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Estimation of genetic components for grain yield and quality traits of rice

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ABSTRACT

The nature of gene interaction in the inheritance of sixteen yield and seven grain quality traits was studied deploying generation mean analysis following 6 parameter model for parents, F_1, F_2, BC_1 and BC_2 generations of three crosses of rice, during wet season. The additive gene effect was significant for all the characters except florets panicle^{-1}, grain length, cooked kernel breadth and cooked kernel L/B ratio in IET 6441 × Dudheswar, grain yield plant^{-1} in IET 8002 × Basmati 385 and cooked kernel length in IET 8002 × Sambamahsuri, while dominance effect was significant for all the characters except days to 50% flowering, panicle length, florets panicle^{-1} and kernel length in IET 6441 × Dudheswar, except for total tillers plant^{-1}, productive tillers plant^{-1}, panicle length, florets panicle^{-1}, filled grains panicle^{-1}, floret fertility, 1000 seed weight, grain yield plant^{-1}, harvest index and cooked kernel L/B ratio in the cross IET 8002 × Basmati 385 and except for panicle length, panicle weight, florets panicle^{-1}, filled grains panicle^{-1}, floret fertility, grain weight panicle^{-1}, grain yield plant^{-1}. Duplicate epistasis played an important role in the inheritance of all the yield and quality related traits except days to 50% flowering, panicle length, florets panicle^{-1} and kernel length in IET 6441 × Dudheswar.

Key words: *rice, generation means, epistasis, quality traits*

Rice is the principal food crop of India and breeding for higher yield is of prime importance. In the Indian scenario, it is estimated that rice demand in 2010 will be 100 million tonnes and in 2025, the demand will be 140 million tonnes (Mishra, 2004). This projected demand can only be met by maintaining steady increase in production over the years. At the same time improvement in rice grain quality has become an important breeding objective as many countries have achieved rice self sufficiency (Juliano and Duff, 1991). The knowledge on the nature of gene action in the inheritance of yield and quality related traits would be useful to formulate a suitable breeding programme and develop better cultivars with higher yield and superior grain quality. Keeping this in view, the present study was initiated to investigate the gene effects controlling different quantitative traits relative to yield and grain quality, deploying appropriate model of generation means analysis. A number of studies have been carried out in the past to study the inheritance of quantitative traits in rice using the generation means analysis (Somrith *et al.*, 1979 and Roy and Panwar, 1993).

MATERIALS AND METHODS

The experimental material consisted of five diverse rice genotypes namely IET 6441, IET 8002, Dudheswar, Basmati 385 and Sambamahsuri among which three crosses namely IET 6441 × Dudheswar, IET 8002 × Basmati 385 and IET 8002 × Sambamahsuri were carried out. The female parents IET 6441 and IET 8002 were semidwarf high yielders whereas, the male parents Dudheswar and Basmati 385 were tall and superior grain quality genotypes and Sambamahsuri was a semidwarf high yielding genotype with fine grain quality. Six generations namely P_1, P_2, F_1, F_2, BC_1 and BC_2 of the three crosses were raised in a randomized block design with four replications during wet season 2004-05 at Bidhan Chandra Krishi Viswavidyalaya, Sub-centre Chakdah, West Bengal. In each replication every entry was transplanted with a single seedling per hill in five rows of 1.8 m length with a spacing of 20 cm between and within the rows. The recommended agronomic practices were followed to obtain a good harvest. For P_1, P_2 and F_1 observations were recorded on five randomly selected plants in each entry in each replication. For BC_1 and BC_2 observations were recorded from 20 randomly selected plants whereas, for F_2 observations were recorded from 40 randomly selected plants in each entry in each replication for the characters plant height (cm), total tillers plant^{-1}, productive tillers plant^{-1}, grain yield (g) plant^{-1} and harvest index (%), but for days to 50% flowering observations were recorded per plot. For panicle traits like panicle length (cm), panicle weight (g), florets panicle^{-1}, filled grains panicle^{-1} and floret fertility, observations were recorded from 10 randomly selected panicles. Observations on grain characters like grain length (mm), grain breadth (mm) and grain L/B ratio were recorded from 10 randomly selected grains. The polished rice samples were analyzed after six months of ageing for the seven quality triats viz. kernel length (mm), kernel breadth (mm), kernel L/B ratio, cooked kernel length (mm), cooked kernel breadth (mm), cooked kernel L/B ratio and linear elongation ratio by recording observations from 10 randomly selected kernels in the laboratory following standard methods (Murthy and Govindaswamy, 1967, Juliano *et al*., 1965 and Little *et al*., 1958). The mean values were used for four scaling tests suggested by Mather (1949) and for calculation of the gene effects from the 6-parameter model suggested by Jinks and Jones (1958). The joint scaling test as proposed by Cavalli (1952) 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 more informative approach.

RESULTS AND DISCUSSION

The analysis of variance of the six generations P_1, P_2, F_1, F_2, BC_1 and BC_2 revealed that the six generations differed significantly for all the 16 yield and seven grain quality traits in the three crosses except for florets/ panicle by the cross C_1. As compared to IET 6441, Dudheswar was the better performer for most of the yield related traits except florets panicle^{-1} and grain breadth whereas, IET 6441 outperformed Dudheswar for most of the grain quality traits except kernel length, kernel L/B ratio and cooked kernel breadth (Table 1). IET 8002 performed better than Basmati 385 in 10 out of 16 yield related traits viz. days to 50% flowering, panicle weight, florets panicle^{-1}, filled grains panicle^{-1}, floret fertility, grain breadth, grain weight panicle^{-1}, 1000 seed weight, grain yield plant^{-1} and harvest index whereas, Basmati 385 outperformed IET 8002 for most of the grain quality traits namely kernel length, kernel L/B ratio, cooked kernel length, cooked kernel L/B ratio and linear elongation ratio. The parent IET 8002 showed superior performance than Sambamahsuri in 12 out of 16 yield related traits except days to 50% flowering, total tillers/plant, productive tillers/plant and grain L/B ratio and in three out of seven quality traits namely kernel length, kernel breadth and cooked kernel breadth.

In case of productive tillers per plant and kernel L/B ratio in the cross combination C_1 and days to 50% flowering, total tillers plant^{-1}, productive tillers plant^{-1}, floret fertility, grain breadth, 1000 seed weight and kernel breadth in the cross C_2 and floret fertility, grain length, grain breadth, 1000 seed weight and kernel length in the cross C_3, the F_1 mean performance was midway between the parental values with inclination towards better parent. This indicated that additive gene effects may be more important for these traits (Table 1). The estimates of gene effects also revealed a similar picture. The low mean performance of F_2's as compared to F_1's was observed for plant height, panicle weight, grain breadth, grain weight panicle^{-1}, 1000 seed weight, grain yield plant^{-1} and kernel breadth indicating inbreeding depression of rice as reported by Sharma *et al*. (1986) and Krishna Veni *et al*. (2005). The value of BC_2 was higher than BC_1 in respect of all the characters studied, except for days to 50% flowering, total tillers plant^{-1}, productive tillers plant^{-1}, grain breadth, grain weight panicle^{-1}, 1000 seed weight, kernel breadth and cooked kernel breadth in the cross C_1 and for days to 50% flowering, total tillers plant^{-1}, panicle weight, florets panicle^{-1}, filled grains panicle^{-1}, floret fertility, grain breadth, grain weight panicle^{-1}, grain yield plant^{-1}, harvest index, kernel breadth and cooked kernel breadth in the cross C_2 and for plant height, panicle length, panicle weight, florets panicle^{-1}, filled grains panicle^{-1}, grain length, grain breadth, grain weight panicle^{-1}, kernel length, kernel breadth, cooked kernel length, cooked kernel breadth, cooked kernel L/B ratio and linear elongation ratio in the cross IET 8002 x Sambamahsuri.

The results of the scaling tests as proposed by Mather (1949) revealed that the additive-dominance model was inadequate in respect of all the characters evaluated except days to 50% flowering and panicle length in the cross C_1, productive tillers plant^{-1}, 1000 seed weight and harvest index in the cross C_2 and kernel

Table 1. Mean performance of different generations of three crosses for grain yield and quality traits in rice

Treatment	Plant height (cm)	Days to 50% flowering	Total tillers plant^{-1}	Productive tillers plant^{-1}	Panicle length (cm)	Panicle weight (g)	Florets panicle^{-1}	Filled grains panicle^{-1}	Floret fertility (%)	Grain length (mm)	Grain breadth (mm)	Grain L/B ratio
C_1 (IET 6441 x Dudheswar)												
P_1 (IET 6441)	89.46	118.75	16.63	10.83	22.04	2.44	159.75	102.35	66.17	8.02	2.44	3.29
P_2 (Dudheswar)	142.20	115.25	27.20	22.10	23.78	2.98	157.85	120.20	82.60	8.17	2.33	3.50
F_1 (P_1 x P_2)	145.72	113.50	27.44	21.66	25.46	3.40	190.75	169.30	88.80	8.31	2.31	3.60
F_2	141.35	114.25	22.85	18.38	23.43	2.30	153.90	135.13	79.81	8.06	1.98	4.08
BC_1 (F_1 x P_1)	114.00	115.25	23.35	16.56	23.42	3.40	155.70	142.36	88.26	8.04	2.68	2.99
BC_2 (F_1 x P_2)	148.13	115.25	17.06	12.35	23.80	3.41	164.07	160.67	92.78	8.37	2.37	3.54
Mean	130.14	115.38	22.42	16.98	23.65	2.99	163.67	138.34	83.07	8.16	2.35	3.50
SEm (±)	1.83	0.62	1.31	1.18	0.37	0.17	9.05	4.74	1.55	0.05	0.02	0.04
CD (P=0.05)	5.51	1.87	3.95	3.56	1.11	0.51	27.27	14.28	4.67	0.15	0.06	0.12
C_2 (IET 8002 x Basmati 385)												
P_1 (IET 8002)	111.50	127.75	14.13	10.63	21.75	2.97	133.07	121.25	88.06	8.04	2.73	2.95
P_2 (Basmati 385)	118.13	130.00	22.69	19.53	25.32	1.53	89.75	64.70	76.83	9.32	2.02	4.63
F_1 (P_1 x P_2)	125.00	130.75	21.50	17.50	26.04	3.78	198.73	168.80	84.76	8.05	2.68	3.01
F_2	120.06	124.75	22.56	17.72	25.34	2.56	155.25	105.30	89.38	8.75	2.32	3.78
BC_1 (F_1 x P_1)	116.10	125.25	19.67	13.97	23.61	3.41	143.20	131.07	92.19	7.99	2.68	2.98
BC_2 (F_1 x P_2)	130.75	124.25	17.25	16.19	24.63	2.32	120.54	95.10	80.95	8.68	2.42	3.58
Mean	120.26	127.13	19.63	15.92	24.45	2.76	140.09	114.37	85.36	8.47	2.47	3.49
SEm (±)	1.26	0.39	1.57	1.19	0.63	0.17	6.64	5.74	1.76	0.05	0.03	0.05
CD (P=0.05)	3.80	1.18	4.73	3.59	1.90	0.51	20.01	17.29	5.30	0.15	0.09	0.15
C_3 (IET 8002 x Sambamahsuri)												
P_1 (IET 8002)	111.53	128.25	14.35	11.08	22.05	2.97	129.65	121.86	87.78	8.03	2.73	2.95
P_2 (Sambamahsuri)	63.85	118.00	19.00	15.28	18.29	1.33	115.30	82.13	72.44	7.47	1.99	3.80
F_1 (P_1 x P_2)	116.25	117.75	23.50	19.53	23.69	3.10	161.25	146.92	87.56	7.98	2.65	3.01
F_2	101.41	116.00	23.00	17.56	24.31	2.81	174.25	154.87	88.77	8.10	2.22	3.65
BC_1 (F_1 x P_1)	114.44	114.00	16.47	13.16	22.75	3.29	159.05	156.83	89.14	8.19	2.67	3.07
BC_2 (F_1 x P_2)	110.63	115.00	18.19	15.35	22.66	2.61	138.15	117.40	89.90	8.13	2.42	3.36
Mean	103.02	116.67	19.09	15.33	22.29	2.68	146.28	130.00	85.93	7.98	2.45	3.31
SEm (±)	1.55	0.46	1.11	0.92	0.65	0.15	9.01	5.29	2.21	0.05	0.03	0.06
CD (P=0.05)	4.67	1.39	3.34	2.77	1.96	0.45	27.15	15.94	6.66	0.15	0.09	0.18

breadth and kernel L/B ratio in the cross C_3 therefore, it suggested the existence of epistasis in the inheritance of these characters (Table 2). These findings were further substantiated by the more robust "Joint Scaling Test" proposed by Cavalli (1952), in which the significant Chi-square values indicated the presence of epistasis and non significant Chi-square values indicated the absence of epistasis in the inheritance of the morpho-physiological characters studied (Table 3). A perusal of six parameter model suggested by Jinks and Jones (1958) indicated that additive effect (d) was significant for all the characters except florets panicle^{-1}, grain length, cooked kernel breadth and cooked kernel L/B ratio in C_1, grain yield/plant in C_2 and cooked kernel length in C_3, while dominance effect (h) was significant for all the characters except days to 50% flowering, panicle length, florets panicle^{-1} and kernel length in the cross C_1, total tillers plant^{-1}, productive tillers plant^{-1}, panicle length, florets panicle^{-1}, filled grains panicle^{-1}, floret fertility, 1000 seed weight, grain yield plant^{-1}, harvest index and cooked kernel L/B ratio in the cross C_2 and panicle length, panicle weight, florets panicle^{-1}, filled grains panicle^{-1}, floret fertility, grain weight panicle^{-1}, grain yield plant^{-1}, harvest index, kernel breadth, kernel L/B ratio and cooked kernel breadth in the cross C_3. However, all the genetic components were significant for the traits plant height, total tillers/plant, productive tillers/plant, grain breadth, grain L/B ratio,

Table 2. Mean performance of different generations of three crosses for quality traits in rice

Treatment	Grain weight panicle^{-1} (g)	1000 seed weight (g)	Grain yield plant(g)$^{-1}$	Harvest Index (%)	Kernel length (mm)	Kernel breadth (mm)	Kernel L/B ratio	Cooked kernel length (mm)	Cooked kernel breadth (mm)	Cooked kernel L/B ratio	Linear elongation ratio
C_1 (IET 6441 x Dudheswar)											
P_1 (IET 6441)	2.01	19.09	25.54	31.35	5.84	2.38	2.46	10.35	3.00	3.34	1.72
P_2 (Dudheswar)	2.56	21.18	55.57	36.37	5.97	2.15	2.79	9.42	3.04	3.11	1.58
F_1 (P_1 x P_2)	3.74	22.89	64.19	37.87	5.82	2.17	2.69	9.42	3.00	3.14	1.62
F_2	2.10	17.09	32.44	30.45	5.64	1.72	3.28	9.17	2.48	3.71	1.63
BC_1 (F_1 x P_1)	3.54	24.61	47.56	32.10	5.75	2.44	2.36	8.46	3.31	2.56	1.47
BC_2 (F_1 x P_2)	3.33	20.95	54.34	41.38	5.83	2.10	2.78	9.42	2.80	3.39	1.62
Mean	2.88	20.97	46.60	34.92	5.81	2.16	2.72	9.37	2.94	3.21	1.61
SEm (±)	0.10	0.45	4.30	0.77	0.02	0.03	0.04	0.21	0.09	0.11	0.03
CD (P=0.05)	0.30	1.36	12.96	2.32	0.06	0.09	0.12	0.63	0.27	0.33	0.09
C_2 (IET 8002 x Basmati 385)											
P_1 (IET 8002)	2.79	25.40	28.03	32.64	5.81	2.40	2.37	9.59	3.00	3.16	1.52
P_2 (Basmati 385)	1.37	20.32	22.51	28.35	6.64	1.89	3.52	11.59	2.70	4.29	1.74
F_1 (P_1 x P_2)	3.99	23.71	60.92	43.86	5.97	2.25	2.66	9.11	3.20	2.86	1.53
F_2	2.51	23.40	39.68	38.70	6.22	2.10	2.97	10.25	2.89	3.56	1.65
BC_1 (F_1 x P_1)	3.03	23.93	39.34	36.16	5.77	2.48	2.33	9.84	3.17	3.11	1.71
BC_2 (F_1 x P_2)	2.36	24.20	32.20	35.55	6.24	2.10	2.97	12.33	3.03	4.10	1.98
Mean	2.68	23.49	37.11	35.88	6.08	2.20	2.80	10.28	3.05	3.42	1.69
SEm (±)	0.10	0.75	2.62	1.04	0.02	0.03	0.04	0.24	0.08	0.14	0.04
CD (P=0.05)	0.30	2.26	7.89	3.13	0.06	0.09	0.12	0.72	0.24	0.42	0.12
C_3 (IET 8002 x Sambamahsuri)											
P_1 (IET 8002)	2.73	25.35	26.78	32.14	5.86	2.41	2.44	9.65	2.97	3.22	1.64
P_2(Sambamahsuri)	0.97	12.45	17.53	27.61	5.10	1.77	2.88	10.25	2.69	3.82	2.01
F_1 (P_1 x P_2)	3.29	23.51	51.06	34.40	5.64	2.42	2.33	10.25	3.06	3.35	1.82
F_2	3.20	21.53	45.39	39.66	5.61	2.27	2.47	11.00	3.06	3.60	1.96
BC_1 (F_1 x P_1)	3.46	23.40	36.07	33.86	5.73	2.45	2.34	10.04	3.21	3.13	1.75
BC_2 (F_1 x P_2)	2.95	25.43	42.41	46.23	5.60	2.10	2.67	8.13	2.88	2.82	1.45
Mean	2.76	21.95	36.54	35.58	5.59	2.24	2.52	9.89	2.98	3.32	1.77
SEm (±)	0.17	0.76	2.40	1.81	0.04	0.03	0.04	0.22	0.06	0.10	0.04
CD (P=0.05)	0.51	2.29	7.23	5.45	0.12	0.09	0.12	0.66	0.18	0.30	0.12

grain weight/panicle and kernel L/B ratio in the cross C_1, for plant height, grain breadth, grain L/B ratio, kernel breadth, kernel L/B ratio, cooked kernel length and linear elongation ratio in the cross C_2 and for plant height, days to 50% flowering, cooked kernel L/B ratio and linear elongation ratio in the cross C_2 and for plant height, days to 50% flowering, cooked kernel L/B ratio and linear elongation ratio in the cross C_3. When the complexity of the inheritance of quantitative characters become more, the contribution of dominance gene effects to their inheritance becomes greater (Gamble, 1962). Conversely, the contribution of additive gene effects was greater for the characters which apparently had less complex inheritance.

Among the components of epistasis, additive × additive interaction was significant and important in all the three crosses for plant height, total tillers/plant, grain breadth, grain L/B ratio, additive × dominance interaction was found to be operative in all the three crosses for plant height, kernel L/B ratio, cooked kernel length and linear elongation ratio whereas, dominance × dominance interaction was significant in all the three crosses for plant height, grain breadth, grain L/B ratio, cooked kernel length and linear elongation ratio. These results are in close agreement with earlier findings of Khaleque *et al*. (1978) and Manna *et al*. (2002). The higher magnitude of estimates of dominance × dominance interaction as compared to additive × additive and additive × dominance interactions suggest the predominant role of dominance × dominance interaction for grain yield, quality and their components which corroborated with the observations of Dikshit

Table 3. Scaling test and gene effects of grain yield and quality characters in three crosses of rice

Cross	Scale				Genetic component						Epistasis
	A	B	C	D	m	(d)	(h)	(i)	(j)	(l)	
Plant height (cm)											
C_1	-7.18**	8.33**	42.28**	20.57**	156.96*	-26.37**	-51.22*	-41.13**	-7.76**	39.98**	D
	(1.45)	(3.91)	(10.11)	(4.69)	* (9.55)	(1.77)	(19.86)	(9.39)	(1.96)	(10.63)	
C_2	-4.31*	18.38**	0.63	-6.72*	101.37*	-3.31**	51.13**	13.44*	-11.34**	-27.51*	D
	(2.17)	(5.08)	(4.28)	(3.20)	* (6.43)	(0.72)	(17.43)	(6.39)	(2.70)	(11.27)	
C_3	1.10	41.15**	-2.25	-22.25**	43.19**	23.84**	159.80**	44.50**	-20.03**	-86.75**	D
	(3.92)	(2.40)	(9.63)	(5.05)	(10.12)	(0.58)	(22.25)	(10.10)	(2.13)	(12.64)	
Days to 50% flowering											
C_1	-1.75	1.75	-4.00	-2.00	113.00*	1.75**	4.50	4.00	-1.75	-4.00	-
	(1.60)	(1.11)	(2.41)	(1.17)	* (2.44)	(0.67)	(5.93)	(2.35)	(0.95)	(3.62)	
C_2	-8.00**	-12.25**	-20.25**	0.00	128.88**	-1.13**	-18.38**	0.00	2.13**	20.25**	D
	(1.17)	(0.90)	(1.68)	(0.74)	(1.49)	(0.24)	(3.88)	(1.47)	(0.59)	(2.74)	
C_3	-9.00**	-5.75**	-8.75**	3.00**	124.63**	0.63*	-27.63**	-6.00**	-1.63*	20.75**	D
	(1.06)	(1.03)	(2.00)	(1.00)	(2.03)	(0.32	(4.85)	(2.00)	(0.66)	(3.05)	
Total tillers per plant											
C_1	2.63	-20.51**	-7.32	5.28**	32.48**	-5.29**	-33.49**	-10.57**	11.57**	28.45**	D
	(3.31)	(3.95)	(5.01)	(1.99)	(4.10)	(1.01)	(11.76)	(3.97)	(2.08)	(8.83)	
C_2	3.71	-9.69*	10.44	8.21*	34.82**	-4.28**	-35.71	-16.42*	6.70*	22.39	-
	(3.86)	(3.96)	(7.19)	(4.00)	(8.07)	(1.06)	(19.52)	(8.00)	(2.62)	(11.98)	
C_3	-4.91*	-6.13**	11.65	11.34**	39.36**	-2.33**	-49.58**	-22.69**	0.61	33.72**	D
	(2.35)	(2.24)	(8.31)	(3.89)	(7.80)	(0.47)	(16.25)	(7.79)	(1.10)	(9.21)	
Productive tillers per plant											
C_1	0.64	-19.06**	-2.74	7.84**	32.15**	-5.64**	-44.59**	-15.69**	9.85**	34.11**	D
	(3.45)	(3.47)	(4.42)	(2.29)	(4.62)	(0.55)	(12.93)	(4.58)	(2.08)	(9.16)	
C_2	-0.19	-4.66	5.72	5.28	25.64**	-4.45**	-23.55	-10.57	2.24	15.41	-
	(3.06)	(2.60)	(6.56)	(3.41)	(6.89)	(1.03)	(15.73)	(6.81)	(1.92)	(9.21)	
C_3	-4.29	-4.12**	4.84	6.62*	26.42**	-2.10**	-28.54*	-13.25*	-0.09	21.66**	D
	(2.95)	(1.28)	(5.72)	(3.07)	(6.16)	(0.47)	(13.93)	(6.14)	(1.51)	(8.11)	
Panicle length (cm)											
C_1	-0.66	-1.64	-3.01	-0.36	22.20**	-0.87**	1.67	0.71	0.49	1.59	-
	(1.09)	(1.13)	(1.73)	(1.11)	(2.23)	(0.20)	(5.59)	(2.22)	(0.77)	(3.46)	
C_2	-0.57	-2.10**	2.21	2.44	28.42**	-1.79**	-9.93	-4.88	0.77	7.55	-
	(1.75)	(0.79)	(3.07)	(1.58)	(3.18)	(0.40)	(7.29)	(3.15)	(0.87)	(4.36)	
C_3	-0.25	3.34*	9.53*	3.22	26.61**	1.88**	-6.27	-6.44	-1.79*	3.35	-
	(1.00)	(1.61)	(3.77)	(1.97)	(3.96)	(0.36	(8.77)	(3.95)	(0.90)	(5.00)	
Panicle weight (g)											
C_1	0.97*	0.43	-3.02**	-2.21**	-1.71*	-0.27*	10.92**	4.42**	0.27	-5.81**	D
	(0.39)	(0.57)	(0.57)	(0.35)	(0.71)	(0.13)	(1.97)	(0.70)	(0.32)	(1.32)	
C_2	0.06	-0.67*	-1.80	-0.60	1.05	0.72**	3.32*	1.20	0.37*	-0.59	D
	(0.37)	(0.29)	(0.94)	(0.39)	(0.79)	(0.12)	(1.65)	(0.78)	(0.15)	(1.01)	
C_3	0.51*	0.79*	0.74	-0.28	1.58	0.82**	3.38	0.57	-0.14	-1.87	-
	(0.24)	(0.34)	(0.94)	(0.49)	(0.98)	(0.09)	(2.12)	(0.97)	(0.20)	(1.18)	
Florets per panicle											
C_1	-39.10*	-20.47	-83.50	-11.97	134.87*	0.95	20.26	23.94	-9.32	35.63	-
	(17.92)	(27.91)	(50.94)	(27.08)	(54.57)	(6.66)	(126.77)	(54.16)	(15.53)	(75.79)	
C_2	-45.40**	-47.41*	0.72	46.76*	204.93**	21.66**	-192.53	-93.53*	1.00	186.33**	-
	(10.01)	(19.29)	(42.60)	(22.85)	(45.76)	(2.34)	(101.96)	(45.70)	(10.26)	(58.39)	
C_3	27.20	-0.25	129.55**	51.30	225.08**	7.18**	-139.48	-102.60	13.73	75.65	-
	(29.15)	(12.37)	(47.92)	(26.90)	(53.86)	(2.61)	(126.23)	(53.80)	(14.89)	(75.71)	
Filled grains per panicle											
C_1	13.06	31.83	-20.62	-32.76**	45.75	-8.93**	233.98**	65.53**	-9.38	-110.43**	D
	(8.95)	(16.51)	(22.81)	(11.69)	(23.45)	(1.85)	(58.43)	(23.38)	(7.95)	(38.44)	
C_2	-27.92*	-43.30*	-102.35**	-15.57	61.84**	28.28**	66.88	31.14	7.69	40.08	-
	(11.91)	(18.47)	(17.26)	(9.47)	(19.15)	(2.81)	(56.27)	(18.95)	(9.53)	(40.32)	
C_3	44.89**	5.76	121.65**	35.50**	172.99**	19.87**	-46.44	-71.01**	19.57*	20.36	-
	(13.53)	(15.31)	(20.78)	(12.06)	(24.19)	(2.00)	(63.05)	(24.11)	(9.20)	(41.51)	

Contd. Table 3

Cross	Scale				Genetic component						Epistasis
	A	B	C	D	m	(d)	(h)	(i)	(j)	(l)	
Floret fertility (%)											
C_1	21.55**	14.16**	-7.13	-21.42**	31.54**	-8.21**	135.81**	42.84**	3.70	-78.55**	D
	(3.87)	(2.18)	(9.78)	(4.93)	(9.90)	(0.79)	(21.44)	(9.87)	(1.97)	(12.14)	
C_2	11.57**	0.31	23.12**	5.62*	93.69**	5.62**	-8.30	-11.25*	5.63	-0.63	-
	(3.94)	(5.18)	(5.67)	(2.80)	(5.84)	(1.71)	(16.47)	(5.59)	(2.99)	(11.32)	
C_3	2.94	19.80**	19.74	-1.50	77.11**	7.67**	36.19	3.00	-8.43**	-25.74	-
	(4.36)	(3.09)	(14.26)	(7.08)	(14.26)	(1.60)	(29.99)	(14.17)	(2.50)	(16.19)	
Grain length (mm)											
C_1	-0.25*	0.26*	-0.56*	-0.29*	7.52**	-0.08	1.37*	0.57*	-0.26**	-0.58	D
	(0.10)	(0.12)	(0.24)	(0.12)	(0.24)	(0.04)	(0.57)	(0.24)	(0.07)	(0.35)	
C_2	-0.09	-0.02	1.56**	0.83**	10.34**	-0.64**	-4.07**	-1.67**	-0.04	1.77**	D
	(0.07)	(0.15)	(0.24)	(0.12)	(0.25)	(0.04)	(0.58)	(0.25)	(0.08)	(0.35)	
C_3	0.36**	0.81**	0.95*	-0.11	7.52**	0.28**	1.85*	0.23	-0.23**	-1.41**	D
	(0.13)	(0.10)	(0.38)	(10.20)	(0.39)	(0.02)	(0.85)	(0.39)	(0.07)	(0.48)	
Grain breadth (mm)											
C_1	0.62**	0.09*	-1.49**	-1.10**	0.19*	0.05**	5.01**	2.19**	0.26**	-2.89**	D
	(0.04)	(0.03)	(0.10)	(0.04)	(0.09)	(0.01)	(0.19)	(0.08)	(0.02)	(0.12)	
C_2	-0.04	0.15**	-0.83**	-0.47**	1.43**	0.36**	2.30**	0.94**	-0.10**	-1.06**	D
	(0.05)	(0.05)	(0.19)	(0.10)	(0.19)	(0.01)	(0.41)	(0.19)	(0.03)	(0.23)	
C_3	-0.04	0.21	-1.12**	-0.65**	1.06**	0.37**	3.06**	1.30**	-0.12	-1.47**	D
	(0.06)	(0.13)	(0.12)	(0.09)	(0.18)	(0.01)	(0.47)	(0.18)	(0.07)	(0.30)	
Grain L/B ratio											
C_1	-0.89**	-0.02	2.35**	1.63**	6.66**	-0.11**	-7.23**	-3.26**	-0.44**	4.18**	D
	(0.07)	(0.07)	(0.28)	(0.13)	(0.27)	(0.03)	(0.56)	(0.27)	(0.04)	(0.31)	
C_2	0.01	-0.47**	1.53**	1.00**	5.78**	-0.84**	-5.24**	-1.99**	0.24**	2.46**	D
	(0.07)	(0.12)	(0.31)	(0.15)	(0.31)	(0.04)	(0.66)	(0.30)	(0.06)	(0.36)	
C_3	0.17	-0.08	1.82**	0.86**	5.10**	-0.43**	-3.72**	-1.73**	0.13	1.64**	D
	(0.10)	(0.22)	(0.27)	(0.17)	(0.34)	(0.02)	(0.85)	(0.34)	(0.12)	(0.53)	
Grain weight per panicle (g)											
C_1	1.33**	0.35	-3.66**	-2.67**	-3.05**	-0.27**	13.79**	5.33**	0.49*	-7.01**	D
	(0.26)	(0.31)	(0.27)	(0.20)	(0.41)	(0.05)	(1.16)	(0.40)	(0.19)	(0.78)	
C_2	-0.72*	-0.65**	-2.09**	-0.36*	1.36**	0.71**	1.99*	0.73*	-0.04	0.64	-
	(0.30)	(0.16)	(0.41)	(0.18)	(0.37)	(0.09)	(0.93)	(0.36)	(0.15)	(0.62)	
C_3	0.94	1.64**	2.56**	-0.01	1.81*	0.86**	4.08	0.02	-0.35	-2.60	-
	(0.64)	(0.32)	(0.68)	(0.44)	(0.88)	(0.07)	(2.29)	(0.88)	(0.34)	(1.48)	
1000 seed weight (g)											
C_1	7.24**	-2.17*	-17.67**	-11.37**	-2.61	-1.04**	53.32**	22.75**	4.70**	-27.82**	D
	(1.41)	(0.84)	(2.59)	(1.30)	(2.61)	(0.27)	(6.01)	(2.60)	(0.71)	(3.68)	
C_2	-1.27	4.38	0.44	-1.34	20.18**	2.54**	9.32	2.68	-2.82	-5.79	-
	(1.36)	(2.75)	(2.29)	(1.71)	(3.47)	(0.51)	(9.47)	(3.43)	(1.51)	(6.13)	
C_3	-2.06	14.89**	1.31	-5.76**	7.38	6.45**	40.49**	11.53**	-8.47**	-24.36**	D
	(1.76)	(1.86)	(4.37)	(2.09)	(4.17)	(0.15)	(9.42)	(4.17)	(0.98)	(5.85)	
Grain yield per plant (g)											
C_1	5.39	-11.07	-79.73**	-37.03**	-33.50	-15.02**	166.06**	74.05**	8.23	-68.38	D
	(9.68)	(15.15)	(7.32)	(8.90)	(17.88)	(1.62)	(52.82)	(17.81)	(8.81)	(35.39)	
C_2	-10.27	-19.03**	-13.66	7.82	40.90**	2.76	-24.90	-15.63	4.38	44.92*	D
	(9.73)	(4.79)	(10.80)	(6.97)	(14.02)	(1.55)	(36.09)	(13.93)	(5.26)	(22.82)	
C_3	-5.71	16.23**	35.13*	12.30	46.76**	4.63**	-9.79	-24.61	-10.97**	14.08	-
	(6.35)	(5.56)	(15.61)	(8.25)	(16.50)	(0.44)	(37.06)	(16.50)	(3.79)	(21.69)	
Harvest index (%)											
C_1	-5.03**	8.53**	-21.65**	-12.57**	8.71	-2.51**	57.80**	25.15**	-6.78**	-28.64**	D
	(1.90)	(2.92)	(5.11)	(2.88)	(5.78)	(0.48)	(13.62)	(5.76)	(1.66)	(8.16)	
C_2	-4.18	-1.11	6.09	5.69	41.86**	2.14**	-14.65	-11.37	-1.53	16.65	-
	(3.65)	(3.94)	(4.81)	(3.13)	(6.30)	(0.65)	(16.76)	(6.27)	(2.53)	(10.92)	
C_3	1.59	30.45**	30.48**	-0.78	28.12*	2.06**	39.87	1.56	-14.43**	-33.59*	D
	(4.58)	(4.45)	(10.02)	(5.76)	(11.55)	(0.67)	(26.88)	(11.53)	(3.13)	(15.81)	

C_1 = IET 6441×Dudheswar; C_2= IET 8002×Basmati 385; C_3=IET 8002×Sambamahsuri; D=Duplicate Epistasis; Values in parenthesis indicate respective standard error (SE ±)

Contd. Table 3

Cross	Scale				Genetic component						Epistasis
	A	B	C	D	m	(d)	(h)	(i)	(j)	(l)	
Kernel length (mm)											
C_1	-0.15**	-0.13*	-0.90**	-0.31**	5.29**	-0.07**	0.87	0.62**	-0.01	-0.34	-
	(0.04)	(0.05)	(0.22)	(0.11)	(0.23)	(0.02)	(0.47)	(0.22)	(0.03)	(0.25)	
C_2	-0.10	-0.13*	0.62**	0.43**	7.01**	-0.49**	-2.13**	-0.86**	0.02	1.09**	D
	(0.08)	(0.06)	(0.10)	(0.05)	(0.10)	(0.01)	(0.27)	(0.10)	(0.04)	(0.19)	
C_3	-0.03	0.46**	0.20	-0.12	5.25**	0.38**	1.05*	0.23	-0.25**	-0.66*	D
	(0.08)	(0.07)	(0.23)	(0.12)	(0.24)	(0.02)	(0.52)	(0.24)	(0.05)	(0.30)	
Kernel breadth (mm)											
C_1	0.34**	-0.12	-1.99**	-1.11**	0.05	0.11**	4.55**	2.21**	0.23**	-2.43**	D
	(0.06)	(0.07)	(0.11)	(0.04)	(0.08)	(0.03)	(0.21)	(0.08)	(0.04)	(0.15)	
C_2	0.31**	0.07	-0.39	-0.38**	1.38**	0.26**	2.01**	0.77**	0.12**	-1.15**	D
	(0.06)	(0.05)	(0.21)	(0.09)	(0.19)	(0.02)	(0.39)	(0.19)	(0.02)	(0.22)	
C_3	0.07	0.01	0.08	0.00	2.09**	0.32**	0.41	0.00	0.03	-0.08	-
	(0.08)	(0.03)	(0.17)	(0.09)	(0.17)	(0.02)	(0.39)	(0.17)	(0.04)	(0.22)	
Kernel L/B ratio											
C_1	-0.42**	0.09	2.51**	1.42**	5.47**	-0.16**	-5.96**	-2.85**	-0.25**	3.18**	D
	(0.08)	(0.09)	(0.13)	(0.05)	(0.11)	(0.03)	(0.29)	(0.11)	(0.05)	(0.21)	
C_2	-0.37**	-0.24**	0.67*	0.64**	4.22**	-0.58**	-3.44**	-1.28**	-0.07*	1.88**	D
	(0.07)	(0.06)	(0.31)	(0.15)	(0.29)	(0.02)	(0.59)	(0.29)	(0.03)	(0.32)	
C_3	-0.09	0.12	-0.09	-0.06	2.53**	-0.22**	-0.04	0.13	-0.10*	-0.16	-
	(0.07)	(0.07)	(0.15)	(0.08)	(0.15)	(0.03)	(0.35)	(0.15)	(0.05)	(0.20)	
Cooked kernel length (mm)											
C_1	-2.85**	0.00	-1.94*	0.46	10.79**	0.46**	-5.13*	-0.91	-1.42**	3.76**	D
	(0.37)	(0.56)	(0.83)	(0.42)	(0.86)	(0.15)	(2.11)	(0.84)	(0.31)	(1.34)	
C_2	1.98*	3.97**	2.62*	-1.67**	6.75**	-1.50**	11.64**	3.34**	-0.99**	-9.29**	D
	(0.78)	(0.48)	(1.26)	(0.63)	(1.27)	(0.09)	(3.05)	(1.27)	(0.38)	(1.95)	
C_3	0.19	-4.25**	3.61**	3.84**	17.62**	-0.30	-19.11**	-7.68**	2.22**	11.74**	D
	(0.45)	(0.51)	(1.16)	(0.52)	(1.05)	(0.18)	(2.33)	(1.03)	(0.27)	(1.43)	
Cooked kernel breadth (mm)											
C_1	0.61**	-0.44	-2.14**	-1.16**	0.71*	-0.02	4.78**	2.31**	0.53**	-2.48**	D
	(0.14)	(0.28)	(0.30)	(0.16)	(0.33)	(0.07)	(0.88)	(0.32)	(0.14)	(0.59)	
C_2	-0.16	0.15	-0.85**	-0.42**	2.15**	0.30**	1.89*	0.85**	-0.15	-0.84	D
	(0.18)	(0.25)	(0.28)	(0.16)	(0.33)	(0.04)	(0.89)	(0.33)	(0.14)	(0.60)	
C_3	0.39**	0.02	0.46*	0.03	2.89**	0.14**	0.53	-0.06	0.19*	-0.35	-
	(0.14)	(0.12)	(0.21)	(0.11)	(0.22)	(0.05)	(0.55)	(0.21)	(0.09)	(0.35)	
Cooked kernel L/B ratio											
C_1	-1.37**	0.53	2.09**	1.47**	6.16**	0.11	-6.80**	-2.94**	-0.95**	3.78**	D
	(0.12)	(0.47)	(0.52)	(0.31)	(0.63)	(0.08)	(1.60)	(0.62)	(0.23)	(1.01)	
C_2	0.76*	1.06*	1.62**	-0.10	3.26**	-0.84**	1.61	0.20	-0.15	-2.01	-
	(0.35)	(0.41)	(0.59)	(0.34)	(0.69)	(0.05)	(1.75)	(0.69)	(0.25)	(1.13)	
C_3	-0.31	-1.52**	0.65	1.24**	6.00**	-0.30**	-6.97**	-2.49**	0.61**	4.32**	D
	(0.23)	(0.23)	(0.35)	(0.15)	(0.31)	(0.07)	(0.81)	(0.30)	(0.13)	(0.57)	
Linear elongation ratio											
C_1	-0.40**	0.04	-0.04	0.17	1.98**	0.07*	-1.06*	-0.33	-0.22**	0.70**	D
	(0.07)	(0.11)	(0.18)	(0.09)	(0.18)	(0.03)	(0.43)	(0.18)	(0.06)	(0.26)	
C_2	0.37**	0.69**	0.29	-0.39**	0.86**	-0.11**	2.50**	0.77**	-0.16**	-1.83**	D
	(0.12)	(0.07)	(0.20)	(0.10)	(0.20)	(0.01)	(0.47)	(0.20)	(0.06)	(0.30)	
C_3	0.05	-0.93**	0.56**	0.72**	3.27**	-0.18**	-3.78**	-1.45**	0.49**	2.33**	D
	(0.09)	(0.09)	(0.16)	(0.07)	(0.13)	(0.03)	(0.33)	(0.13)	(0.05)	(0.23)	

* Significant at 5% level; ** Significant at 1% level; C_1 = IET 6441 × Dudheswar; C_2= IET 8002×Basmati 385; C_3=IET 8002×Sambamahsuri; D=Duplicate Epistasis; Values in parenthesis indicate respective standard error (SE ±)

Table 4. Chi-square test for means of different generations for grain yield and quality traits in rice

Character	C_1 (IET 6441 x Dudheswar)		C_2 (IET 8002 x Basmati 385)		C_3 (IET 8002 x Sambamahsuri)	
	Chi-square value	Epistasis	Chi-square value	Epistasis	Chi-square value	Epistasis
Plant height (cm)	53.22*	Present	18.07**	Present	306.96**	Present
Days to 50% flowering	6.29	Absent	205.14**	Present	87.67**	Present
Total tillers plant^{-1}	36.86**	Present	11.43**	Present	14.79**	Present
Productive tillers plant^{-1}	37.49**	Present	5.12	Absent	14.01**	Present
Panicle length (cm)	4.98	Absent	9.63*	Present	11.04*	Present
Panicle weight (g)	54.42**	Present	11.76**	Present	9.11*	Present
Florets panicle^{-1}	8.54*	Present	24.73**	Present	8.31*	Present
Filled grains panicle^{-1}	9.29*	Present	40.49**	Present	38.25**	Present
Floret fertility (%)	67.37**	Present	18.02**	Present	41.66**	Present
Grain length (mm)	20.89**	Present	51.24**	Present	64.09**	Present
Grain breadth (mm)	722.13**	Present	32.40**	Present	88.89**	Present
Grain L/B ratio	272.53**	Present	55.08**	Present	47.26**	Present
Grain weight panicle^{-1} (g)	305.78**	Present	28.41**	Present	32.86**	Present
1000 seed weight (g)	91.93**	Present	3.63	Absent	89.78**	Present
Grain yield plant^{-1} (g)	127.90**	Present	16.43**	Present	14.76**	Present
Harvest index (%)	33.70**	Present	4.00	Absent	54.52**	Present
Kernel length (mm)	31.10**	Present	89.77**	Present	41.78**	Present
Kernel breadth (mm)	938.56**	Present	48.28**	Present	0.85	Absent
Kernel L/B ratio	825.13**	Present	48.11**	Present	5.34	Absent
Cooked kernel length	64.18**	Present	72.76**	Present	124.06**	Present
Cooked kernel breadth (mm)	158.06**	Present	11.54**	Present	11.24*	Present
Cooked kernel L/B ratio	212.94**	Present	12.96**	Present	83.58**	Present
Linear elongation ratio	40.14**	Present	115.05**	Present	237.33**	Present

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

and Mani (1988) and Chauhan *et al*. (1993), who reported the importance of all the three types of interactions in the inheritance of different traits. Considering the sign of dominance (h) and dominance × dominance (l), the nature of epistasis was identified as duplicate in majority of the crosses for most of the yield and quality related traits except days to 50% flowering, panicle length, florets/panicle and kernel length in the cross C_1, total tillers/plant, productive tillers/ plant, panicle length, florets/panicle, filled grains/panicle, floret fertility, grain weight/panicle, 1000 seed weight, harvest index and cooked kernel L/B ratio in the cross C_2 and panicle length, panicle weight, florets/panicle, filled grains/panicle, floret fertility, grain weight/panicle, grain yield/plant, kernel breadth, kernel L/B ratio and cooked kernel breadth in the cross C_3. Duplicate epistasis as observed in most of the crosses for majority of the characters may result in decreased variation in F_2 and subsequent generations and may decrease heterosis and also hinder the pace of progress through selection (Singh *et al*., 2006).

The present study demonstrates the importance of additive, dominance and epistatic gene effects in the inheritance of grain yield, quality and their attributing traits. Under this situation breeders may opt for one of the two alternatives. On one hand the crop can be conventionally handled as self fertilizing species practising selection in segregating generations, following diallel selective mating system as suggested by Jensen (1970). Another, perhaps more promising alternative is the exploitation of heterosis.

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