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Heterosis and genetic studies on yield and associated physiological traits in rice (*Oryza sativa* L.)

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ABSTRACT

Studies indicated that the amount of heterosis for leaf area index (LAI) at tillering stage, crop growth rate (CGR) from tillering to heading, harvest index, 100-grain weight and grain yield plant^{-1} was high and the inheritance of LAI, CGR net assimilation rate (NAR), harvest index (HI), days to 50% flowering, productive tillers plant^{-1}, filled grains panicle^{-1} and grain yield plant^{-1} were predominantly under the control of non-additive gene action. Whereas, 100-grain weight was largely governed by additive gene action. The parents IR 20 for LAI, RDR 763 for LAI, NAR and productive tillers plant^{-1} and Lunisree for CGR, HI, Biological yield and 100-grain weight were identified as good general combiners. The per se performance of the parents was found to be good indicator of their general combining ability. The best specific crosses with high SCA effects mostly involved parents with high x low or low x low GCA effects, hence heterosis breeding would be more rewarding to achieve another quantum jump in rice yields through exploitation of physiological traits.

Key words: *Heterosis, combining ability, rice, physiological traits*

To increase the yield levels of rice it would be necessary to investigate critically the factors imposing yield ceiling and alleviate them. It is obvious that further improvement in yield is most likely to come from increasing the physiological efficiency or functional aspects of the plants. Such approach involves a thorough understanding of heterosis as well as the inheritance of physiological parameters and identification of physiologically efficient donors/combiners. Combining ability studies help in the identification of parents with high general combining ability (GCA) and crosses with high specific combining ability (SCA) effects. The gene action (additive and non-additive) estimated through this analysis would be useful for suggesting an appropriate breeding strategy (exploitation of heterosis or isolation of purelines). The present paper reports the results of studies conducted on heterosis and genetics of yield and associated physiological traits in rice.

MATERIALS AND METHODS

Seven rice varieties *viz.*, IR 20, Shiva, Tellahamsa, Lunisree, WGL-NDL-2, Erramallelu and RDR 763 were selected and crossed in 7x7 diallel fashion without reciprocals. The resultant 21F_1 derivative hybrids were raised along with their parents in a randomized block design during Dry seasons 1999-2000 in three replications at Agricultural Research Station, Warangal. Each entry was grown in 2 rows of 3m long, at a spacing of 20 x 15 cm. Thirty days old seedlings were transplanted following a fertilizer dose of 100 N, 60 P_2O_5 and 40 K_2O kg ha^{-1}. Data were recorded on 10 plants in each replication. For the purpose of estimation of dry matter, samples containing 5 plants each were collected every time and oven-dried. The observations were recorded on seven yield components *viz.*, days to 50% flowering (DFF), productive tillers plant^{-1}, plant height (cm), panicle length (cm), filled grains panicle^{-1}, 100-grain weight (g) and grain yield plant^{-1} (g) and seven physiological parameters such as leaf area index (LAI) at tillering and heading, crop growth rate (CGR) from tillering to heading (T-H) and heading to ripening (H-R) in g m^{-2} day^{-1}, net assimilation rate (NAR) from tillering to heading in mg dm^{-2} day^{-1}, harvest index (HI) in percentage and biological yield (BY) were computed by applying formulae as described by Yoshida *et al.* (1976). Heterosis and heterobeltiosis were estimated using standard formula and test of significance was done as suggested by Arunachalam (1976). Combining ability analysis was carried out according to Griffing (1956) Method II and Model I.

RESULTS AND DISCUSSION

Analysis of variance revealed that there were significant differences among the parents and hybrids for all the characters studied (Table 1).

High heterosis for LAI was observed at tillering stage with four crosses *viz.*, Tellahamsa / WGL-NDL-2, Tellahamsa/RDR-763, Shiva/Erramallelu and Shiva/ Tellahamsa manifesting superiority over their respective better parents to the extent as high as 90 per cent, whereas, at heading stage, only three crosses, *viz.*, Shiva/ Erramallalu, Shiva/Tellahamsa and Lunisree/ WGL-NDL-2 exhibited significant positive heterobeltiosis for LAI (Table 2). Similar findings were also earlier reported by Niranjana Murthy and Kulkarni (1996), Khan *et al*, (1998) and Seetharamaiah *et.al.*, (1998).

Although eight hybrids were superior to their respective better parent at tillering, only three hybrids, by the time they attained flowering stage and two hybrids *viz.*, Lunisree / RDR 763 and Tellahamsa / Lunisree were consistent in their performance. Nguyen *et al.*, (1993) observed significant positive heterosis and heterobeltiosis for CGR from tillering to heading and heading to flowering, but the number of heterotic crosses decreased from tillering to heading as observed in present study. The heterotic crosses for CGR (pre and post flowering) involved medium x low parental mean combinations. Interestingly, the crosses with high heterotic values had high *per se* performance. These findings suggest that low x low parental mean combinations do not workout to exploit heterosis for CGR in rice. Higher magnitude of heterosis was observed for harvest index in most of the crosses and the best crosses *viz.*, IR-20 / RDR-763, Tellahamsa / RDR-763, WGL-NDL-2/RDR-763 and IR-20/WGL-NDL-2 which exhibited significant heterobeltosis involved the parents with low x medium parental means.

Out of 21 crosses evaluated, 8 were superior to their respective better parents for productive tillers per plant as reported earlier by several workers. Grafius (1959) stated that heterosis for grain yield is the result of interaction of simultaneous increase in the expression of heterosis for individual yield components in barley. The crosses *viz.*, Lunisree/RDR-763, Tellahamsa / Lunisree, Shiva / Tellahamsa and Shiva / Lunisree which exhibited heterobeltoisis in yield were also heterotic for other yield components and physiological traits (LAI, CGR and NAR).

Table 1. Mean squares for physiological and yield characters of 7 parents and 21 F_1s

Source	df	LAI at tillering	LAI at heading	CGR (T-H)	CGR (H-R)	NAR (T-H)	HI	BY plant^{-1}
Replications	2	0.131	0.028	4.962	14.301	31.285	5.258	1.862
Genotypes	27	0.900**	2.744**	33.506**	103.368**	616.470**	46.756**	174.675**
Parents	6	0.379**	4.428**	10.006**	66.588**	422.079**	74.138**	148.308**
Hybrids	20	0.696**	2.213**	38.538**	118.524**	704.109**	18.492**	186.521**
Parents Vs Hybrids	1	8.100**	3.259**	73.850**	20.915**	30.035NS	447.73**	95.953**
Error	54	0.031	0.042	1.869	4.33	52.75	3.23	8.756

Source	df	Days to 50% flowering	Productive tillers plant^{-1}	Plant height	Panicle length	Filled grains panicle^{-1}	100-grain weight	Grain yield plant^{-1}
Replications	2	1.940	0.136	3.359	0.964	45.398	0.003	1.120
Genotypes	27	154.533**	20.471**	355.394**	8.705**	1064.088**	0.510**	70.276**
Parents	6	152.428**	11.274**	248.75**	15.052**	1674.76**	0.834**	42.738**
Hybrids	20	136.049**	21.768**	400.909**	7.178**	911.23**	0.422**	72.343**
Parents Vs Hybrids		537.396**	49.68**	84.935**	1.146**	457.112**	0.317**	194.164**
Error	54	1.187	0.626	4.807	0.190	28.52	0.002	3.396

Table 2. Estimates of heterosis (H1), heterobeltiosis (H2) for physiological and yield characters

Cross	LAI at tillering		LAI at heading		CGR (T-H)		CGR (H-R)		NAR (T-H)		HI		BY plant^{-1}	
	H1	H2	H1	H2	H1	H2	H1	H2	H1	H2	H1	H2	H1	H2
IR 20/Shiva	91.34**	35.38**	-28.88*	-36.36**	25.10**	24.93**	-17.00	-25.05**	6.71	-14.80	17.81**	10.77**	6.63	-0.48
IR 20/Tellahamsa	81.38**	32.81**	-10.20*	-19.93*	-37.53**	-38.88**	5.67	-8.11	-49.83**	-58.43**	15.99**	10.59**	12.20**	11.98**
IR 20/Lunisree	59.36**	27.87**	-26.12*	-44.62**	9.96	2.14	3.30	-3.93	-4.76	-24.24**	8.56*	-2.04	-15.88*	-19.29*
IR 20/WGL-NDL 2	24.46*	-14.03	-36.02*	-55.10**	5.23	-12.60	10.96	-12.98	0.63	-20.69*	17.94**	11.78*	-13.25	-34.49**
IR 20/Erramallelu	89.59**	40.32**	0.39	-18.32*	14.59	12.37	-25.67**	-29.51**	-22.19*	-41.30**	13.21*	3.43	6.92	0.56
IR 20/RDR 763	116.36**	62.06**	-27.22*	-30.72**	25.45**	19.37*	-29.57**	-33.82**	22.81*	4.17	28.35**	25.11**	-16.11*	-17.77*
Shiva/Tellahamsa	101.35**	90.64**	27.35*	26.84**	41.84**	38.98**	28.87**	2.84	-8.56	-12.76	8.14*	6.56*	24.99**	16.87*
Shiva/Lunisree	80.62**	52.29**	-9.06	-25.78*	-6.36	-12.90	58.96**	34.59**	-27.92**	-28.28**	3.37	-1.08	33.45**	29.66**
Shiva/WGL-NDL 2	76.18**	69.05**	-16.53*	-36.94**	30.62**	8.60	21.54	3.63	14.29	12.32	3.53	2.66	13.95	-9.46
Shiva/Erramallelu	109.71**	95.47**	41.76**	27.19**	71.05**	67.53**	5.04	-9.51	-0.47	-7.83	4.26	1.11	25.30**	24.27**
Shiva/RDR 763	44.16**	32.14	-3.21	-17.07*	40.38**	33.41**	-8.46	-12.27	23.08**	14.29	17.77**	8.11*	-6.56	-11.13
Tellahamsa/Lunisree	88.54**	66.67**	-7.31	-24.11*	52.73**	44.82**	32.85**	23.51**	15.96	10.10	8.85*	2.72	25.19**	20.34**
Tellahamsa/WGL-NDL 2	172.43**	148.09**	-1.83	-25.63**	34.19**	13.45	-14.56	-39.32**	-16.01	-21.18*	11.41**	10.71**	11.31	-15.82*
Tellahamsa/Erramallelu	82.85**	79.84**	-12.25*	-20.98*	-17.58*	-20.88*	1.78	-7.16	-35.29**	-42.61**	7.15*	2.44	4.24	-1.78
Tellahamsa/RDR 763	122.59**	115.08**	-42.78*	-51.14*	12.73	5.08	-16.30*	-30.95**	8.09	5.06	23.17**	14.60**	-9.53	-11.14
Lunisree/WGL-NDL 2	43.89**	17.32	32.77*	20.03*	-0.46	-11.88	47.41**	9.75	-30.67**	-31.53**	0.45	-4.64	28.80*	0.17
Lunisree/Erramallelu	53.37**	37.58*	-23.53*	-31.33*	-14.41	-21.91*	14.29*	11.95	-21.96**	-27.39**	1.03	-0.34	-1.30	-3.32
Lunisree/RDR 763	53.05**	39.54**	-18.90*	-41.15**	44.61**	28.33**	67.05**	46.70**	28.42**	18.69*	12.54**	-0.74	41.49**	38.41**
WGL-NDL-2/Erramallelu	56.42**	40.33*	-28.36*	-41.14**	-5.45	-22.68*	-6.84	-29.67**	-5.31	-10.87	-11.34*	-14.72**	4.91	-17.15***
WGL/NDL-2/RDR 763	20.90	6.75	-37.19*	-57.14**	28.56**	2.66	-15.40	-30.35**	47.71**	34.98**	21.99**	12.85**	-8.31	-29.79**
Erramallelu/RDR 763	68.89**	65.87**	-15.53*	-33.82**	23.60**	19.85*	-37.86**	-44.43**	14.07	-1.30	8.18*	-3.43	-22.48*	-25.69**
SE±	0.12	0.14	0.14	0.16	0.96	1.11	1.47	1.70	5.13	5.93	1.27	1.46	2.09	2.41

* Significant at 5% level ** Significant at 1% level

Cross	Days to 50% flowering H1	Days to 50% flowering H2	Productive tillers $plant^{-1}$ H1	Productive tillers $plant^{-1}$ H2	Plant height H1	Plant height H2	Panicle length H1	Panicle length H2
IR 20/Shiva	0.48	-1.25	20.85**	11.85*	-1.66	-3.16	-2.32	-2.79
IR 20/Tellahamsa	3.00*	-3.44*	14.12*	6.60	0.77	-0.85	6.21*	3.67*
IR 20/Lunisree	-17.06*	-24.06*	-10.88**	-12.57*	-6.47*	-10.00*	-6.80*	-11.99**
IR 20/WGL-NDL 2	-6.12*	-13.75*	-5.08	-14.89**	-16.99*	-23.71*	-6.80*	-12.98**
IR 20/Erramallelu	2.65*	-3.12*	16.83*	9.26	2.93	-1.00	2.68**	2.54
IR 20 RDR 763	-11.96*	-13.75*	-13.91*	-23.71**	-15.35*	-23.44*	-0.89	-13.26**
Shiva/Tellahamsa	-3.57*	-8.09*	39.91**	21.64**	0.95	0.85	2.52	-0.42
Shiva/Lunisree	-8.87*	-15.21**	44.69**	31.58**	4.16**	1.74	-4.90*	-10.61*
Shiva/WGL-NDL 2	-8.84*	-14.89*	14.23**	10.36	-2.83	-11.94*	-3.08**	-9.92*
Shiva/Erramallelu	-4.55*	-8.41*	38.91**	20.90**	-5.40*	-10.34*	-1.34	-1.96
Shiva/RDR 763	-11.36*	-11.65*	51.84**	25.82**	-7.21*	-17.22*	2.24	-10.89**
Tellahamsa/Lunisree	-6.96*	-9.29*	24.27*	18.21**	9.03*	6.60*	-1.00	-4.30*
Tellahamsa/WGL-NDL 2	-4.01*	-6.07*	-5.94	-20.58**	-4.53**	-13.55*	-7.60*	-11.70**
Tellahamsa/Erramallelu	5.32*	4.58*	-7.79	-7.92	-4.90*	-9.95*	1.88	-0.42
Tellahamsa/RDR 763	-9.71*	-13.68*	8.82**	2.82	-3.89**	-14.33*	5.39*	-5.78*
Lunisree/WGL-NDL 2	-5.62*	-5.97*	14.43**	0.88	13.17*	0.43	1.20	0.00
Lunisree/Erramallelu	-8.00*	-10.92*	5.28	0.26	-0.88	-8.12*	-6.66*	-11.74*
Lunisree/RDR 763	-7.50*	-13.68*	41.67**	27.70**	16.94*	2.20	4.82*	-3.33
WGL-NDL-2/Erramallelu	-5.07*	-7.75*	-13.62**	-26.98**	-19.53*	-23.26*	-8.17*	-14.14**
WGL/NDL-2/RDR 763	-8.17*	-14.01**	31.30**	5.87	-13.27*	-14.78*	2.70	-4.23**
Erramallelu/RDR 763	-10.66*	-14.01*	17.16*	10.56*	-10.6*	-16.15*	-4.92*	-16.69*
SE±	0.77	0.88	0.55	0.64	1.55	1.79	0.30	0.35

Cross	Filled grains $panicle^{-1}$ H1	Filled grains $panicle^{-1}$ H2	100-grain weight H1	100-grain weight H2	Grain yield $plant^{-1}$ H1	Grain yield $plant^{-1}$ H2
IR 20/Shiva	10.52*	4.98	5.82*	-6.79*	26.32**	25.47*
IR 20/Tellahamsa	-0.55	-10.38*	8.70*	-7.15*	30.32**	24.38*
IR 20/Lunisree	0.03	-12.28*	1.82	-19.54*	-8.16	-13.95*
IR 20/WGL-NDL 2	-14.28*	-20.78**	14.85*	3.37	4.33	-18.17*
IR 20/Erramallelu	15.84**	11.20**	9.78*	0.33	22.10**	18.31*
IR 20 RDR 763	4.69	-4.94	8.80*	6.53*	7.80	3.23
Shiva/Tellahamsa	-5.33	-10.45*	16.57*	12.48**	35.39**	28.40**
Shiva/Lunisree	-6.11**	-13.72*	8.81*	-4.14*	37.69**	28.19**
Shiva/WGL-NDL 2	-15.04*	-25.10**	8.15*	-12.97*	17.9**	-7.06
Shiva/Erramallelu	-7.99*	-9.00*	16.73*	12.07*	30.69**	25.80**
Shiva/RDR 763	-10.70*	-14.85*	10.37*	-4.52*	10.54	6.54
Tellahamsa/Lunisree	12.19**	8.80*	10.42*	0.46	36.76**	34.12**
Tellahamsa/WGL-NDL 2	-7.27*	-22.08*	3.31*	-19.07*	24.52*	-5.56
Tellahamsa/Erramallelu	8.03*	1.13	4.91*	-2.66	12.07	10.34
Tellahamsa/RDR 763	-0.69	-1.52	3.59	-13.04*	11.71	2.31
Lunisree/WGL-NDL 2	-2.66	-20.21**	8.48*	-20.57*	27.65**	-4.45
Lunisree/Erramallelu	-9.24*	-17.43**	5.27	-10.46*	-0.15	-3.56
Lunisree/RDR 763	20.18**	15.60**	-0.59	-22.64*	59.44**	43.47**
WGL-NDL 2/Erramallelu	-41.83**	-48.22**	-4.14	-20.33*	-7.79	-29.30**
WGL/NDL 2/RDR 763	-10.03*	-23.88**	7.21*	-1.65	14.42	-7.24
Erramallelu/RDR 763	-1.47	-7.03**	-2.93	-12.95*	-15.68	-21.66**
SE±	3.77	4.36	0.036	0.04	1.30	1.50

Table 3. Combining ability analysis for physiological characters and yield components

Source	df	LAI at tillering	LAI at heading	CGR (T-H)	CGR (H-R)	NAR (T-H)	HI	BY plant^{-1}
GCA	6	0.617**	2.349**	18.693**	101.004**	456.707**	9.082**	146.854**
SCA	21	0.209**	0.504**	9.018**	15.442**	133.713**	17.443**	32.902**
Error	54	0.010	0.014	0.623	1.446	17.584	1.076	2.918
σ^2 GCA		0.067	0.259	2.007	11.062	48.791	0.889	15.992
σ^2 SCA		0.199	0.490	8.395	13.996	116.128	16.366	29.983
σ^2 GCA/σ^2 SCA		0.338	0.528	0.239	0.790	0.420	0.054	0.054

Source	df	Days to 50% flowering	Productive tillers plant^{-1}	Plant height	Panicle length	Filled grains panicle^{-1}	100-grain weight	Grain yield plant^{-1}
GCA	6	134.299**	15.759**	397.111**	10.401**	535.456**	0.714**	59.437**
SCA	21	27.865**	4.270**	38.851**	0.759**	303.050**	0.014**	13.136**
Error	54	0.395	0.208	1.60	0.063	9.508	0.001	1.132
σ^2 GCA		14.878	1.727	43.945	1.148	58.438	0.079	6.478
σ^2 SCA		27.470	4.061	37.248	0.695	293.541	0.013	12.004
σ^2 GCA/ σ^2 SCA		0.541	0.42	1.179	1.651	0.199	5.692	0.539

** Significant at 1% Level

Combining ability analysis indicated that both additive and non-additive gene actions were important, as the mean squares due to general combining ability (GCA) and specific combining ability (SCA) were significant for all the characters (Table 3).

The estimates of SCA variances, were relatively higher than those of GCA variance for all the physiological parameters (LAI, CGR, NAR, HI and BY) indicating the predominant role of non-additive gene action in expression of these traits. Similar observations were also reported earlier by Reddy (1981) and Murthy (1994) for LAI; Prasanthi (1993) and Nguyen *et al.* (1993) for CGR; Nguyen *et al.* (1993) for NAR; Singh *et al.* (1998) for HI and Verma *et al.* (1995) for biological yield. According to Ali *et al.* (1993) the mean performance was good indicator of GCA. In the present study, the analysis of mean performance and their GCA effects revealed that *per se* performance of the parents was a direct reflection of their respective GCA effects in most of the cases. Accordingly, the parents, IR 20 for LAI (tillering and heading); RDR 763 for LAI (heading), CGR (T-H) and NAR and Lunisree for CGR (H-R), HI and BY were identified as potential donors to increase physiological efficiency of hybrid derivatives and hybrids (Table 4).

Study of GCA/SCA variances (Table 3) for yield components revealed that expression of days to 50% flowering (Ram *et al.*, 1993), productive tillers plant^{-1} (Singh *et al.*, 1998), filled grains panicle^{-1} (Padmavathi *et al.*, 1997) and grain yield plant^{-1} (Ram *et al.*, 1998) were predominantly governed by non-additive gene action, whereas plant height, panicle length and 100-grain weight (Geetha *et al.*, 1998) chiefly by additive genetic proportions. The parents WGL-NDL-2 (days to 50% flowering and filled grains panicle^{-1}), RDR-763 (productive tillers plant^{-1}), Lunisree and Tellahamsa (100-grain weight) with high GCA effects and *per se* performance were identified as good general combiners for yield attributes (Table 4).

The best specific cross combinations (Table 5) with high sca effects and *per se* performance *viz.*, IR-20/RDR 763 and Tellahamsa/WGL-NDL 2 (LAI at tillering); Shiva/Erramallelu and Shiva/ Tellahamsa (LAI at heading); Shiva/Erramallelu and Tellahamsa/Lunisree (CGR from tillering to heading); Lunisree/RDR 763, and Shiva/Lunisree (CGR from heading to maturity); Tellahamsa/Lunisree (NAR); WGL-NDL-2/RDR-763, IR-20/RDR-763 (HI) and Lunisree/RDR-763 and Shiva/Erramallelu (BY) registered for different physiological parameters possessed the parental combinations of either high x low or low X low GCA, which indicated involvement of non-additive gene action in their inheritance. The superior crosses for HI involved low x low general

Table 4. Estimates of mean and general combining ability effects for physiological and yield characters

Source	LAI tillering		LAI heading		CGR (H-R)		CGR (T-H)		NAR		HI		BY $plant^{-1}$	
	$\overline{X}$	GCA	$\overline{X}$	GCA	$\overline{X}$	GCA	$\overline{X}$	GCA	$\overline{X}$	GCA	$\overline{X}$	GCA	$\overline{X}$	GCA
IR 20	1.68	0.543**	4.70	0.340**	12.43	-0.504	18.23	-1.661**	39	-13.090**	47.40	-0.497	41.40	0.177
Shiva	0.70	-0.123*	3.76	0.446**	12.40	1.644**	14.70	-0.635	65	3.206	53.83	0.243	35.93	2.073*
Tellahamsa	0.78	0.055	3.73	0.172**	11.90	-0.334	24.60	3.595**	59	-5.608**	52.26	0.584	41.30	3.729**
Lunisree	1.02	-0.027	2.38	-0.512**	10.66	-0.871*	21.20	5.498**	66	-0.090	58.90	1.717*	38.10	3.714**
WGL-NDL 2	0.64	-0.291**	1.92	-0.848**	8.22	-2.141**	10.36	-3.872**	67	4.577*	52.93	-0.942	21.16	-8.031**
Erramallelu	0.81	-0.084	2.99	-0.082	12.93	0.203	20.33	-0.528	76	3.280	57.30	0.140	36.53	-0.894
RDR 763	0.84	-0.074	5.27	0.484**	13.76	2.003**	16.03	-2.398**	56	7.725**	45.00	-1.246*	39.83	-0.768
SE±		0.048		0.055		0.372		0.566		1.976		0.489		0.805
Source	**Days to 50% flowering**		**Productive tillers $plant^{-1}$**		**Plant height**		**Panicle length**		**Filled grains $panicle^{-1}$**		**100-grain weight**		**Grain yield $plant^{-1}$**	
	$\overline{X}$	GCA	$\overline{X}$	GCA	$\overline{X}$	GCA	$\overline{X}$	GCA	$\overline{X}$	GCA	$\overline{X}$	GCA	$\overline{X}$	GCA
IR 20	106	5.577**	10.96	-1.148**	86	-0.010	23.63	0.895**	163	13.38**	1.68	-0.167**	19.63	-0.224
Shiva	103	2.947**	9.33	0.312	89	3.620**	23.86	1.021**	147	-3.013*	2.21	0.156**	19.36	1.294*
Tellahamsa	93	0.466	12.63	0.378	89	4.627**	22.50	0.703**	131	-4.557**	2.37	0.201*	21.60	2.339**
Lunisree	88	-5.868**	11.40	0.341	94	10.231**	21.00	-0.583**	123	-7.361**	2.98	0.437**	22.46	2.81**
WGL-NDL 2	89	-3.831**	8.70	-2.122**	72	-7.399**	20.50	-1.023**	192	8.332**	1.34	-0.361**	11.16	-4.832**
Erramallelu	94	0.651*	12.40	0.163	80	-3.347**	23.56	0.654**	150	-2.520	2.03	-0.017	20.93	-0.395
RDR 763	102	0.058	14.20	2.075**	70	-7.721**	17.73	-1.668**	133	-4.261**	1.61	-0.249**	17.96	-0.998
SE±		0.296		0.215		0.596		0.118		1.453		0.014		0.501

* Significant at 5% level   ** Significant at 1% level

Table 5. Estimates of mean and specific combining ability effects for physiological and yield characters

Cross	LAI at tillering		LAI at heading		CGR (T-H)		CGR (H-R)		NAR (T-H)		HI		BY plant^{-1}	
	$\overline{X}$	GCA	$\overline{X}$	GCA	$\overline{X}$	GCA	$\overline{X}$	GCA	$\overline{X}$	GCA	$\overline{X}$	GCA	$\overline{X}$	GCA
IR 20/Shiva	2.28	0.399**	3.03	-0.959**	15.53	1.010	13.66	-2.835	55	5.157	59.63	3.369**	41.26	0.832
IR 20/Tellahamsa	2.24	0.178	3.81	0.099	7.60	-4.946**	22.66	1.935	24	-17.028**	57.80	1.195	46.43	4.344*
IR 20/Lunisree	2.15	0.176	2.64	-0.394**	12.70	0.691	20.36	-2.269	50	2.787	57.70	-0.038	33.46	-8.608**
IR 20/WGL-NDL 2	1.45	-0.266*	2.14	-0.558**	10.86	0.128	15.86	2.602	53	1.787	59.16	4.088**	27.16	-3.164
IR 20/Erramallelu	2.36	0.443**	3.89	0.429**	14.53	1.451	14.33	-2.276	45	-5.583	59.26	3.106*	41.70	4.232*
IR-20 RDR 763	2.73	0.800**	3.65	-0.377*	16.43	1.551	12.06	-2.672	58	3.306	59.30	4.525**	34.10	-3.494
Shiva/Tellahamsa	1.49	0.097	4.77	0.950**	17.23	2.539**	25.36	3.609*	57	-0.991	57.36	0.021	48.26	4.281*
Shiva/Lunisree	1.55	0.239*	2.79	-0.346*	10.80	-3.357**	28.50	4.872**	47	-16.176**	58.26	-0.212	49.40	5.429*
Shiva/WGL-NDL 2	1.18	0.133	2.37	-0.430**	10.46	0.579	15.20	0.943	76	7.824	55.26	-0.553	32.53	0.306
Shiva/Erramallelu	1.58	0.326*	4.78	1.216**	21.66	6.436**	18.40	0.765	70	3.787	57.93	1.032	45.40	6.036**
Shiva/RDR 763	1.11	-0.157	4.37	0.238	18.36	1.336	14.06	-1.698	74	3.343	58.20	2.684*	35.40	-4.090
Tellahamsa/Lunisree	1.70	0.208	2.83	-0.032	17.23	5.054**	30.46	2.576	72	17.972**	60.50	1.681	49.70	4.073
Tellahamsa/WGL-NDL 2	1.94	0.715**	2.77	0.247	13.50	2.591**	14.96	-3.554*	53	-6.028	58.60	2.440	34.76	0.884
Tellahamsa/Erramallelu	1.45	0.021	2.95	-0.346*	10.23	-3.020**	22.90	1.035	44	-14.065**	58.70	1.458	40.56	-0.453
Tellahamsa/RDR 763	1.80	0.362**	2.57	-1.285**	14.46	-0.586	17.03	-2.961	62	-0.176	59.90	4.044**	36.70	-4.445*
Lunisree/WGL-NDL 2	1.19	0.050	2.85	1.011**	9.40	-0.972	23.26	2.843	46	-18.546**	56.16	-1.127	38.16	4.299*
Lunisree/Erramallelu	1.40	0.049	2.05	-0.559**	10.10	-2.616**	23.70	-0.035	55	-7.917	58.20	0.325	36.83	-4.171
Lunisree/RDR 763	1.42	0.060	3.10	-0.075	17.66	3.151**	31.10	9.202**	78	10.306*	58.46	1.477	55.13	14.003**
WGL-NDL-2/Erramallelu	1.13	0.047	1.76	-0.516**	10.00	-1.446	14.30	-0.098	68	0.083	48.86	-6.849**	30.26	1.006
WGL/NDL-2/RDR 763	0.89	-0.202	2.26	-0.582**	14.43	0.887	11.10	-1.361	91	18.639**	59.73	5.403**	27.96	-1.419
Erramallelu/RDR 763	1.39	0.087	3.49	-0.118	16.50	0.910	11.30	-4.572**	75	4.269	55.33	-0.079	29.60	-6.923
SE±		0.127		0.147		0.984		1.499		5.23		1.294		2.13

* Significant at 5% level ** Significant at 1% level

Source	Days to 50% flowering		Productive tillers plant^{-1}		Plant height		Panicle length		Filled grains panicle^{-1}		100-grain weight		Grain yield plant^{-1}	
	$\overline{X}$	GCA	$\overline{X}$	GCA	$\overline{X}$	GCA	$\overline{X}$	GCA	$\overline{X}$	GCA	$\overline{X}$	GCA	$\overline{X}$	GCA
IR 20/Shiva	105	4.333**	12.26	0.366	86	1.542	23.20	-0.343	171	16.502**	2.06	-0.059	24.63	1.911
IR 20/Tellahamsa	103	4.481**	13.46	1.499**	89	2.768	24.50	1.276**	146	-7.054	2.20	0.042	26.86	3.100*
IR 20/Lunisree	81	-11.185**	9.96	-1.964**	84	-7.269**	20.80	-1.139**	143	-7.350	2.33	-0.067	19.33	-4.911**
IR 20/WGL-NDL 2	92	-2.222**	9.33	-0.134	66	-7.940**	20.56	-0.931**	152	-13.776**	1.74	0.138**	16.06	-0.530
IR 20/Erramallelu	103	4.630**	13.76	2.014**	86	7.742**	24.23	1.057**	181	26.176**	2.04	0.094*	24.76	3.733**
IR 20 RDR 763	92	-6.111**	10.83	-2.831**	66	-7.384**	20.50	-0.354	155	1.550	1.79	0.079*	20.26	-0.163
Shiva/Tellahamsa	94	-1.222	15.36	1.940**	90	0.671	23.76	0.417	131	-5.461	2.67	0.186**	27.73	2.448
Shiva/Lunisree	87	-2.222**	15.00	1.610**	95	0.134	21.33	-0.731*	126	-7.457	2.67	0.057	28.80	3.037*
Shiva/WGL-NDL 2	87	-3.926**	10.30	-0.627	78	1.064	21.50	-0.124	144	-5.717	1.92	-0.002	18.00	-0.115
Shiva/Erramallelu	94	-1.741*	15.20	2.021**	80	-1.555	23.40	0.098	136	-2.365	2.47	0.208**	26.33	3.781**
Shiva/RDR 763	91	-4.481**	17.86	2.744**	74	-3.347*	21.26	0.287	125	-12.224**	2.11	0.073*	20.63	-1.315
Tellahamsa/Lunisree	84	-2.407**	14.93	1.477**	100	3.694*	21.53	-0.213	142	9.887*	2.91	0.145**	30.13	3.326*
Tellahamsa/WGL-NDL 2	87	-1.444	10.03	-0.960	77	-1.244	19.86	-1.439**	150	1.661	1.92	-0.047	20.40	1.241
Tellahamsa/Erramallelu	99	5.407**	11.63	-1.645**	80	-2.062	23.46	0.483	152	14.413**	2.31	0.000	23.83	0.237
Tellahamsa/RDR-763	88	-4.667**	14.60	-0.590	76	-1.621	21.20	0.539	131	-4.546	2.06	-0.015	22.10	-0.893
Lunisree/WGL-NDL 2	84	1.222	11.50	0.544	94	9.919**	21.00	0.980**	153	8.065*	2.30	0.098**	21.46	1.830
Lunisree/Erramallelu	84	-2.926**	12.63	-0.608	86	-2.166	20.80	-0.898**	123	-10.683**	2.59	0.047	21.66	-2.407
Lunisree/RDR 763	88	1.667*	18.13	2.981**	96	11.908**	20.30	0.924**	154	21.091**	2.24	-0.074*	32.23	8.763**
WGL-NDL-2/Erramallelu	87	-1.963*	9.20	-1.579**	61	-9.303**	20.23	-1.024**	99	-50.763**	1.62	-0.132**	14.80	-1.626
WGL/NDL-2/RDR 763	88	-0.704	15.03	2.344**	62	-4.462**	19.63	0.698*	146	-2.102	1.58	0.067	16.66	0.844
Erramallelu/RDR 763	88	-5.185**	15.70	0.725	67	-3.281*	19.63	-0.980**	139	1.850	1.77	-0.093*	16.40	-3.859**
SE±		0.784		0.569		1.578		0.314		3.845	1.62	0.037		1.327

* Significant at 5% level ** Significant at 1% level

combiners suggesting that epistatic gene action, might be due to genetic diversity in the form of heterozygous loci. Hence, these crosses could be utilized through heterosis breeding and the best crosses identified on over all basis for this purpose were Lunisree/RDR-763, Shiva/Erramallelu and Shiva/Lunisree.

Grain yield is the ultimate result, which is dependent on its components. Grafius (1959) suggested that there would be no separate gene system for yield *per se* and yield is an end product of multiplicative interaction between yield and its components. Interestingly, the parents with high GCA effects for yield also possessed high GCA effects for other yield components. Similarly, crosses with high *per se* performance and SCA effects (Lunisree/RDR 763, Tellahamsa/ Lunisree, Shiva/Lunisree and Shiva/ Erramallelu) for grain yield also had exhibited high SCA effects for other yield components and physiological parameters in the material studied.

The superior crosses, with high SCA effects (Table 5) for productive tillers plant^{-1} (Lunisree/RDR 763, Shiva/RDR 763 and Shiva/Erramallelu) and filled grains panicle^{-1} (IR 20/Erramallelu, Lunisree/RDR 763 and IR-20/Shiva) mostly involved parents with medium x high, high x low, and low x low GCA effects, for such crosses simple pedigree breeding would not be sufficient to improve these characters, instead, population improvement *i.e.,* mass selection with recurrent random mating in early segregating generations (Redden and Jensen, 1974) could be a perspective breeding for yield improvement in rice.

The yield components *viz.,* panicle length and 100-grain weight were largely governed by additive genetic proportions, as such the best cross combinations *viz.,* IR 20/Tellahamsa, IR 20/Erramallelu (Panicle length) and Shiva/Tellahamsa, Tellahamsa/Lunisree (100-grain weight) which involved parents with high x high gca effects could straight away be utilized for improvement through single plant selections in early segregating generations by adopting pedigree method of breeding, as they are most likely to give pure lines with high test weight. The cross Tellahamsa/Lunisree (high x high) was also superior in terms of grain yield plant^{-1}.

From this study, it can be concluded that, limited yield improvement is possible through conventional breeding and a quantum jump in yield may be expected by following heterosis breeding by combining the physiological efficiency of plants. Fortunately, high amount of heterosis was exhibited for important physiological traits like CGR, LAI and HI coupled with non-additive gene action. The best specific crosses were Lunisree / RDR 763, Shiva / Erramallelu, Shiva / Lunisree and IR 20 / Erramallelu.

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