)iallel analysis in rice (*Oryza sativa* L.) for physiological traits

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Abstract: Genetic components and combining ability analyses of various physiological traits were carried out by using seven parents diallel mating design excluding reciprocals. Results revealed that both additive and non-additive gene effects were important for the inheritance of characters studied with preponderance of latter for all traits, except plant height and harvest index in both F_1 and F_2 generations. The significance of gene distribution indicated the presence of gene asymmetry. At least one major group of genes controlled the inheritance of each trait. High narrow-sense heritability further suported the importance of additive gene effects for harvest index and plant height. NDR 359, Sarjoo 52, Mahsuri, T 21 and Jal Lahari were good general combiners. The promising cross combinations were NDR 359/Jal Lahari, NDR 359/T 21, Mahsuri/ T 21, Sarjoo 52/NDR 359 and Sarjoo 52/T 21. Since non-additive/dominance components were higher than the additive for all the characters in both F_1 and F_2 generations, therefore, biparental mating and/or reciprocal recurrent selection could be used for genetic improvement of these characters.

Key words : Physiological traits, additive and non-additive gene effects, heritability, dominance.

ntroduction

Crop breeding for economic traits had eceived attention since long and this factor ˌas been fully exploited in rice. Among different nethods to assess the nature of gene action n the parents, the diallel cross technique (Hayman, 1954a) is a systematic method. Acharya *et al.* (1998) laid emphasis on physiological components for increasing the yield. Now the yield level ıas almost reached a plateau, further breakthrough n yield level may be obtained by exploiting certain physiological traits related to yied. Yield components of HYVs varies with different levels of interactions depending on the genetic constitution of the parents. The information on genetic ıature of physiological traits is, therefore, important for developing potential genotypes for targetted ecosystem by manipulating these traits. With this view, the present study was undertaken to understand the genetics of six physiological trait in progenies in order to select suitable parent for different eco-geographical situations of rice cultivation.

Materials and Methods

The materials consisted of seven eco-culturally different rice varieties *viz.*, IR 24, Sarjoo 52, NDR 359 and T 21 (irrigated and widely adoptable), Mahsuri (Shallow water), Jal Lahari and NS 19 (semi-deepwater). All possible 21 crosses excluding reciprocal were made in wet season 1994 and half of the hybrid seeds were grown in off-season 1994 at International Rice Research Institute, Manila, Philippines to advance the generation following rapid generation advance (RGA) technique. The final experiment comprising 21 F_1, 21 F_2 and seven parents was conducted at New Diary Farm Kalyanpurm, Kanpur (Chandra Shekhar Azad University of Agriculture and Tecnology, Kanpur, Uttar Pradesh) during wet season 1995 following randomized complete block design with three replications. Each parent and F_1 was represented by two rows; and F_2 had five rows per block. The rows were five meter long and 20 cm apart and plants were spaced at 15 cm. Observations on plant height, flag-leaf area, grain-filling period, biological yield, harvest index and grain yield plant^{-1} were recorded on ten randomly selected competitive plants from parents and F_1 plants and fifty plants from F_2. The statistical procedures of Hayman (1954b) for genetic component analysis and Griffing (1956) Method 1, Model 2 for combining ability analysis; Crumpacker and Allard (1962) and Verhalen and Murray (1969) for narrow-sense heritability in F_1 and F_2, respectively, were followed.

Table 1. Estimation of various components and related statistics for 6 characters in a 7 parents diallel mating design of rice (F_1s and F_2s)

Variance components	Plant height		Flag-leaf area		Grain filling period		Biological yield (g)		Harvest index		Grain yield plant^{-1} (g)	
G	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
Additive gene effects D	352.08** ±55.03	352.06** ±40.13	13.62 ±8.53	13.69** ±2.83	8.38* ±4.25	8.29* ±4.22	47.28 ±40.05	47.52 ±35.63	19.07** ±3.76	19.02** ±2.88	12.69* ±6.00	12.66** ±2.54
Dominance effects H_1	515.98** ±132.47	2047.16* ±386.43	78.79** ±20.53	77.73** ±27.24	33.89** ±10.23	199.33** ±40.67	377.62** ±96.42	1040.03* ±43.10	56.64** ±9.06	101.09** ±27.73	61.48** ±14.43	123.17** ±24.42
H_2	486.91** ± 116.73	1648.39* ± 340.50	70.68** ± 18.09	63.24** ± 24.00	24.91** ± 9.02	160.99** ± 35.84	316.31** ± 84.96	921.20** ±302.32	47.74** ±7.98	72.88** ±24.43	52.35** ±12.72	100.21** ±21.52
h^2	669.68** ±78.40	3.71 ±57.17	30.22 ±12.15	1.03 ±4.03	1.00 ±6.06	2.13 ±6.02	117.54* ±57.06	14.27 ±50.76	43.73** ±5.36	-0.16 ±4.10	56.61** ±8.54	2.08 ±3.61
Gene distribution F	55.26 ±132.01	551.74** ±192.53	-2.71 ±20.46	16.58 ±13.57	4.54 ±10.20	8.32 ±20.26	0.67 ±96.08	60.58 ±170.94	16.86 ±9.03	29.34* ±13.81	-5.17 ±14.38	15.34 ±12.17
Environmental effects E	0.71 ±19.45	0.72 ±14.19	0.34 ±3.02	0.28 ±1.00	0.14 ±1.50	0.23 ±1.49	0.90 ±14.16	0.66 ±12.60	0.37 ±1.33	0.42 ±1.02	0.10 ±2.12	0.14 ±0.9[illegible]
Mean degree of dom. $(H_1/D)^{1/2}$	1.21	2.41	2.41	2.38	2.01	4.90	2.83	4.68	1.69	2.31	2.20	3.12
Gene asymmetry $(H_2/4H_1)$	0.24	0.20	0.22	0.20	0.18	0.20	0.21	0.22	0.22	0.18	0.21	0.20
Proportion of dom.& recessive genes	1.14	1.96	0.92	1.68	1.31	1.23	1.01	1.32	1.71	2.01	0.83	1.48
h^2/H_2	1.37	0.002	0.42	0.016	0.04	0.01	0.37	0.01	0.91	0.00	1.08	0.0[illegible]
r (Wr+Vr)yr^{1}	-0.86*	-0.80*	0.24	-0.77*	0.49	-0.06	-0.16	-0.44	-0.67	0.30	-0.22	-0.5[illegible]

Mean degree of dom. in F_2 = $[1/4\,(H_1/D)^{1/2}]$; KD/KR=$[(4DH_1)^{1/2}F] / [(4DH_1)^{1/2}-F]$ in F_1; KD/KR=$[(1/4DH_1)^{1/2}+1/2F] / [(4DH_1)^{1/2}-1/2F]$ in F_2;
*, ** Significant at P<0.05 and Significant at P<0.01, respectively.

Table 2. ANOVA for combining ability and related statistics

Source of variation	d.f.	G.	Plant height	Flag leaf area	Grain filling period	Biological yield (g)	Harvest index	Grain yield plant^{-1} (g)
GCA	6	F_1	735.55**	46.68**	23.23**	189.30**	23.06**	50.09**
		F_2	445.58**	21.41**	24.58**	94.82**	27.02**	22.96**
SCA	21	F_1	149.79**	19.87**	7.34**	90.71**	14.51**	16.22**
		F_2	114.66**	4.55**	11.34**	61.78**	5.58**	7.05**
Error	54	F_1	0.71	0.34	0.13	0.89	0.36	0.1
		F_2	0.72	0.27	0.22	0.65	0.42	0.13
σ^2_g		F_1	81.64	5.14	2.56	20.93	2.52	5.55
		F_2	49.42	2.34	2.70	10.46	2.95	2.53
σ^2_s		F_1	149.08	19.53	7.21	89.82	14.15	16.12
		F_2	113.94	4.28	11.12	61.13	5.16	6.92
σ^2_g/σ^2_s		F_1	0.55	0.26	0.36	0.23	0.18	0.34
		F_2	0.43	0.55	0.24	0.17	0.57	0.37
GPR		F_1	0.52	0.34	0.41	0.32	0.26	0.41
		F_2	0.46	0.52	0.39	0.25	0.58	0.42
$(\sigma^2_s/\sigma^2_g)^{0.05}$		F_1	1.35	1.95	1.67	2.07	2.37	1.70
		F_2	1.51	1.35	2.02	2.42	1.32	1.65

*, ** Significant at P<0.05 and Significant at P<0.01, respectively, GPR = General Predictabiltiy Ratio, $(\sigma^2_s/\sigma^2_g)^{0.05}$= Degree of dominance

Results and Discussion

(I) Genetic component analysis

The genetic components and relative proportion of various components and narrow-sense h^2 are furnished in Table 1. The component of variance analysis revealed that both additive (D) and dominant (H_1 and H_2) components were positive and significant for all the physiological traits except flag-leaf area in F_1 and biological yield in both F_1 and F_2 generations for the additive component. The non-significance of D for these traits was further attested by low values of narrow-sense heritability. However, estimates of dominant components were higher than additive components suggesting that dominance variances were more important. The imoprtant of dominance variances has also been reported earlier in rice by Mishra and Singh (1998) for plant height, biological yield, harvest index and grain yield. The estimate of H_2 component was smaller than H_1 for all the traits in both the generations reflecting unequal proportion of positive and negative alleles at loci governing these physiological traits in parents. This was further confirmed by the ratio ($h^2/4H_1$). The positive and significant values of h^2 and F except flag-leaf area and grain yield in F_1 indicated that dominant genes were frequently distributed than the recessive ones for all the characters. The values of mean degree of dominance exhibited over dominance with a value above the unity for all the traits in both the generations. The non-significant component (E) indicated the least influence of environment in the expression of these traits. The proportion of positive and negative alleles in the parents was found to be symmetrical for most of the traits as evident by their close approach to theoretical value (0.25). The ratio of dominant and recessive genes (KD/KR) in the parents indicated distribution of dominant alleles for all the traits in both the generations except flag-leaf area and grain yield in F_1. The magnitude of (h^2/H_2) was found to be depressed except plant height in

Table 3. Ranking of five desirable parents on the basis of *per se* performance and *gca* effects for six characters in a 7-parent-diallel cross of rice (F_1s and F_2s)

Characters	Best parent based on per se performance	Best general combiner		Best common parent based on per se performance and gca effects
		F1	F2	
Plant height	IR 24 NDR 359 Sarjoo 52 Mahsuri T 21	IR 24** NDR 359** Sarjoo 52 Mahsuri** Jal Lahri**	IR 24** Sarjoo 52** Mahsuri** NDR 359** T 21**	IR 24 NDR 359 Sarjoo** Mahsuri
Flag leaf area	T 21 Jal Lahri NS 19 NDR 359 Sarjoo 52	T 21** NDR 359** Jal Lahri** Sarjoo 52** NS 19**	T 21** Jal Lahri** NS 19** NDR 359** IR 24**	T 21 Jal Lahri NS 19 NDR 359
Grain filling period	Sarjoo 52 IR 24 Mahsuri NS 19 NDR 359	Sarjoo 52** NS 19** Mahsuri** Jal Lahri** T 21**	Sarjoo 52** T 21** NS 19** Mahsuri IR 24**	Sarjoo 52** Mahsuri
Biological yield	NDR 359 Sarjoo 52 T 21 Jal Lahri IR 24	NDR 359** IR 24** Sarjoo 52** T 21** Mahsuri**	NDR 359** Mahsuri** Sarjoo 52 IR 24** NS 19**	NDR 359 Sarjoo 52 IR 24
Harvest index	T 21 NDR 359 Jal Lahri IR 24 Sarjoo 52	T 21** NDR 359** IR 24** Sarjoo 52** Jal Lahri	T 21** NDR 359** IR 24** Jal Lahri Mahsuri**	T 21 NDR 359 Jal Lahri IR 24
Grain yield plant^{-1} (g)	NDR 359 Sarjoo 52 T 21 Jal Lahri Mahsuri	NDR 359** T 21** IR 24** Sarjoo 52** Mahsuri**	NDR 359** T 21** Mahsuri* IR 24** Sarjoo 52**	NDR 359 Sarjoo 52 T 21 Mahsuri

*, ** Significant at P<0.05 and Significant at P<0.01, respectively.

F_1 only, suggesting the presence of at least one major group of genes controlling the inheritance. The negative values of coefficient of correlation between parental order of dominance and parental measurement was observed for all the traits except grain-filling period and flag leaf area in F_1 and harvest index in F_2 generation. These are in close agreement with those of Mohapatra and Debjani (2000) and Acharya *et al.* (2000) on estimates of various components and related statistics for harvest index and grain yield.

High h^2 estimates were observed for plar height, flag-leaf area and harvest index. Dwivec and Senadhira (1999) also reported high ł for plant height in rice. High h^2 were du to greater contribution of additive geneti component and thus these traits could be improve by adopting progeny selection. In general, ł estimate in F_2 was higher than the F_1 fc all the traits except grain-filling period. It indicate that selection for these traits would be mor effective in early generations.

Table 4. Best specific combiners of grain yield plant-1 and their performance in other related traits in a 7-parents diallel mating design of F_1s and F_2s in rice

Desirable/ economic cross	SCA effect		*Per se* performance		GCA effect				Traits for which cross also exhibited desirable *sca* effect
					F_1		F_2		
	F_1	F_2	F_1	F_2	P_1	P_2	P_1	P_2	
Mahsuri/ IR 24	8.64**	0.61**	29.87	18.14	-0.72**	0.37**	0.02*	-0.13**	I,II,IV,V
NDR 359/ Jal Lahri	4.81**	3.77**	28.49	23.33	4.12**	-2.02**	3.08**	-1.16**	IV, V
NDR 359/ T 21	4.75**	-2.29**	31.63	18.84	4.12**	1.18**	3.08**	0.41**	II,IV,V
IR 24/ NS 19	3.91**	3.06**	22.65	18.51	0.37**	-3.20**	-0.13**	-2.06**	II,III,IV
T 21/ NS 19	0.46**	5.19**	20.02	21.18	1.18**	-3.20**	0.41**	-2.06**	I,II,V

*, ** Significant at P<0.05 and Significant at P<0.01, respectively
I = Plant height (cm), II = Flag - leaf area, III = Grain filling period, VI = Biological yield, V = Harvest index

(II) Combining ability analysis

An analysis of variances demonstrated the presence of highly significant genetic variability within diallel population for all the traits under study. The mean square due to *gca* and *sca* effects were highly significant indicating the importance of both additive and non-additive type of gene effects in controlling these traits (Table 2). Greater values of σ^2s than σ^2g, higher value of degree of dominance and lower predictability ratio were observed for all the physiological characters, indicating the greater importance of non-additive gene action. By and large combining ability effects of the parents were associated with their *per se* performance in most of the characters. The best common parents identified on the basis of *per se* performance and *gca* effects were NDR 359 (for grain yield, plant height, flag-leaf area, biological yield and harvest index); Sarjoo 52 and Mahsuri (for grain-filling period, plant height and grain yield); T21 and Jal Lahari (for flag-leaf area and harvest index) (Table 3). As regards the grain-filling period, the shortest filled grain hybrid Sarjoo 52/NS 19 had parents with negative *gca* effect indicating the presence of additive x additive genes. Parents NS 19, Jal Lahari and T 21 possessed high positive *gca* effects for tallness while their hybrids were intermediate to tall type. Similar findings were also reported by Manonmani and Ranganathan (1998) for plant height and grain yield. Recently, Yu *et al.* (2002) have demonstrated the importance of epistatic interactions in the genetic bases of heading date and plant height by using Mapmarker/Quantitative trait loci (QTLs).

T21 and Jal Lahari had highest positive gca effect for flag-leaf area and their hybrids had positive and highly significant sca effect. In contrast, the hybrids Sarjoo 52/NS 19, IR 24/NDR 359 and Mahsuri/IR 24 had parents with negative gca effects (low X low combinations) and produced highest positive interaction effect indicating over-dominance and epistatic interactions. This may be due to genetic diversity in the form of homozygous loci. The hybrids IR 24/NS 19 and Mahsuri/IR 24 showing highest positive *sca* effect for biological yield, had parents possessing high x low *gca* effects indicated interaction effect. In case of harvest index crosses including Sarjoo 52/NS 19 and NDR 359/NS

19 had positive and negative general combiners to produce a hybrid with highest positive *sca* effect indicating the interaction effects between the different alleles. Peng and Virmani (1990) reported about the possibility of interaction between positive alleles from good combiner and negative alleles from poor combiners in high x low combining crosses and suggested for the exploitation of heterosis in F_1 as their high yield potential would be unfixable in succeeding generations. Crosses involving dominant x recessive gene interaction might tend to be non-fixable. Lavanya (2000) also observed similar trend of genetic interactions for yield and its certain related physiological traits.

Significant *sca* effects for yield plant^{-1} were observed for Mahsuri/IR 24 and NDR 359/ T21 in F_1 and T21/NS 19, NDR 359/ Jal Lahari and IR 24/NS 19 in F_2 generation. These combinations also possessed high sca effect for related physiological traits in both the generations. It is evident that the crosses involving either both or at least one high *gca* parent produced hybrids with high *sca* effects (Table 4). Therefore, it could be concluded that *sca* effects varied greatly from cross to cross; and that moderate to poor general combiners also produced good cross combinations. The perusal of Table 4 also revealed that the hybrids with high *per se* performance need not be the ones with high sca effects and vice versa as indicated by Rahman *et al.* (1981) and Lavanya (2000). Thus, desirable hybrids should be selected on the basis of *per se* performance coupled with sca effects.

Genetic components and combining ability analyses revealed significant contribution of both fixable and non-fixable gene effects with preponderance of latter in the inheritance of various physiological traits studied. NDR 359, Sarjoo 52, Mahsuri, T 21 and Jal Lahari were observed to be good general combiners and these parents may be utilized in yield improvement along with related physiological traits in targeted ecosystems. Therefore, biparental mating following by selection in F_3 & F_4 generations could be the most effective breeding method for improving these physiological traits to increase yield in rice of diverse eco-cultural types.

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