Combining Ability and Gene Action in Rice under Salinity

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ABSTRACT. *Combining ability for 8 quantitative traits and Na-K ratio in rice genotypes under salinity was studied through Line x Tester analysis involving 4 saline tolerant genotypes as lines and 4 locally adapted cultivars as testers. The study revealed that variance due to lines x testers was significant for all the characters except panicle length. The estimates of SCA and GCA and their ratio indicated preponderance of non-additive gene action for all the traits except grain number panicle*[-1] *and panicle length. Based on mean performance and gca effects, IET 14543, IET 14552, CO 43 and TRY 1 were found to be better parents for most of the traits studied. On the basis of mean performance, sca effects and standard heterosis, 2 hybrids viz., SSRC 92058/TRY 1 and SSRC 92076/CO 43 were found to be promising for heterosis breeding. The genetics of salinity tolerance in rice was investigated by adopting generation mean analysis, for 8 crosses involving 4 salt tolerant genotypes viz., IET 14543, IET 14552, SSRC 92058 and SSRC 92076 and 2 susceptible cultivars namely TKM 9 and ADT 36. The P_1, P_2, F_1, F_2, BC_1 and BC_2 generations were studied for 7 metric traits. As evidenced from the scaling tests, an epistatic digenic model was assumed for all the crosses. Since non-additive gene action is predominant for majority of the traits, 1 or 2 cycles of recurrent selection followed by pedigree breeding is suggested. Duplicate epistasis was more towards complementary type. Among the interaction effects, dominance x dominance (l) was predominant. Due to preponderance of dominance component for all the traits except grain yield plant*[-1]*, heterosis breeding is also suggested as a suitable breeding methodology under salinity.*

INTRODUCTION

Salinity is one of the main obstacles to high yields in deltas, estuaries and coastal fringes in the humid tropics. It is also a serious impediment to the growth of irrigated rice in arid and semi-arid areas (Ponnamperuma, 1977). While various methods such as reclamation, irrigation, and drainage are advocated to reduce soil salinity, they are not always economical or practical. Therefore, development of salt tolerant cultivars is undoubtedly a viable alternative (Lee *et al.*, 1996).

Rice (*Oryza sativa* L.) is moderately sensitive to salinity (Akbar *et al.*, 1972). To effect and infuse salt tolerance, the rice plant itself is now genetically modified. However, progress made so far is slow, primarily due to inadequate knowledge of the genetics and mechanism of salinity tolerance (Gregorio and Senadhira, 1993). The potassium ion, which plays an important role in activating enzymes and which affects opening and closure of the stomata, correlated well with salt tolerance through its accumulation in the shoots

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(Ponnamperuma, 1984). Moreover, a Na-K imbalance adversely affected grain yield (Devitt et al., 1981). Qatar (1991) stressed the importance of Na-K ratio as a criterion in selection of salt tolerant lines. A tolerant rice compared with a salt sensitive variety, maintains a lower concentrations of Na^+, a higher concentration of K^+, and low Na-K ratio in the shoot (Bal et al., 1986; Thomas and Nambisan, 1999). Several workers have reported the presence of considerable genetic variation in salinity tolerance among rice cultivars (Akbar et al., 1972; Akbar and Yabuno, 1975; Ikehashi and Ponnamperuma, 1978). The response of the rice plant to soil salinity is a complex phenomenon. Some plant breeders have reported that salinity tolerance is governed by polygenes (Akbar and Yabuno, 1975; Akbar et al., 1985; Mishra et al., 1996). Consequently, it has been suggested that several donor parents be included for infusing salt tolerance through pyramiding of desirable genes (Yeo and Flowers, 1984).

The choice of the breeding methodology is a function of genetic architecture of the economic traits in the crop to be improved upon. Combining ability is an effective tool which gives useful genetic information for the choice of parents in terms of the performance of their hybrids (Dhillon, 1975). Even though many studies have been made on the combining ability and gene action for yield and its components in rice, information under salinity is very much limited. Hence an attempt has been made to get further insights into the combining ability of Na-K ratio, yield and its components through Line x Tester analysis and epistatic gene action of salt tolerance, adopting generation mean analysis.

MATERIALS AND METHODS

The experimental materials consisted of 4 saline tolerant genotypes viz., IET 14543, IET 14552, SSRC 92058 and SSRC 92076 as lines and 4 popular cultivars consisting 2 short duration varieties viz., TKM 9 and ADT 36 and 2 medium duration varieties viz., CO 43 and TRY 1 as testers and their 16 hybrids obtained through crossing in Line x Tester mating design. The parents and F_1s were grown in randomised block design replicated thrice, spaced with 15×20 cm at Pandit Jawaharlal Nehru College of Agriculture and Research Institute, Karaikal, during Kharif season (June-July) 1997, under natural saline environment. The characteristics of soil and irrigation water are presented below :

Source	EC (dSm⁻¹)	pH	SAR	RSC (meq/l)
Soil	0.90	7.85	-	-
Irrigation Water	2.44	8.40	22.40	18.60

As per United States Salinity Laboratory (USSL) classification (Richards, 1973), the irrigation water used in the present study is saline-alkaline as indicated by high sodium adsorption ratio (SAR) and residual sodium carbonate (RSC) values. Five random competitive plants were used to record observations on days to 50% flowering, plant height, productive tillers $plant^{-1}$, grain number $panicle^{-1}$, spikelet sterility, 100 grain weight, panicle length, grain yield $plant^{-1}$ and Na-K ratio. Sodium and potassium in plant samples

at the time of flowering were estimated by adopting the method suggested by Standford and English (1949) and Na-K ratio was calculated. Combining ability analysis was done following the method suggested by Kempthorne (1957).

Genetic components of variances (d, h, i, j and l) of salinity tolerance in rice were investigated using 8 cross combinations *viz.*, IET 14543/TKM 9, IET 14543/ADT 36, IET 14552/TKM 9, IET 14552/ADT 36, SSRC 92058/TKM 9, SSRC 92058/ADT 36, SSRC 92076/TKM 9 and SSRC 92076/ADT 36 involving 4 salt tolerant genotypes (IET 14543, IET 14552, SSRC 92058 and SSRC 92076) and 2 susceptible genotypes (TKM 9 and ADT 36). The resultant 6 generations *viz.*, P_1, P_2, F_1, F_2, BC_1 and BC_2 of each cross were raised in randomized block design with 3 replications during summer (February) 1998 under natural saline environment. The characteristics of soil and irrigation water were the same as that of the previous season *kharif* 1997. The total number of plants raised in each replication was 30 in parents and F_1, 60 in backcross generations and 200 in F. Observations on days to 50% flowering, plant height, productive tillers plant^{-1}, grain number panicle^{-1}, spikelet sterility, panicle length and grain yield plant^1 were recorded on 10 plants each on parents and F_1, 120 plants in F_2 and 35 plants each in BC_1 and BC_2 generations. The means and variances of seven biometric traits were computed for each generation of all the cross. The adequacy of data for simple additive dominance model and digenic interaction model were tested adopting the methods suggested by Mather and Jinks (1971) and Cavalli (1952) respectively. The genetic effects were estimated by adopting perfect fit equation given by Jinks and Jones (1958).

RESULTS AND DISCUSSION

The analysis of variance revealed that variation between genotypes (parents and hybrids) was highly significant for all the 9 characters studied. The Line x Tester interactions were significant for all the characters except panicle length (Table 1).

Table 1.   Analysis of variance for different characters.

Source of variance	df	Mean square								
		Days to 50% flowering	Plant height (cm)	Productive tillers plant^{-1}	Grain number panicle^{-1}	Spikelet sterility (%)	100 grain weight (g)	Panicle length (cm)	Grain yield plant^{-1} (g)	Na-K ratio
Genotypes	23	226.44**	117.48**	27.17**	440.08**	109.10**	0.027**	11.68**	28.23**	0.034**
Lines (L)	3	102.85**	195.69**	27.11**	1537.47**	58.83**	0.005	47.65**	52.79**	0.03**
Testers (T)	3	551.83**	60.19**	11.70**	36.96	163.00**	0.053**	13.11**	10.88**	0.0002
L×T	9	162.06**	50.24**	16.45**	141.90**	29.30**	0.020*	3.22	19.00**	0.037**
Error	46	6.62	14.00	0.65	14.16	2.45	0.002	1.18	1.05	0.0003
GCA		13.77	6.47	0.25	53.78	6.80	0.0007	2.26	1.07	- 0.002
SCA		51.81	12.07	5.27	42.58	8.95	0.006	0.68	5.98	0.012
GCA/SCA		0.27	0.54	0.05	1.26	0.76	0.122	3.33	0.18	- 0.140

* Significance at 5% level   ** Significance at 1% level

The mean performance and *gca* effects of lines and testers are given in Tables 2 and 3. In the present investigation, none of the lines and testers registered significant *gca* effects for all the characters studied. However, the line SSRC 92076 showed desirable *gca* effects for 3 traits including grain yield plant[1] and testers CO 43 and TRY 1 had desirable *gca* effects for majority of the traits including grain yield plant[1]. Evaluation of parents

Table 2. **Mean performance of parents for different characters.**

Hybrids	Days to 50% flowering	Plant height (cm)	Productive tillers plant[1]	Grain number panicle[1]	Spikelet sterility (%)	100 grain weight (g)	Panicle length (cm)	Grain yield plant[1] (g)	Na-K ratio
Lines									
IET 14543	108.62**	106.81	9.42**	73.71**	25.06**	2.19**	19.74	11.92	0.35**
IET 14552	114.75	106.41	11.21**	70.96**	32.43	2.14**	18.45	7.83**	0.42**
SSRC 92058	119.75**	105.75	13.79**	72.38**	25.62**	2.30**	18.54	14.29**	0.33**
SSRC 92076	109.71**	101.31	15.25**	41.62**	40.87**	2.05**	17.29	10.90	0.40**
Testers									
TKM 9	91.87**	89.08**	6.37**	58.83**	30.94**	2.35**	14.83**	10.69**	0.70**
ADT 36	106.83**	103.54	8.01**	78.91**	27.44	2.10**	18.92	10.28**	0.54
CO 43	120.43**	110.47**	12.62**	69.75	23.14**	2.27**	20.07**	15.88**	0.49**
TRY 1	114.89**	109.00**	13.92**	65.75	26.98	2.28**	18.93	15.82**	0.45**
Grand Mean	110.86	104.05	11.32	66.49	30.31	2.21	18.35	12.20	0.46
S.E. (M)	0.86	1.15	2.46	0.47	2.41	0.07	0.02	0.71	0.009
C.D. (5%)	2.60	3.48	3.48	1.41	7.30	3.26	0.07	2.16	0.028

* Significance at 5% level   ** Significance at 1% level

Table 3. **General combining ability effects of parents for different characters.**

Parents	Days to 50% flowering	Plant height (cm)	Productive tillers plant[1]	Grain number panicle[1]	Spikelet sterility (%)	100 grain weight (g)	Panicle length (cm)	Grain yield plant[1] (g)	Na-K ratio
Lines									
IET 14543	-2.68**	-2.92**	-1.94**	-14.85**	0.36	-0.03**	-2.84**	-0.84**	-0.05**
IET 14552	3.70**	4.76**	0.79**	2.64**	2.76**	-0.001	1.05**	-2.11**	-0.04**
SSRC 92058	-1.98**	1.91	-0.36	12.52**	-0.55	7.71	1.65**	0.13	0.03**
SSRC 92076	0.97	-3.75**	1.51**	0.31	-2.58**	2.10	0.14	2.83**	0.06**
S.E.	1.50	2.17	0.47	2.19	0.91	0.03	0.63	0.60	0.10
Testers									
TKM 9	-8.41**	-2.10	-1.03**	-0.25	4.15**	-1.48	0.62	-0.71**	0.007
ADT 36	-2.41**	-1.75	-0.63**	1.76	-1.32**	-3.48**	-1.56**	-0.91**	-0.004
CO 43	6.61**	1.66	1.05**	0.82	-4.40**	-4.81**	0.43	1.00**	-0.04**
TRY 1	4.21**	2.19**	0.06**	-2.33**	1.56**	9.77**	0.52	0.62**	-0.003
S.E.	1.50	2.17	0.47	2.19	0.91	0.03	0.63	0.60	0.10

* Significance at 5% level   ** Significance at 1% level

based on mean and *gca* effects separately, resulted in identification of different sets of parents as promising ones, but assessing the parents using both these parameters would be more relevant. This led to identification of IET 14543 and IET 14552 among the lines and CO 43 and TRY 1 among the testers as the best parents since they registered high mean performance coupled with high *gca* effects for most of the characters studied. These parents can be extensively used in breeding programmes for fixing desirable recombinants.

The mean performance, *sca* effects and standard heterosis of hybrids are presented in Tables 4, 5 and 6. Seven hybrids for Na-K ratio, five hybrids each for earliness and productive tillers plant^{-1} and grain yield plant^{-1}, four hybrids for grain number panicle^{-1} and three hybrids for spikelet sterility showed desirable *sca* effects. None of the hybrids exhibited significant *sca* effects for all the characters. However, *sca* effects coupled with mean performance and standard heterosis were found to be very effective in locating superior cross combinations for the exploitation of hybrid vigour through heterosis breeding (Richharia and Singh, 1983). In the present study, none of the hybrids exhibited higher order of expression for all the 3 genetic parameters. However, 2 hybrids *viz.*, SSRC 92058/TRY 1 and SSRC 92076/CO 43 registered all the aforesaid parameters and were adjudged as the best hybrids for grain yield plant^{-1}.

Table 4.   Mean performance of hybrids for different characters.

Hybrids	Days to 50% flowering	Plant height (cm)	Productive tillers plant^{-1}	Grain number panicle^{-1}	Spikelet sterility (%)	100 grain weight (g)	Panicle length (cm)	Grain yield plant^{-1} (g)	Na-K ratio
IET 14543/TKM 9	99.21**	105.33**	13.63	61.75**	28.28**	2.19	18.00	12.54**	0.38**
IET 14543/ADT 36	108.34	107.25	7.75**	70.93	21.14	2.14	12.56**	15.00	0.35**
IET 14543/CO 43	109.30	107.34	13.84	58.21**	15.58**	2.13	15.94**	14.81	0.33**
IET 14543/TRY 1	110.37	107.84	14.71	51.34**	22.56	2.12	15.47**	13.76	0.38**
IET 14552/TKM 9	113.88**	116.07**	13.29**	75.75	23.90**	2.13	19.18	15.84	0.45**
IET 14552/ADT 36	113.50**	113.13	16.25**	76.04	26.61**	2.08**	18.86	11.22**	0.33**
IET 14552/CO 43	113.13**	119.72**	15.71**	76.00	19.25**	2.06**	19.89**	12.81**	0.40
IET 145552/TRY 1	112.21	109.58	15.58**	84.42**	27.42**	2.42**	19.60	11.15**	0.29**
SSRC 92058/TKM9	98.63**	108.27	10.09**	95.54**	28.37**	2.11**	19.76**	10.58**	0.40
SSRC 92058/ADT 36	105.71**	108.02	16.29**	83.84**	14.73**	2.15	19.21	15.34	0.33**
SSRC 92058/CO 43	115.88**	110.56	15.58**	88.88**	17.74**	2.14	20.17**	15.79	0.41
SSRC 92058/TRY 1	109.79	120.23**	14.25	83.46**	23.10	2.32**	20.80**	18.27**	0.63**
SSRC 92076/TKM 9	92.58**	101.37**	16.54**	67.58**	22.18	2.20	18.85	17.68**	0.43
SSRC 92076/ADT 36	100.75**	104.04**	14.87	77.86	18.39**	2.18	16.44**	14.26	0.61**
SSRC 92076/CO 43	126.09**	108.46	16.75**	81.84**	15.96**	2.17	19.06	20.08**	0.50**
SSRC 92076/TRY 1	122.38**	110.58	15.54**	73.13	19.28**	2.23	19.52	18.78**	0.33**
Grand Mean	109.48	109.86	14.44	75.41	21.53	2.17	18.33	14.87	0.41
S.E.	1.53	2.23	0.48	2.24	0.93	0.03	0.65	0.61	0.01
C.D. (5%)	3.08	4.48	0.97	4.51	1.88	0.06	1.30	1.23	0.02

* Significance at 5% level   ** Significance at 1% level

Table 5. Specific combining ability effects of hybrids for different characters.

Hybrids	Days to 50% flowering	Plant height (cm)	Productive tillers plant⁻¹	Grain number panicle⁻¹	Spikelet sterility (%)	100 grain weight (g)	Panicle length (cm)	Grain yield plant⁻¹ (g)	Na-K ratio
IET 14543/TKM 9	0.82	0.49	2.18**	1.45	2.24**	0.06**	1.89**	-0.78	0.01
IET 14543/ADT 36	3.94**	2.06	-4.10**	8.62**	0.56	0.03	-1.37**	1.89**	-0.006
IET 14543/CO 43	-4.12**	-1.26	0.30	-3.17	-1.91**	0.04	0.01	-0.22	-0.03**
IET 14543/TRY 1	-0.64	-1.30	1.62**	-6.90**	-0.89	-0.12**	-0.54	-0.89	0.02**
IET 14552/TKM 9	9.12**	3.54	0.88	-2.04	-4.55**	-0.02	-0.82	3.79**	0.08**
IET 14552/ADT 36	2.73	0.26 ·	1.67**	-3.77	3.63**	-0.06**	1.04	-0.62	-0.03**
IET 14552/CO 43	-6.67**	3.44	-0.55	-2.87	-0.65	-0.07**	0.08	-0.95	0.03**
IET 145552/TRY 1	-5.17**	-7.24**	-0.23	8.69**	1.57	0.15**	-0.30	-2.23**	-0.07**·
SSRC 92058/TKM9	-0.47	1.39	-2.94**	7.87**	3.23**	-0.05	-0.84	-3.70**	-0.04**
SSRC 92058/ADT 36	0.62	-2.00	2.86**	-5.85**	-4.94**	0.004	0.79	1.26**	0.11**
SSRC 92058/CO 43	1.76	-2.87	0.48	0.13	1.15	0.01	-0.25	-0.21	-0.04**
SSRC 92058/TRY 1	-1.91	6.26**	-0.40	-2.14	0.56	0.04	0.30	2.66**	0.19**
SSRC 92076/TKM 9	-9.46**	-2.64	1.65**	-7.27**	-0.93	0.02	-0.23	0.69	-0.04**
SSRC 92076/ADT 36	-7.29**	-0.32	-0.43	1.00	0.75	0.02	-0.46	-2.52**	0.15**
SSRC 92076/CO 43	9.02**	-0.69	-0.23	5.91**	1.41	0.02	0.16	1.38**	0.03**
SSRC 92076/TRY 1	7.72**	2.27	-0.99**	0.35	-1.23	-0.06**	0.54	0.46	-0.14**
S.E.	2.99	4.35	0.94	4.37	1.82	0.05	1.26	1.19	0.02

* Significance at 5% level   ** Significance at 1% level

Table 6. Extent of standard heterosis (%) for different characters.

Hybrids	Days to 50% flowering	Plant height (cm)	Productive tillers plant⁻¹	Grain number panicle⁻¹	Spikelet sterility (%)	100 grain weight (g)	Panicle length (cm)	Grain yield plant⁻¹ (g)	Na- K ratio
IET 14543/TKM 9	-17.62**	-4.64**	7.95	-11.46**	22.21**	-3.81*	-10.30*	-20.10**	-22.97**
IET 14543/ADT 36	-10.04**	-2.91	-38.58**	1.70	-8.66	-5.72**	-37.40**	-5.52	-29.05**
IET 14543/CO 43	-9.24**	-2.84	9.61	-16.54**	-32.67**	-6.16**	-20.58**	-6.72	-33.11**
IET 14543/TRY 1	-8.35**	-2.38	16.53**	-26.40**	-2.51	-6.74**	-22.92**	-13.35	-22.97**
IET 14552/TKM 9	-5.44**	5.07	5.30	8.61	3.28	-6.16**	-4.43	-0.20	-8.11**
IET 14552/ADT 36	-5.75**	2.41	28.73**	9.03*	14.98**	-8.50**	-6.01	-29.31**	-33.11**
IET 14552/CO 43	-6.06**	8.37**	24.45	8.97*	-16.81**	-9.53**	-0.80	-19.34	-18.92**
IET 145552/TRY 1	-6.82**	-0.81	23.44**	21.03**	18.51**	6.30**	-2.34	-29.80**	-41.22**
SSRC 92058/TKM9	-18.10**	-1.99	-20.01**	36.99**	22.60**	-7.04**	-1.54	-33.34*	-18.92**
SSRC 92058/ADT 36	-12.22**	-2.22	29.07**	20.20**	-36.36**	-5.43**	-4.29	-3.40	-33.11**
SSRC 92058/CO 43	-3.78**	0.08	23.45**	27.43**	-23.35**	-5.87**	0.40 ·	-0.50	-17.57**
SSRC 92058/TRY 1	-8.83**	8.83**	12.91**	19.66**	-0.17	2.05	3.64	15.07**	27.71**
SSRC 92076/TKM 9	-23.13**	-8.24**	31.03**	-3.11	-4.15	-3.23	-6.08	11.36*	-12.84**
SSRC 92076/ADT 36	-16.34**	5.82*	17.78**	11.63*	-20.53**	-4.11*	-18.09**	-10.18	23.65**
SSRC 92076/CO 43	4.70**	1.82	32.70**	17.33**	-31.01**	-4.55**	-5.03	26.45**	1.35
SSRC 92076/TRY 1	1.61**	0.09	23.11**	4.85	-16.67**	-2.05	-2.72	18.27**	-33.78**
S.E.	1.49	2.16	0.47	2.17	0.90	0.027	0.63	0.59	0.01

* Significance at 5% level   ** Significance at 1% level

The proportional contributions by lines and testers to total variance revealed that the lines and lines x testers (Table 7) have contributed more than the testers for all the characters studied.

Table 7.   Proportional contribution of lines, testers and line × tester to total value.

Characters	Proportional contribution due to		
	Lines (%)	Testers (%)	Line × Tester (%)
Days to 50% flowering	9.02	48.37	42.62
Plant height	48.13	14.80	37.07
Productive tillers plant[-1]	30.75	13.28	55.97
Grain number panicle[-1]	76.86	1.85	21.28
Spikelet sterility	18.99	52.62	28.38
100 grain weight	4.21	44.67	51.13
Panicle length	67.66	18.61	13.73
Grain yield plant[-1]	43.75	9.01	47.24
Na-K ratio	23.32	0.19	76.50

In the present study, GCA/SCA ratio was observed (Table 1) to be more than unity for grain number panicle[-1] and panicle length, indicating the influence of additive gene action, while the remaining characters including Na-K ratio are under the influence of non-additive gene action. Similar results were obtained by Edwin and Subbaraman (1997). However, additive and non-additive gene action for Na-K ratio were reported by Gregorio and Senadhira (1993) and Mishra et al. (1998). For the improvement of these traits, breeder can exploit non-additive variance through heterosis breeding or other breeding methodologies like biparental mating, recurrent selection and diallel selective mating.

The scaling tests and estimates of genetic parameters viz., (m), (d), (h), (i), (j) and (l) for 7 traits are presented in Table 8.

An epistatic digenic interaction model was assumed as evidenced from the significance of any one of the scales for all the traits in all the crosses. In general, the dominance effect (h) was predominant for all the traits except grain yield plant[-1]. The predominance of dominant effect for these traits was earlier reported by many workers in rice under salinity (Edwin and Subbaraman, 1997; Narayanan et al., 1990). However, for grain yield plant[-1], both additive and dominance effects were important (Mishra et al., 1996).

Among the interaction components, dominance x dominance (l) gene effect was predominant for all the traits except for productive tillers plant[-1] and grain yield plant[-1] where both additive x dominance (j) and dominant x dominant (l) gene effects were

Table 8. Genetic effects of different characters.

Character	Cross	A	B	C	m	d	h	i	j	l	Type of epistasis
Days to 50% flowering	IET 14543 x TKM 9	*	*	*	123.97**±1.77	**	-**	-**	-**	**	D
	IET 14543 x ADT 36	*	*	*	150.89**± 1.86	**	-**	-**	-**	**	D
	IET 14552 x TKM 9	*	*	-	126.71**±1.98	**	-**	-**	-	**	D
	IET 14552 x ADT 36	*	*	*	78.69**± 0.96	**	**	**	**	-**	D
	SSRC 92058 x TKM 9	*	*	*	77.37**±2.05	**	**	**	-**	-**	D
	SSRC 92058 x ADT 36	*	*	*	13.99**±0.98	**	**	**	-**	-**	D
	SSRC 92076 x TKM 9	*	*	*	62.43**±2.03	**	**	**	-**	-**	D
	SSRC 92076 x ADT 36	*	*	*	78.79**±1.98	**	**	**	**	-**	D
Plant height	IET 14543 x TKM 9	*	*	*	214.56**±1.57	**	-**	-**	-**	**	D
	IET 14543 x ADT 36	*	*	*	11.75**±0.97	**	-**	-**	-	**	D
	IET 14552 x TKM 9	*	*	-	95.37**±1.98	**	**	-	-**	-	D
	IET 14552 x ADT 36	*	*	*	121.96**±2.37	**	-**	-**	-**	**	D
	SSRC 92058 x TKM 9	*	*	*	154.88**±2.08	**	-**	-**	-**	**	D
	SSRC 92058 x ADT 36	*	*	*	110.77**±1.56	**	-**	-**	-**	**	D
	SSRC 92076 x TKM 9	*	-	-	95.34**±1.87	**	-	-	-**	**	D
	SSRC 92076 x ADT 36	*	*	*	111.41**±2.08	-**	-**	-**	-**	**	D
Productive tillers plant⁻¹	IET 14543 x TKM 9	-	*	-	12.25**±1.44	**	-*	-**	**	**	D
	IET 14543 x ADT 36	*	*	-	-11.09**±1.38	**	**	**	-**	-**	D
	IET 14552 x TKM 9	*	-	*	6.05**±1.26	**	-	*	-**	-	C
	IET 14552 x ADT 36	*	*	*	13.09**±1.09	**	-	-**	**	-	D
	SSRC 92058 x TKM 9	*	*	*	-0.58±1.41	**	**	**	-**	-**	D
	SSRC 92058 x ADT 36	-	*	*	-9.12**±0.91	**	**	**	-**	-**	D
	SSRC 92076 x TKM 9	*	*	*	-0.31±1.49	**	**	**	-**	-**	D
	SSRC 92076 x ADT 36	*	*	*	7.31**±1.43	**	**	**	-**	-**	D
Grain number panicle⁻¹	IET 14543 x TKM 9	*	*	*	88.71**±3.00	**	-**	-**	**	**	D
	IET 14543 x ADT 36	*	*	*	36.87**±2.29	-**	**	**	**	-**	D
	IET 14552 x TKM 9	*	*	*	12.99**±3.09	**	**	**	-**	-**	D
	IET 14552 x ADT 36	*	-	*	126.27**±4.95	-**	-**	-**	-**	**	D
	SSRC 92058 x TKM 9	*	*	*	67.38**±2.91	**	-**	-	-**	**	D
	SSRC 92058 x ADT 36	*	*	*	34.70**±6.59	-**	**	**	**	-	C
	SSRC 92076 x TKM 9	*	*	*	-44.73**±2.90	-**	**	**	-	**	D
	SSRC 92076 x ADT 36	*	*	*	45.46**±3.92	**	-	**	**	**	C

Cont'd..

Table 8.   Continued ....

Character	Cross	A	B	C	m	d	'h	i	j	l	Type of epistasis
Spikelet sterility	IET 14543 x TKM 9	*	*	*	-36.30**±1.73	-**	.	-**	**	-**	D
	IET 14543 x ADT 36	*	*	*	11.09**±1.09	-**	**	**	-**	-**	D
	IET 14552 x TKM 9	-	-	*	55.36**±1.79	*	-**	-**	-**	**	D
	IET 14552 x ADT 36	*	*	*	1.14±0.94	**	**	**	-**	-**	D
	SSRC 92058 x TKM 9	*	*	*	11.06**±1.73	-**	**	**	**	-**	D
	SSRC 92058 x ADT 36	*	*	*	26.01**±2.21	-**	**	.	-**	-**	D
	SSRC 92076 x TKM 9	*	*	*	6.05**±1.80	**	**	**	**	-**	D
	SSRC 92076 x ADT 36	*	*	*	41.30**±2.76	**	.	-**	-**	-**	C
Panicle length	IET 14543 x TKM 9	*	*	-	31.98**±1.15	**	-**	-**	-**	**	D
	IET 14543 x ADT 36	*	*	-	1.50±1.15	**	**	**	-**	-**	D
	IET 14552 x TKM 9	-	*	-	19.74**±1.14	**	.	-**	**	*	D
	IET 14552 x ADT 36	*	*	*	-1.26±1.12	-**	**	**	-**	-**	D
	SSRC 92058 x TKM 9	-	-	*	26.13**±1.07	**	-**	-**	.	**	D
	SSRC 92058 x ADT 36	*	*	*	-17.12**±1.96	**	**	**	-**	-**	D
	SSRC 92076 x TKM 9	*	-	-	11.12**±1.40	**	**	**	**	-**	D
	SSRC 92076 x ADT 36	-	*	*	17.85**±2.09	-	-	-**	-	*	D
Grain yield plant^{-1}	IET 14543 x TKM 9	*	*	*	0.06±1.38	*	**	**	-**	-**	D
	IET 14543 x ADT 36	-	*	*	21.29**±2.19	-	**	-	-*	-	C
	IET 14552 x TKM 9	*	*	*	10.20**±1.39	-**	*	-	**	-	D
	IET 14552 x ADT 36	-	*	*	37.89**±2.38	-	-**	-**	*	**	D
	SSRC 92058 x TKM 9	*	*	*	-14.01**±1.18	**	**	**	-**	-**	D
	SSRC 92058 x ADT 36	*	-	-	19.91**±2.19	-	-	-	-*	-	D
	SSRC 92076 x TKM 9	*	*	*	14.56**±1.43	-	-**	-**	-	**	D
	SSRC 92076 x ADT 36	*	-	*	23.43**±2.23	-**	.	-**	**	-	C

prominent. Hence, among the interaction components, the unfixable gene effects played a major role in all the traits studied.

In majority of the crosses, (h) and (l) effects had opposite signs for all the traits. Therefore, duplicate kind of epistasis played a prominent role in governing all the traits than complimentary type of interaction.

As a whole, the dominance and epistatic interaction effects appear to govern grain yield plant^{-1} and its components. Since there is preponderance of non-additive gene action

for majority of the traits, improvement of these traits appeared to be difficult as simple pedigree breeding method may not be suitable to fix useful segregants in the early generations. Hence, 1 or 2 cycles of recurrent selection followed by pedigree breeding will be more effective and useful for the improvement of these traits (Nadarajan and Sree Rengasamy, 1992). In another approach, the improvement of these characters could also be achieved by adopting biparental mating in F_2 among the selected plants or following selection procedures such as diallel selective mating (Jensen, 1970). Due to presence of considerable amount of dominance component for most of the traits, heterosis breeding will also be rewarding for the improvement of the economic traits, adopting cytoplasmic male sterility system.

CONCLUSIONS

Combining ability analysis based on mean performance and *gca* effects, revealed that the parents *viz.*, IET 14543, IET 14552, CO 43 and TRY 1, were found to be better for most of the characters. On the basis of mean performance, *sca* effects and standard heterosis, two hybrids *viz.*, SSRC 920758/TRY 1 and SSRC 92076/CO 43 were found to be promising for grain yield plant[-1]. These hybrids are recommended for commercial exploitation of heterosis. Generation mean analysis indicated non-additive gene action, which is predominant for majority of the traits. Hence, 1 or 2 cycles of recurrent selection followed by pedigree breeding is suggested. Due to preponderance of dominance component for all the traits except grain yield plant[-1], heterosis breeding is also more relevant under salinity.

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