006; Saleem et al., 2010). In all cases, a low specific heritability (h_n^2) was obtained (18.2 to 26.3%), although the highest specific heritability was calculated for total number of kernels (26.3%), again indicating that non-additive effects play an important role in controlling the traits. Ahmadikhah (2008) also reported a low specific heritability for yield-related traits and Wu et al. (1986) reported a low specific heritability for tiller number and grain yield. Therefore, it seems that hybridization must be a choice for utilizing the putative heterosis in special crosses.

Abbreviations

ANOVA, Analysis of variance; **S.E.**, standard error; **GCA**, general combining ability; **SCA**, specific combining ability; **MP**, mid-parent; **BP**, better parent; δ_A^2 , additive variance; δ_D^2 , dominance variance; δ_G^2 , genotypic variance; δ_P^2 , phenotypic variance; δ_E^2 , environmental variance; h_b^2 , general heritability; h_n^2 , specific heritability; **d**, degree of dominance.

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