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Genetic dissection of yield and yield components related to sodicity tolerance in rice (*Oryza sativa* L.)

M. Gopikannan* and S.K. Ganesh

Anbil Dharmalingam Agricultural College and Research Institute. Department of Plant Breeding and Genetics, Trichy-620009, Tamil Nadu Agricultural University, Tamil Nadu, India

***Corresponding author: kannan.gk007@gmail.com**

Abstract

Understanding of gene actions governing the sodicity tolerance provides useful information for constructing breeding programs in rice. Inheritance of sodicity tolerance was studied in four crosses viz., IR 20 / FL 478, IR 20 / CSR 23, ADT 49 / TRY 2 and CO (R) 50 / CSR 23. The parents, F_1, F_2 and backcross generations were studied under sodicity conditions (ESP 23). The data on 10 physio-morphological traits viz., days to 50 per cent flowering, plant height, number of productive tillers per plant, panicle length, spikelet fertility percentage, single plant yield, Na^+: K^+ ratio, proline content, chlorophyll a/b ratio and chlorophyll stability index were recorded. Generation means analysis of the data revealed that all these traits exhibit significant non-allelic interactions and suggested that complex epistatic interactions have major role in controlling sodicity tolerance traits. Duplicate dominant type of epistasis was found to be governing the inheritance of all traits under investigation. In consideration of demonstrable additive and non-additive effects in controlling measured traits, the conventional breeding technology needs some modification for capitalizing the genetic effects. Instead of continuous selfing for a number of generations prior to selection, alternative intermating and selfing might be adopted to increase the span of selections. This would enhance the frequency of potential transgressive segregants in such materials. The involvement of dominance × dominance interactions for some traits indicated that it might be useful to postpone selections at later generations. As epistatic interactions might govern the inheritance of most of the traits studied, either the selection could be postponed to later generations or *inter se* matings among selected segregants might be advocated to break any undesirable linkages and to allow accumulation of favorable genes for improvement of rice under salinity / sodicity.

Keywords: Rice, inheritance, epistatic interactions, sodicity tolerance, generation means analysis.
Abbreviations: ESP- exchangeable sodium percentage, Na^+- sodium ions, K^+- potassium ions.

Introduction

Globally rice is planted to about 160 million ha and 685 million tons of produced harvested annually. Of this, Asia accounts for 90 per cent of the production and consumption of rice. India has the world's largest area under rice with 44 million ha and is the second largest producer (96 million tones) next only to China. It contributes 21.50 per cent of global rice production. However, productivity of rice is only 2.10 tones/ha (milled rice) which is lower than worlds average productivity of 2.90 tones/ha (FAO, 2009). Salinity /or sodicity is a limiting environmental factor for plant production, and is becoming more prevalent as the intensity of agriculture increases. Around the world, 100 million ha or 5 per cent of arable land, is adversely affected by high salt concentrations, which reduce crop growth and yield (Gunes et al., 2007). Approximately 6.50 per cent of the world land area is affected by either salinity or sodicity. In salt susceptible (glycophytes) plant species, biochemical, physiological and morphological characteristics are negatively affected, leading to abnormal growth and development and eventual plant death (Nishimura et al., 2011). Salts are detrimental to the various processes of crops such as seed germination, seedling growth and vigor, vegetative growth, flowering and fruit set and ultimately it causes diminished economic yield and also quality of produce (Sairam and Tyagi, 2004).Yield is the complex phenomenon and also is the end product of combination of the yield components. The complexity get worsen when rice crop interacts with abiotic stress like sodicity. The number of productive tillers per plant is an important yield parameter under sodicity because it determines the grain bearing panicles. The decrease in tillering capacity might be due to the toxic effect of salt on plant growth. The development of more tillers may be a mechanism of salt tolerance by dilution of salts in plants (Aslam et al., 1989). Under salinity / sodicity, poor seed setting is due to significant inhibition of starch synthetase activity in developing rice grains. Starch synthetase is the first enzyme in the pathway of starch metabolism which is responsible for transfer of a glucose moiety from ADP-G to the starch primer. The severe inhibitory effects of salts on fertility may be due to the differential competition in carbohydrates supply between vegetative growth and constrained its distribution to the developing panicles (Murty and Murty, 1982). Salt tolerance is related to exclusion of Na^+ ion and distribution of almost uniform concentration of this ion in all leaves (Haq et al., 2009). Overall control mechanism (before flowering) of sodium uptake through root properties and its subsequent distribution in different vegetative and floral parts especially in leaves where it causes leaf mortality thereby reduces transportation of total assimilates to the growing region

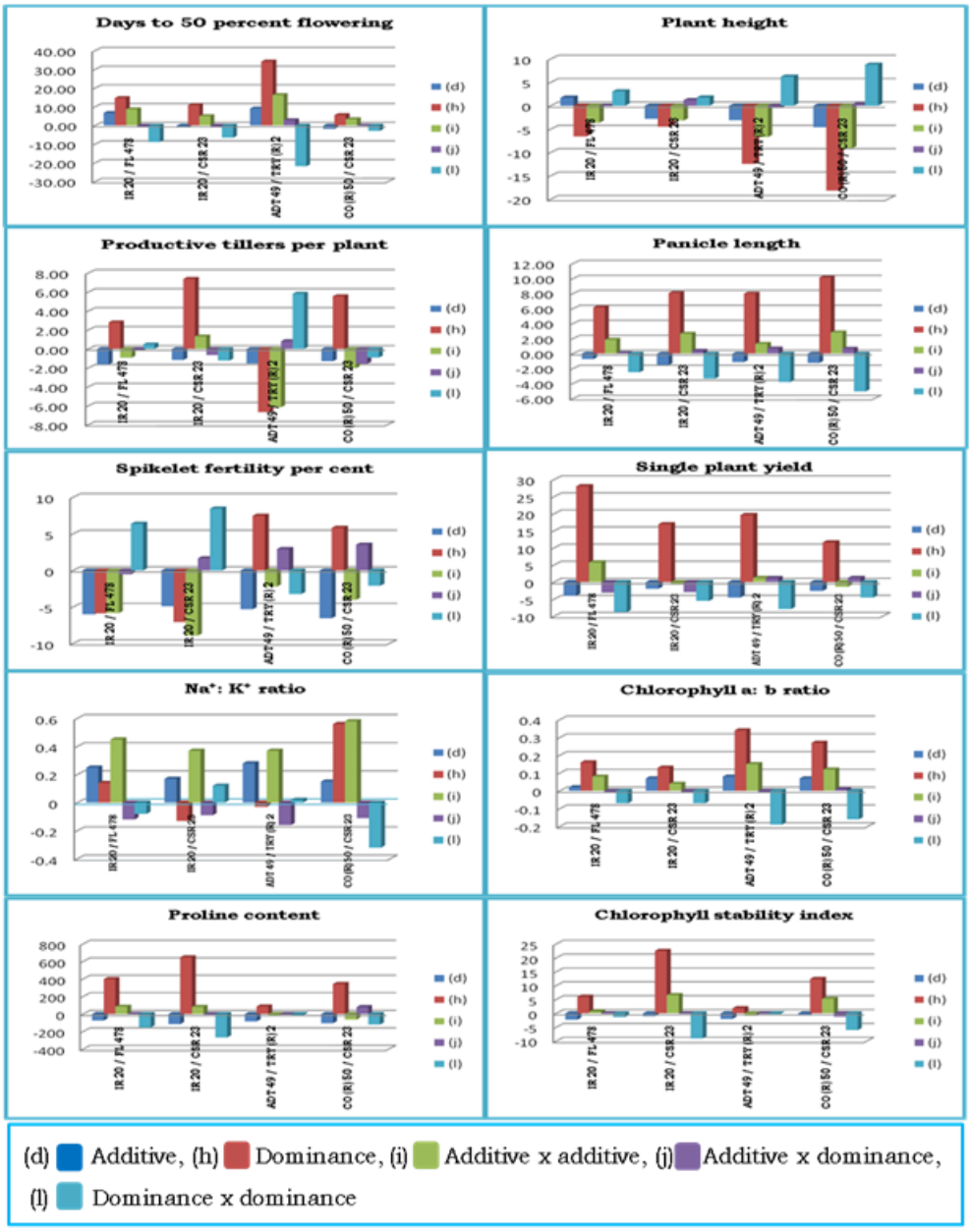

Fig 1. Genetic effects of different traits under sodicity.

(Munns, 2002). Maintenance of a low Na^+: K^+ ratio in cells is essential for plants tolerance to salt stress (Maathuis and Amtmann, 1999). One of the most notable effects of salt stress is the alteration of photosynthetic pigment biosynthesis (Maxwell and Johnson, 2000). The decrease in chlorophyll content under salt stress is a commonly reported phenomenon and in various studies and the chlorophyll concentration is used as a sensitive indicator of the cellular metabolic state (Chutipaijit et al., 2011). Chlorophyll a: b ratio has often been considered as a measure of the activity of chlorophyll synthesizing mechanism in plants under stress condition. Chlorophyll a: b ratio was lower in the salt tolerant cultivars (Kupke and Huntington, 1963). The accumulation of osmolytes such as proline is a well-known adaptive mechanism in plants against salt stress conditions. It has also been suggested that proline accumulation can serve as a selection criterion for the tolerance of most species to stressed conditions (Parida and Das, 2005; Ashraf and Foolad, 2007; Ahmad et al., 2009). The loss of turgor due to salt stress triggers proline accumulation in plants contributing to osmotic adjustment and stress tolerance (Aslam et al., 1989). Besides this, proline can serve as a protector of enzyme denaturation, a reservoir of nitrogen and carbon or as a stabilizer of the machinery for protein synthesis (Hamada and Khulaef, 1995). Rice is a salt-sensitive monocot (Darwish et al., 2009; Shereen et al., 2005). Breeding rice varieties with in-built salt tolerance is realized as the most promising, less resource consuming, economically viable and socially acceptable approach. Salt tolerance is a multigenic trait that allows plants to grow and maintain economic yield in the presence of non-physiologically high and relatively constant levels of salt (Hurkman, 1992). The strategies for mitigating salinity problems in crop production include both development of management options (Shannon, 1997) and genetic improvement of salinity tolerance in current cultivars (Epstein et al., 1980). Although the use of some management

options can improve yield under salinity stress, implementation is often limited due to cost and availability of good quality water resources. Therefore, the need for genetic improvement of salt tolerance is great and is expected to increase dramatically in near future. To plan efficient breeding programs for developing salt tolerant varieties, information on the genetic basis of salt tolerance, mode of inheritance, magnitude of gene effects and their mode of actions are necessary (Munns et al., 2006). Generation means analysis, provides an opportunity to estimate genetic components and measure of epistasis. This also helps us to understand the performance of parents used in the crosses and the potentials for crosses to be used for heterosis exploitation or pedigree selection (Sharma et al., 2003). However, studies on the genetics of sodicity tolerance in rice have been limited, inhibiting the realization of breeder's goal. Keeping it mind in addressing the need based research priorities, the present study was undertaken to predict the nature of gene action governing the inheritance of sodicity tolerant, yield and its components using generation means analysis in selected four crosses.

Results and discussion

The estimates of mean and standard error for six generations of each assumption of a simple additive-dominance gene action without non-allelic interaction and perfect fit estimate of the six genetic parameters *viz.*, m, (d), (h), (i), (j) and (l) on the assumption of an additive-dominance model with digenic interaction were presented in Tables 1 to 6 and Fig. 1 for 10 traits under study. Digenic epistasis model was found to be fit for all traits, since scaling tests were significant in all crosses under investigation except for number of productive tillers per plant in cross IR 20 / FL 478 and for chlorophyll stability in crosses IR 20 / FL478 and ADT 49 / TRY (R) 2. Duplicate epistasis had to be assumed as seen from opposite signs of both (h) and (l) effects in all 10 traits under study. Complimentary type of epistasis was evident in cross IR 20 / FL 478 for productive tillers per plant and in two crosses viz., IR 20 / CSR 23 and CO (R) 50 / CSR 23 for chlorophyll a/b ratio. Similar results were reported by (Farshadfar et al., 2001; Dashti et al., 2012). Positive additive x additive type of interaction with duplicate epistasis were observed for panicle length in all crosses and for single plant yield in cross IR 20 / FL 478. Hence these crosses might throw superior transgressive segregants in later generations.

Inheritance of days to 50 per cent flowering and plant height

For days to 50 per cent flowering, the cross ADT 49 / TRY (R) 2 exhibited dominance x dominance (l) type of gene interaction. In cross IR 20 / FL 478, additive x dominance (j) and dominance x dominance (l) type of gene actions might govern the inheritance of the trait. These results showed that non additive gene effect was found to be more important in controlling the trait. In two crosses viz., IR 20 / CSR 23 and CO (R) 50 / CSR 23 additive and dominance x dominance gene interactions were found to play a major role. Inter mating of selected segregants followed by one or two generations of selfing might yield an array of segregants varying in maturity groups, which would make the selection process meaningful. Dominance x dominance type of interaction for days to 50 per cent flowering was reported by Dashti et al. (2010). Short stature in rice reduces the susceptibility to lodging and increases the harvest index (Tsunoda, 1962). For plant height, three crosses viz., IR 20 / FL 478, ADT 49 / TRY (R) 2 and CO (R) 50 / CSR 23 exhibited additive, dominance and additive x additive (i) type of interactions which indicated the existence of both fixable and non-fixable gene actions. To have a positive shift in the phenotypic mean expression, it is essential to harness both additive and non-additive effects. Hence intermating of selected segregants followed by one or two generations of selfing could be suggested to break undesirable linkages. Dashti et al. (2010) reported that plant height was the only trait affected by six parameters.

Inheritance of number of productive tillers per plant and panicle length

Tillering is one of the most important agronomic traits because tiller number per plant determines panicle number, a key component of grain yield. Regarding number of productive tillers per plant, the cross ADT 49 / TRY (R) 2 had additive x dominance (j) interactions, which could be partly fixable and dominance x dominance gene interactions were prevalent. In crosses viz., IR 20 / CSR 23 and CO (R) 50 / CSR 23 dominant gene action alone predominantly found to be present. Hence, in those crosses, a diallel selective mating would be the appropriate breeding method to harness dominant type of gene interactions governing the inheritance of the trait. Thirumeni et al., 2003 reported predominance of all the three type of gene interactions except (l) component. The genetic architecture of panicle length in cross IR 20 / FL 478 was governed by dominance and additive x additive gene interactions, while dominance, additive x additive and dominance x dominance gene interactions were prevalent in remaining crosses. For exploiting these types of gene actions, intermating among the segregating populations to accumulate fixable type of gene effects and at the same time maintaining heterogygousity for exploiting dominance gene effects would be the ideal method of breeding for the improvement of the trait.

Inheritance of spikelet fertility and single plant yield

The reasons for increasing sterility under salt stress conditions are impaired meiosis in both male and female organs, impaired pollen germination and pollen tube growth and reduced ovule viability. As regard to spikelet fertility, dominance (h) and additive x dominance (j) gene actions were pronounced in cross ADT 49 / TRY (R) 2. In cross IR 20 / FL 478 dominance x dominance gene interaction was predominant. The cross IR 20 / FL 478 exhibited pronounced additive x dominance and dominance x dominance type of interactions. In those crosses, multiple crossing among the selected segregants and selection in advanced generation would help to improve this trait. The importance of additive x dominance and dominance x dominance interactions in governing the inheritance of spikelet fertility were already reported by Thirumeni et al. (2003). Regarding to single plant yield, two crosses viz., ADT 49 / TRY (R) 2 and CO (R) 50 / TRY (R) 2 dominance (h) and additive x dominance gene interactions influenced the inheritance of this trait. Hence, intermating programme among F_2 segregants (or) multiple crossing programme with selected segregants would help in realization of superior genotypes with improved yield under stress. In cross IR 20 / CSR 23 dominance gene action was found to control the trait. Since dominant gene action was present, postponement of selections to later generation might help in improvement of yield. Dominance gene action and

Table 1. Generation means, scaling tests and genetic effects for days to 50 per cent flowering and plant height.

	days to 50 percent flowering				plant height			
Generations	IR 20 xFL 478	IR 20xCSR 23	ADT 49xTRY (R) 2	CO (R) 50xCSR 23	IR 20 xFL 478	IR 20xCSR 23	ADT 49xTRY (R) 2	CO (R) 50xCSR 23
$Parent_1$	103.05 ± 0.26	103.85 ± 0.22	109.60 ± 0.24	101.80 ± 0.27	77.75 ± 0.20	77.90 ± 0.23	70.80 ± 0.36	74.05 ± 0.33
$Parent_2$	89.60 ± 0.21	105.90 ± 0.25	91.40 ± 0.25	105.40 ± 0.25	74.30 ± 0.16	83.50 ± 0.20	77.00 ± 0.25	83.30 ± 0.31
F_1 (Hybrid)	93.50 ± 0.22	104.23 ± 0.18	96.63 ± 0.24	102.93 ± 0.15	76.17 ± 0.20	81.13 ± 0.29	74.37 ± 0.30	78.47 ± 0.26
F_2	92.77 ± 0.32	103.65 ± 0.07	95.86 ± 0.28	102.30 ± 0.10	77.14 ± 0.14	82.06 ± 0.17	75.92 ± 0.19	80.93 ± 0.20
Back $cross_1$	97.83 ± 0.19	104.07 ± 0.14	105.93 ± 0.18	102.20 ± 0.13	77.07 ± 0.19	80.47 ± 0.22	72.47 ± 0.21	76.50 ± 0.21
Back $cross_2$	92.07 ± 0.21	105.77 ± 0.23	93.93 ± 0.16	104.10 ± 0.14	75.40 ± 0.21	82.07 ± 0.27	76.03 ± 0.24	80.80 ± 0.29
Scales								
A	0.88 ± 0.51	0.05 ± 0.40	5.63* ± 0.51	-0.33 ± 0.40	0.22 ± 0.43	1.90* ± 0.57	-0.23 ± 0.63	0.48 ± 0.60
B	1.03 ± 0.52	1.40* ± 0.55	-0.17 ± 0.47	-0.13 ± 0.41	0.33 ± 0.58	-0.50 ± 0.64	0.70 ± 0.61	-0.17 ± 0.71
C	-8.55* ± 1.41	-3.61* ± 0.57	-10.84* ± 1.29	-3.83* ± 0.63	4.18* ± 0.75	4.56* ± 0.95	7.16* ± 1.07	9.43* ± 1.06
D	-4.35* ± 0.71	-2.53* ± 0.31	-8.15* ± 0.62	-1.68* ± 0.28	1.81* ± 0.42	1.58* ± 0.49	3.35* ± 0.50	4.56* ± 0.54
Genetic effects								
m	87.63* ± 1.43	99.82* ± 0.64	84.19* ± 1.25	100.23* ± 0.59	79.65* ± 0.85	83.86* ± 1.00	80.60* ± 1.03	87.79* ± 1.11
(d)	6.72* ± 0.17	-1.02* ± 0.17	9.10* ± 0.17	-1.80* ± 0.18	1.72* ± 0.13	-2.80* ± 0.15	-3.10* ± 0.22	-4.62* ± 0.22
(h)	14.72* ± 3.16	10.93* ± 1.80	34.22* ± 2.77	5.60* ± 1.52	-6.56* ± 2.21	-4.48 ± 2.55	-12.46* ± 2.58	-18.17* ± 2.80
(i)	8.70* ± 1.42	5.06* ± 0.61	16.31* ± 1.24	3.37* ± 0.56	-3.63* ± 0.84	-3.16* ± 0.98	-6.70* ± 1.01	-9.11* ± 1.08
(j)	-0.96* ± 0.33	-0.67 ± 0.32	2.90* ± 0.30	-0.10 ± 0.26	-0.06 ± 0.33	1.20* ± 0.38	-0.47 ± 0.39	0.32 ± 0.43
(l)	-8.85* ± 1.82	-6.51* ± 1.22	-21.78* ± 1.62	-2.90* ± 0.99	3.08 ± 1.43	1.76 ± 1.68	6.23* ± 1.67	8.79* ± 1.79

(m) - mid parent, (d) - additive, (h) - dominance, (i) - additive x additive, (j) - additive x dominance, (l) - dominance x dominance

* Significant at 5% level

Table 2. Generation means, scaling tests and genetic effects productive tillers per plant and panicle length.

	productive tillers per plant				panicle length			
Generations	IR 20 xFL 478	IR 20xCSR 23	ADT 49xTRY (R) 2	CO (R) 50xCSR 23	IR 20 xFL 478	IR 20xCSR 23	ADT 49xTRY (R) 2	CO (R) 50xCSR 23
$Parent_1$	9.05 ± 0.18	9.20 ± 0.1	8.45 ± 0.22	9.15 ± 0.21	19.67 ± 0.14	19.67 ± 0.14	18.86 ± 0.10	20.23 ± 0.06
$Parent_2$	12.35 ± 0.27	11.55 ± 0.22	11 ± 0.55	11.75 ± 0.20	21.15 ± 0.05	22.73 ± 0.13	21.15 ± 0.05	22.73 ± 0.13
F_1 (Hybrid)	16.30 ± 0.17	15.23 ± 0.16	15.30 ± 0.20	17.13 ± 0.15	22.26 ± 0.05	23.27 ± 0.09	22.92 ± 0.06	23.76 ± 0.10
F_2	13.50 ± 0.14	12.46 ± 0.17	14.27 ± 0.24	15.04 ± 0.26	21.04 ± 0.05	21.75 ± 0.06	21.76 ± 0.09	22.47 ± 0.06
Back $cross_1$	12.37 ± 0.16	11.87 ± 0.20	12.37 ± 0.18	13.10 ± 0.18	21.16 ± 0.04	21.84 ± 0.06	21.86 ± 0.08	22.88 ± 0.05
Back $cross_2$	14.17 ± 0.19	13.70 ± 0.17	13.10 ± 0.17	15.97 ± 0.14	21.84 ± 0.07	22.99 ± 0.05	22.32 ± 0.08	23.47 ± 0.04
Scales								
A	-0.62 ± 0.41	-0.70 ± 0.46	0.98 ± 0.46	-0.08 ± 0.44	0.37* ± 0.17	0.73* ± 0.21	1.93* ± 0.19	1.77* ± 0.16
B	-0.32 ± 0.50	0.62 ± 0.43	-0.65 ± 0.45	3.05* ± 0.38	0.26 ± 0.15	-0.03 ± 0.19	0.56* ± 0.18	0.45* ± 0.18
C	0.00 ± 0.75	-1.39 ± 0.83	6.49* ± 1.10	5.01* ± 1.11	-1.21* ± 0.28	-1.97* ± 0.36	1.20* ± 0.39	-0.60 ± 0.35
D	0.47 ± 0.38	-0.65 ± 0.44	3.08* ± 0.54	1.02 ± 0.56	-0.92* ± 0.13	-1.33* ± 0.15	-0.65* ± 0.21	-1.41* ± 0.14
Genetic effects								
m	11.63* ± 0.78	9.06* ± 0.88	16.15* ± 1.10	12.49* ± 1.13	18.57* ± 0.28	18.54* ± 0.32	18.71* ± 0.42	18.66* ± 0.29
(d)	-1.65* ± 0.16	-1.17* ± 0.14	-1.55* ± 0.16	-1.30* ± 0.15	-0.74* ± 0.07	-1.53* ± 0.09	-1.14* ± 0.06	-1.25* ± 0.07
(h)	2.80 ± 1.96	7.39* ± 2.14	-6.68* ± 2.49	5.56* ± 2.51	6.18* ± 0.68	8.09* ± 0.78	8.01* ± 1.00	10.15* ± 0.68
(i)	-0.93 ± 0.76	1.31 ± 0.87	-6.15* ± 1.09	-2.04 ± 1.12	1.85* ± 0.27	2.66* ± 0.30	1.30* ± 0.42	2.82* ± 0.28
(j)	-0.15 ± 0.30	-0.66 ± 0.29	0.82* ± 0.29	-1.57* ± 0.27	0.06 ± 0.11	0.38* ± 0.13	0.68* ± 0.12	0.66* ± 0.10
(l)	0.47 ± 0.38	-1.23 ± 1.32	5.82* ± 1.47	-0.92 ± 1.44	-2.49* ± 0.42	-3.36* ± 0.50	-3.80* ± 0.59	-5.05* ± 0.43

(m) - mid parent, (d) - additive, (h) - dominance, (i) - additive x additive, (j) - additive x dominance, (l) - dominance x dominance

* Significant at 5% level

Table 3. Generation means, scaling tests and genetic effects for spikelet fertility per cent and single plant yield.

	spikelet fertility per cent				single plant yield			
Generations	IR 20 xFL 478	IR 20xCSR 23	ADT 49xTRY (R) 2	CO (R) 50xCSR 23	IR 20 xFL 478	IR 20xCSR 23	ADT 49xTRY (R) 2	CO (R) 50xCSR 23
$Parent_1$	63.75 ± 0.22	63.65 ± 0.25	62.45 ± 0.24	60.25 ± 0.27	10.28 ± 0.13	10.42 ± 0.15	7.66 ± 0.12	9.19 ± 0.14
$Parent_2$	75.80 ± 0.30	73.50 ± 0.27	73.10 ± 0.24	73.35 ± 0.28	18.27 ± 0.12	14.33 ± 0.15	16.70 ± 0.18	14.37 ± 0.13
F_1 (Hybrid)	76.13 ± 0.15	78.87 ± 0.25	74.23 ± 0.24	74.57 ± 0.20	27.78 ± 0.15	24.57 ± 0.14	22.69 ± 0.16	20.22 ± 0.12
F_2	74.28 ± 0.37	76.06 ± 0.35	72.92 ± 0.27	73.22 ± 0.28	20.34 ± 0.26	20.24 ± 0.27	18.79 ± 0.28	17.82 ± 0.26
Back $cross_1$	69.53 ± 0.22	72.20 ± 0.28	71.17 ± 0.20	70.70 ± 0.22	18.23 ± 0.11	17.60 ± 0.11	17.44 ± 0.16	16.81 ± 0.10
Back $cross_2$	76.10 ± 0.15	75.47 ± 0.18	73.57 ± 0.16	73.73 ± 0.23	25.33 ± 0.18	22.49 ± 0.15	20.76 ± 0.15	18.15 ± 0.11
Scales								
A	-0.82 ± 0.52	1.83* ± 0.66	5.65* ± 0.52	6.58* ± 0.56	-1.58* ± 0.30	0.21 ± 0.31	4.53* ± 0.37	4.20* ± 0.28
B	0.27 ± 0.46	-1.43* ± 0.52	-0.20 ± 0.46	-0.45 ± 0.57	4.61* ± 0.40	6.07* ± 0.37	2.13* ± 0.39	1.71* ± 0.29
C	5.29* ± 1.60	9.36* ± 1.52	7.66* ± 1.25	10.16* ± 1.24	-2.74* ± 0.11	7.04* ± 1.12	5.43* ± 1.18	7.29* ± 1.07
D	2.92* ± 0.80	4.45* ± 0.77	1.11 ± 0.61	2.01* ± 0.64	-2.88* ± 0.57	0.38 ± 0.56	-0.62 ± 0.60	0.69 ± 0.54
Genetic effects								
m	75.61* ± 1.60	77.48* ± 1.55	70.00* ± 1.22	70.83* ± 1.30	8.51* ± 0.03	13.14* ± 1.13	10.94* ± 1.20	13.15* ± 1.08
(d)	-6.02* ± 0.19	-4.92* ± 0.18	-5.32* ± 0.17	-6.55* ± 0.20	-4.00* ± 0.09	-1.95* ± 0.10	-4.52* ± 0.11	-2.59* ± 0.10
(h)	-5.87 ± 3.45	-7.07 ± 3.47	7.48* ± 2.73	5.84 ± 3.01	28.05* ± 2.47	16.95* ± 2.44	19.65* ± 2.62	11.61* ± 2.28
(i)	-5.84* ± 1.60	-8.91* ± 1.54	-2.21 ± 1.21	-4.03* ± 1.28	5.76* ± 1.13	-0.76 ± 1.13	1.24 ± 1.20	-1.37 ± 1.07
(j)	-0.54 ± 0.33	1.66* ± 0.38	2.92* ± 0.30	3.52* ± 0.38	-3.09* ± 0.23	-2.93* ± 0.22	1.20* ± 0.25	1.24* ± 0.18
(l)	6.39* ± 1.91	8.46* ± 2.02	-3.24 ± 1.61	-2.10 ± 1.78	-8.79* ± 1.39	-5.52* ± 1.36	-7.90* ± 1.48	-4.54* ± 1.24

(m) - mid parent, (d) - additive, (h) - dominance, (i) - additive x additive, (j) - additive x dominance, (l) - dominance x dominance

* Significant at 5% level

Table 4. Generation means, scaling tests and genetic effects for Na^+: K^+ ratio and chlorophyll a: b ratio.

	Na^+: K^+ ratio				chlorophyll a: b ratio			
Generations	IR 20xFL 478	IR 20xCSR 23	ADT 49xTRY (R) 2	CO (R) 50xCSR 23	IR 20 xFL 478	IR 20xCSR 23	ADT 49xTRY (R) 2	CO (R) 50xCSR 23
$Parent_1$	1.13 ± 0.005	1.13 ± 0.01	1.25 ± 0.005	1.09 ± 0.01	1.76 ± 0.004	1.76 ± 0.004	1.82 ± 0.004	1.75 ± 0.003
$Parent_2$	0.62 ± 0.01	0.78 ± 0.57	0.69 ± 0.005	0.79 ± 0.004	1.73 ± 0.004	1.62 ± 0.004	1.6.7 ± 0.004	1.62 ± 0.005
F_1 (Hybrid)	0.49 ± 0.15	0.57 ± 0.01	0.59 ± 0.005	0.60 ± 0.005	1.75 ± 0.002	1.71 ± 0.003	1.73 ± 0.003	1.68 ± 0.004
F_2	0.47 ± 0.01	0.55 ± 0.01	0.59 ± 0.01	0.55 ± 0.01	1.72 ± 0.002	1.69 ± 0.003	1.71 ± 0.002	1.66 ± 0.003
Back $cross_1$	0.65 ± 0.004	0.68 ± 0.004	0.74 ± 0.004	0.72 ± 0.004	1.75 ± 0.003	1.73 ± 0.003	1.78 ± 0.002	1.73 ± 0.004
Back $cross_2$	0.52 ± 0.004	0.60 ± 0.005	0.62 ± 0.004	0.68 ± 0.004	1.74 ± 0.003	1.67 ± 0.004	1.71 ± 0.003	1.65 ± 0.003
Scales								
A	-0.31* ± 0.01	-0.33* ± 0.01	-0.36* ± 0.01	-0.24* ± 0.01	-0.01 ± 0.01	0.003 ± 0.01	0.01 ± 0.01	0.03* ± 0.01
B	-0.07* ± 0.01	-0.16* ± 0.01	-0.03* ± 0.01	-0.02 ± 0.01	-0.002 ± 0.01	0.02* ± 0.01	0.02* ± 0.01	0.01 ± 0.01
C	-0.83* ± 0.03	-0.84* ± 0.05	-0.76* ± 0.04	-0.85* ± 0.04	-1.00* ± 0.01	-0.02 ± 0.01	-0.12* ± 0.01	-0.08* ± 0.01
D	-0.23* ± 0.01	-0.19* ± 0.02	-0.19* ± 0.02	-0.29* ± 0.02	-0.04 *± 0.01	-0.02* ± 0.01	-0.08* ± 0.01	-0.06* ± 0.01
Genetic effects								
m	0.42* ± 0.03	0.58* ± 0.05	0.60* ± 0.04	0.36* ± 0.04	1.66* ± 0.01	1.64* ± 0.01	1.59* ± 0.01	1.56* ± 0.01
(d)	0.25* ± 0.004	0.17* ± 0.004	0.28* ± 0.004	0.15* ± 0.004	0.02* ± 0.003	0.07* ± 0.003	0.08* ± 0.003	0.07* ± 0.003
(h)	0.14 ± 0.10	-0.13 ± 0.10	-0.03 ± 0.09	0.56* ± 0.09	0.16* ± 0.03	0.13* ± 0.04	0.34* ± 0.03	0.27* ± 0.04
(i)	0.45* ± 0.03	0.37* ± 0.05	0.37* ± 0.04	0.58* ± 0.04	0.08* ± 0.01	0.04* ± 0.01	0.15* ± 0.01	0.12* ± 0.01
(j)	-0.12* ± 0.01	-0.09* ± 0.01	-0.16* ± 0.01	-0.11* ± 0.01	-0.01 ± 0.005	-0.01 ± 0.01	-0.01 ± 0.005	0.01 ± 0.005
(l)	-0.08 ± 0.04	0.12 ± 0.05	0.02 ± 0.05	-0.32* ± 0.05	-0.07* ± 0.02	-0.07* ± 0.02	-0.19* ± 0.02	-0.16* ± 0.02

(m) - mid parent, (d) - additive, (h) - dominance, (i) - additive x additive, (j) - additive x dominance, (l) - dominance x dominance

* Significant at 5% level

additive x additive type of non-allelic interactions were prevalent in cross IR 20 / FL 478. Inter se matings followed by pedigree breeding or a selective diallel mating system might sound useful in improving sodicity tolerance in rice. The preponderance of dominance, additive x additive and additive x dominance were reported by Thirumeni et al. (2003).

Inheritance of Na^+: K^+ ratio and proline content

High Na^+ accumulation in salt-sensitive rice leaves have been reported to result in an enhanced membrane damage, electrolyte leakage and oxidative damage (Mandhania et al., 2006). For Na^+: K^+ ratio, none of the crosses exhibited additive, dominance and additive x additive interaction effects. In three crosses viz., IR 20 / FL 478, IR 20 / CSR23 and ADT 49 / TRY (R) 2 exhibited pronounced additive x dominance type of gene interactions. In cross CO (R) 50 / TRY (R) 2 dominance x dominance gene interaction was prevalent. Since, this non-fixable epistasis (h) and (l) was observed, for improvement in this trait intermating and selection in advanced generations would be of very much useful. Dashti et al. (2010) reported additive x additive and additive x dominance interactions governing the inheritance of Na^+: K^+ ratio. Dehdari et al. (2007) reported the importance of dominance x dominance interactions on this trait. Rapid accumulation of free proline is a typical response to salt stress (Parida et al., 2008). Regarding the inheritance of proline content, dominance and additive x additive gene interaction played a major role in crosses IR 20 / FL 478 and IR 20 / CSR 23. For exploiting these types of gene actions, intermating among the segregating populations to accumulate fixable type of gene effects and at the same time maintaining the heterogygousity for exploiting dominance gene effects would be ideal method of breeding. In cross ADT 49 / TRY (R) 2 dominance gene action was alone prevalent. The dominance and additive x dominance gene interaction were exhibited by CO (R) 50 / CSR 23. The involvement of dominance × dominance interactions indicated that it would be necessary to postpone selection for salt tolerance of rice to advanced generations, when sufficient epistatic interactions had become fixed. Similar results were reported by Farshadfar et al. (2008).

Inheritance of chlorophyll a/b ratio and chlorophyll stability index (CSI)

Chlorophyll a/b ratio increased under salinity stress suggesting more damage to Chlorophyll *b* than Chlorophyll *a* under salt stress (Fang et al., 1998). The epistatic effect (j) was significant in all crosses, indicating that these effects were not fixable by selection under selfing conditions. The chlorophyll stability index (CSI) is an indication of the stress tolerance capacity of plants. A high CSI value means that the stress did not have much effect on chlorophyll content of plants. The genetic architecture of this trait was decided in terms of dominance and additive x additive interaction effects (i) in two crosses *viz.*, IR 20 / CSR 23 and CO (R) 50 / TRY (R) 2. Thus, the trait was under the control of non- fixable and fixable gene effects. For exploiting these types of gene actions, bi-parental mating would be the ideal method of breeding for the improvement of this trait under sodicity

Materials and methods

Soil characteristics

The present investigation was carried out at the Research farm of Department of Plant Breeding and Genetics, Anbil Dharmalingam Agricultural College and Research Institute, Trichy district, Tamil Nadu, India where, the soil was found to be sodic in nature. The soil possessed a pH of 9.50 and ESP 23. The water used for irrigating the experimental field was taken from the bore well with pH of 9.10 and RSC is10 meq/l.

Plant materials

Based on combining ability and heterosis studies, four hybrids *viz.*, IR 20 / FL 478, IR 20 / CSR 23, ADT 49 / TRY (R) 2 and CO (R) 50 / CSR 23 were selected to undertake generation means analysis. In the selected crosses, using F_1 s as female parents and respective two parents (P_1 and P_2) as male parents, back crosses *viz.*, BC_1 (F_1 / P_1) and BC_2 (F_1 / P_2) were effected. Twenty five days old seedlings were transplanted to main field in a randomized block design with three replications. Single seedling was planted per hill adopting the recommended spacing of 20 x 15 cm during rabi 2012-2013 season. Recommended package of practices were followed to establish the crop.

Biometrical observations

The data on 10 physio-morphological traits *viz.*, days to 50 per cent flowering, plant height, number of productive tillers per plant, panicle length, spikelet fertility percentage, single plant yield, Na^+: K^+ ratio, proline content, chlorophyll a/b ratio and chlorophyll stability index were recorded. The biometrical observations were recorded for yield and its component traits under sodicity as per the Standard Evaluation System (SES) for rice (IRRI).

Sodium and potassium ratio (Na^+ / K^+ ratio)

Sodium and potassium content were estimated by flame photometer method using triple acid extract of dry sample at maturity stage, using the method proposed by Jackson (1973) and the ratio was calculated.

Proline content

The amino acid proline content was estimated in fully expanded leaves at flowering stage following the method of Bates et al. (1973) and expressed on µg g^{-1} on fresh weight basis.

Chlorophyll a: b ratio

The contents of chlorophyll 'a' and chlorophyll 'b' were estimated by adopting the method of Yoshida et al. (1976) and the ratio was calculated.

Chlorophyll Stability Index

Using the values of chlorophyll content, CSI was calculated as described by Murthy and Majumdar (1962) and expressed in per cent.

Table 5. Generation means, scaling tests and genetic effects for proline content.

Generations	IR 20 xFL 478	IR 20xCSR 23	ADT 49xTRY (R) 2	CO (R) 50xCSR 23
$Parent_1$	611.40 ± 1.16	613.20 ± 1.43	573.05 ± 0.93	633.55 ± 1.04
$Parent_2$	760.25 ± 0.94	845.35 ± 1.18	742.20 ± 1.41	845.90 ± 1.24
F_1 (Hybrid)	846.67 ± 0.80	1028.73 ± 1.01	793.13 ± 0.97	1025.27 ± 0.73
F_2	763.38 ± 3.34	905.15 ± 7.27	721.95 ± 4.03	944.48 ± 6.12
Back $cross_1$	746.50 ± 0.87	864.37 ± 1.01	673.43 ± 0.87	914.90 ± 0.85
Back $cross_2$	822.00 ± 0.86	986.60 ± 0.89	764.37 ± 1.02	942.20 ± 0.72
Scales				
A	33.93* ± 2.24	86.80* ± 2.68	-19.32* ± 2.21	170.98* ± 2.11
B	36.08* ± 2.12	99.12* ± 2.36	-6.60* ± 2.66	13.23* ± 2.06
C	-13.45 ± 13.55	104.58* ± 29.00	-14.12 ± 16.34	247.92* ± 24.59
D	-41.73* ± 6.80	-40.67* ± 14.50	5.90 ± 8.18	31.85* ± 12.29
Genetic effects				
m	602.36* ± 13.62	647.93* ± 29.01	669.42*± 16.38	803.43* ± 24.60
(d)	-74.42* ± 0.75	-116.07* ± 0.93	-84.57* ± 0.85	-106.17* ± 0.82
(h)	398.79* ± 27.85	648.06* ± 58.37	86.01* ± 33.38	342.35* ± 49.50
(i)	83.46* ± 13.60	81.34* ± 29.00	-11.79 ± 16.36	-63.70* ± 24.59
(j)	-1.07 ± 1.44	-6.16* ± 1.64	-6.36* ± 1.58	78.87* ± 1.38
(l)	-153.48*± 14.42	-267.26*± 29.49	-11.79 ± 16.36	-120.51*± 25.00

(m) - mid parent, (d) - additive, (h) - dominance, (i) - additive x additive, (j) - additive x dominance, (l) - dominance x dominance

* Significant at 5% level

Table 6. Generation means, scaling tests and genetic effects for chlorophyll stability index.

Generations	IR 20xFL 478	IR 20xCSR 23	ADT 49xTRY (R) 2	CO (R) 50xCSR 23
P_1	69.85 ± 0.18	70.15 ± 0.33	67.15 ± 0.29	71.25 ± 0.27
P_2	74.50 ± 0.26	72.20 ± 0.24	71.20 ± 0.25	72.25 ± 0.20
F_1	76.13 ± 0.22	78.03 ± 0.21	71.57 ± 0.19	72.90 ± 0.19
F_2	74.17 ± 0.21	73.59 ± 0.16	70.86 ± 0.14	71.23 ± 0.10
B_1	73.10 ± 0.19	74.63 ± 0.20	69.53 ± 0.21	71.67 ± 0.18
B_2	75.57 ± 0.24	75.83 ± 0.19	71.77 ± 0.21	73.40 ± 0.22
Scales				
A	0.22 ± 0.48	1.08 ± 0.56	0.35 ± 0.54	-0.82 ± 0.49
B	0.50 ± 0.58	1.43* ± 0.50	0.77 ± 0.53	1.65* ± 0.53
C	0.07 ± 1.00	-4.05* ± 0.87	1.96 ± 0.79	-4.39* ± 0.66
D	-0.32 ± 0.52	-3.28* ± 0.43	0.42 ± 0.41	-2.61* ± 0.35
Genetic effects				
m	71.53* ± 1.05	64.61* ± 0.88	70.01 ± 0.85	66.53* ± 0.73
(d)	-2.32* ± 0.16	-1.02* ± 0.20	-2.02 ± 0.19	-0.50 ± 0.17
(h)	5.97 ± 2.54	22.51* ± 2.21	1.83 ± 2.21	12.42* ± 2.00
(i)	0.64 ± 1.04	6.56* ± 0.85	-0.84 ± 0.83	5.22* ± 0.71
(j)	-0.14 ± 0.34	-0.17 ± 0.34	-0.21 ± 0.35	-1.23* ± 0.33
(l)	-1.36 ± 1.58	-9.08* ± 1.41	-0.28 ± 1.43	-6.05* ± 1.33

(m) - mid parent, (d) - additive, (h) - dominance, (i) - additive x additive, (j) - additive x dominance, (l) - dominance x dominance

Statistical analysis

The mean of the different generations *viz.*, P_1, P_2, F_1, F_2, BC_1 and BC_2were used to test the adequacy of additive-dominance model. To confirm the results of scaling tests, the procedure proposed by Caveli (1952) was adopted. Three parameters m, (d) and (h) defining the additive dominance model was estimated by the weighed least square method (Mather and Jinks, 1981). When the scales A, B, C and D were significantly different from zero, a digenic interaction model was assumed and six parameters m, (d), (h), (i), (J) and (l) were estimated (Jinks and Jones, 1958).

Conclusion

A detailed genetic dissection based on different generations using generation means analysis would be an important step forward to fully elucidate the nature and magnitude of gene actions. Generation means analysis of the data revealed additive and non-additive types of gene effects governing most of yield, yield contributing traits and salt tolerance. Results suggested that complex epistatic effects were important in controlling sodicity tolerance traits. Hence, the breeding method that would accumulate fixable type of additive gene effects and at the same time maintaining considerable heterozygosity for exploiting dominance genetic effects might prove appropriate for yield improvement in rice under sodicity.

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