Genetic Analysis of Sodicity Tolerance in Rice (Oryza Sativa L.)

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Abstract

In order to estimate gene actions for sodicity tolerance, grain yield and its related traits in rice, six basic generations were evaluated in a randomized complete block design with three replications. Inheritance of salinity tolerance was determined in a cross between two rice cultivars, "ASD 18" (P_1) a susceptible cultivar and "TRY" (R) 2 (P_2) a tolerant one. The parents, F1, F2 and backcross generations were studied under sodic environment. The parents, F_1 , F_2 and backcross generations were studied under sodic environment. The parents, F_1 , F_2 and backcross generations were studied under sodic environment. The parents, F_1 , F_2 and backcross generations were studied under sodic environment. The parents, F_1 , F_2 and backcross generations were studied under sodic environment. The parents, F_1 , F_2 and backcross generations were studied under sodic environment. The parents, F_1 , F_2 and backcross generations were studied under sodic environment. The parents, F_1 , F_2 and backcross generations were studied under sodic environment. The parents, F_1 , F_2 and backcross generations (Exchangeable Sodium Percentage 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 suggest that complex epistatic interactions are more important in controlling sodicity tolerance traits. The simple additive dominance model was adequate to explain the inheritance of chlorophyll stability index. Due to the presence of greater non-additive gene effects, selection for almost all of the studied traits in this cross, especially in early generations, would be complex in conventional methods. Regarding the existence of additive

Highlights

- Dominance and epistatic gene interactions were predominant.
- Dominance x dominance gene interaction was prevalent.
- Intermating of selected segregants and postponement of selection to later generations might be suggested to break undesirable linkages in order to improve yield under sodicity.

Keywords: Rice, sodicity, tolerance, Generation means analysis, Epistasis

About 6.5% (831 million ha) of the world's total area (12.78 billion ha) is affected by salt in soils (FAO). Area under salt stress is on the increase due to many factors including climate change, underlying rocks rich in harmful salts etc., Vast areas of land are not utilized due to salinity and alkalinity problems. In recent years the development of salt-resistant

varieties has been proposed as a means of expanding agriculture into the regions affected by salinity. Salinisation of agricultural land hampers food production in many areas of the world (Munns and Tester, 2008). 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). Sangita et al. (2002) reported that the presence or retention of K⁺ in rice callus was a key factor for salt tolerance as it was found to be positively correlated with growth while proline was probably the last metabolic device that rice calluses opted for when exposed to salt stress. Screening of rice genotypes based on traits like spikelet sterility, Na⁺: K⁺ ratio is being followed by breeders in salt affected soils. A high percentage of spikelet sterility relates to a low level of salt tolerance in rice. Salt tolerance in plants is often linked to the restriction of Na⁺ accumulation and maintenance of a high K⁺/Na⁺ ratio in the shoots (Moller and Tester, 2007). Zeng et al. (2000) reported that the reduction in spikelet number per panicle was a major cause of yield loss under salinity. Ansari et al. (2003) have reported that sodium uptake increased and potassium decreased with increasing salinity. An assessment of plant materials by an evaluation of important agronomic traits appears to be a practical method to determine salt injury. Generation means analysis can determine types of genes action and also estimate their effects and genetic components in a cross. It helps us in understanding the performance of the parents used in crosses and potential of crosses to be used either for heterosis exploitation or pedigree selection (Sharma and Sain, 2003). The nature of gene action governing the inheritance of sodicity tolerant, yield and its components was therefore studied using generation means analysis in selected five crosses in the present investigation.

Materials and Methods

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 is found to be sodic in nature. The soil in the experimental field was sodic soil with 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. Based on combining ability and heterosis studies, one hybrid *viz.*, ASD 18 / TRY (R) 2 was selected to undertake generation means analysis. In the selected crosses, using F_1 s as female parents, back crosses *viz.*, BC₁ (F_1 / P_1) and BC₂ (F_1 / P_2) were effected. The experiment was laid out in randomized complete block design with three replications adopting a

recommended spacing of 20 x 15 cm in field during 2012-2013. Recommended package of practices were followed to establish the crop. 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). The mean of the different generations viz, P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2 were used to test the adequacy of additive-dominance model. To confirm the result of scaling tests, the procedure proposed by Caveli (1952) was adopted. The three parameters m, (d) and (h) defining the additive dominance model was estimated by the weighed least square method (Mather and Jinks, 1982). When the scales A, B, C and D were significantly different from zero, a digenic interaction model was assumed and the following six parameters m, (d), (h), (i), (J) and (l) were estimated (Jinks and Jones, 1958).

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 (1) on the assumption of an additive-dominance model with digenic interaction are presented for the ten traits studied in Tables 1 and 2. Highly significant variation for this trait among different generations of the cross indicated that the present material was suitable for estimation of additive and dominance gene effects and non-allelic interactions through generation means analysis. Digenic epistasis model was found to be fit for all traits except chlorophyll stability index since scaling tests were significant. The presence of duplicate dominant type of interaction was inferred by opposite sign of (h) and (l) effects in days to 50 percent flowering, number of productive tillers per plant, panicle length, spikelet fertility and chlorophyll a/b ratio. For days to 50 per cent flowering, apart from significant dominance x dominance interaction effect, there would be prevalence of significant additive type of gene action governing the inheritance. Since additive and dominance x dominance gene interactions were found to play a major role in governing the inheritance of the trait, inter mating of selected segregants followed by one or two generations of selfing might yield an array of segregants varying in maturity groups. The selection of early and mid-early duration groups

| Generations | DFF | PH | NPT | PL | SFP | SPY | Na+: K+ ratio |
|-----------------|---------------------------|----------------------|----------------------|----------------------|----------------------|--------------------|----------------------|
| P ₁ | 77.15 ± 0.18 | 63.85 ± 0.25 | 6.40 ± 0.18 | 17.35 ± 0.09 | 56.10 ± 0.46 | 6.13 ± 0.10 | 77.15 ± 0.18 |
| P ₂ | 92.30 ± 0.19 | 77.05 ± 0.29 | 11.90 ± 0.26 | 20.88 ± 0.82 | 73.10 ± 0.36 | 16.55 ± 0.18 | 92.30 ± 0.19 |
| F ₁ | 83.60 ± 0.22 | 72.43 ± 0.21 | 14.43 ± 0.18 | 21.73 ± 0.09 | 77.70 ± 0.20 | 19.19 ± 0.11 | 83.60 ± 0.22 |
| F ₂ | 81.66 ± 0.24 | 74.13 ± 0.29 | 12.42 ± 0.22 | 20.16 ± 0.07 | 74.39 ± 0.53 | 17.12 ± 0.23 | 81.66 ± 0.24 |
| B ₁ | 80.93 ± 0.13 | 70.50 ± 0.19 | 9.37 ± 0.19 | 20.18 ± 0.07 | 67.33 ± 0.20 | 13.77 ± 0.09 | 80.93 ± 0.13 |
| B, | 87.57 ± 0.21 | 75.56 ± 0.21 | 75.56 ± 0.18 | 21.42 ± 0.07 | 74.67 ± 0.22 | 18.42 ± 0.11 | 87.57 ± 0.21 |
| Scales | | | | | | | |
| А | $1.17 * \pm 0.39$ | $4.72^*\pm0.50$ | $-2.10^{*} \pm 0.44$ | $1.23^*\pm0.19$ | 0.87 ± 0.64 | $2.21^*\pm0.23$ | $1.17 * \pm 0.39$ |
| В | $\textbf{-0.77} \pm 0.51$ | $1.65^*\pm0.55$ | 0.80 ± 0.45 | 0.22 ± 0.19 | -1.47 ± 0.61 | $1.10^*\pm0.30$ | -0.77 ± 0.51 |
| С | $-10.01* \pm 1.08$ | $10.76^* \pm 1.31$ | $2.50^*\pm1.01$ | $-1.05^{*} \pm 0.35$ | $12.97* \pm 2.22$ | $7.41^*\pm0.99$ | $-10.01* \pm 1.08$ |
| D | $-5.18* \pm 0.54$ | $2.20^*\pm0.65$ | $1.90^*\pm0.50$ | $-1.25^* \pm 0.17$ | $6.78^*\pm1.09$ | $2.05^*\pm0.49$ | $-5.18* \pm 0.54$ |
| Genetic effects | | | | | | | |
| m | $74.36^{*} \pm 1.09$ | $74.84^{*} \pm 1.32$ | $12.95^* \pm 1.01$ | $16.61^*\pm0.35$ | $78.17^*\pm2.21$ | $15.44^* \pm 0.99$ | $74.36^{*} \pm 1.09$ |
| (d) | $-7.57* \pm 0.13$ | $-6.60^{*} \pm 0.19$ | $-2.75^* \pm 0.16$ | $-1.77* \pm 0.06$ | $-8.50^{*} \pm 0.29$ | $-5.21* \pm 0.10$ | $-7.57* \pm 0.13$ |
| (h) | $19.94^* \pm 2.48$ | -0.44 ± 2.97 | -3.61 ± 2.32 | $9.08^*\pm0.85$ | $-14.64* \pm 4.67$ | 2.96 ± 2.09 | $19.94^* \pm 2.48$ |
| (i) | $10.36^*\pm1.08$ | $-4.39* \pm 1.31$ | $-3.80^{*} \pm 1.00$ | $2.50^*\pm0.34$ | $-13.57* \pm 2.19$ | $-4.10^*\pm0.98$ | $10.36^*\pm1.08$ |
| (j) | $0.94^*\pm0.28$ | $1.53^*\pm0.34$ | $-1.45^{*} \pm 0.28$ | $0.50^*\pm0.12$ | $1.17^*\pm0.42$ | $0.55^*\pm0.18$ | $0.94^*\pm0.28$ |
| (1) | $-10.71^* \pm 1.48$ | -1.97 ± 1.73 | $5.10^*\pm1.38$ | $-3.96^{*} \pm 0.53$ | $14.17^*\pm2.52$ | 0.79 ± 1.14 | $-10.71^* \pm 1.48$ |

Table 1: Generation means, scaling tests and genetic effects for different biometrical traits.

apart from possessing inherent tolerance to sodicity might have escaping mechanisms to alleviate salt injury. Dominance x dominance type of interaction for days to 50 per cent flowering was reported by Dashti *et al.*, (2010).

The genetic architecture of plant height was decided in terms of additive and additive x additive (i) type of interactions indicated the existence of fixable gene actions. Hence, improvement of plant height in this cross through pedigree method might be effective. The additive x additive epistasis and duplicate interaction indicated that segregants with desirable plant stature either of parents could be selected through direct selection. Tillering is one of the most important agronomic traits because tiller number per plant determines panicle number, a key component of grain yield. In according to the outcome of generation means analysis dominance x dominance (1) gene interactions were alone essential among the genetic components. Hence, diallel selective mating would be the appropriate breeding method to not only to (1) interaction but also to break any undesirable linkage. Thirumeni et.al., (2003) reported dominance x dominance gene interaction for productive tillers per plant.

Since, panicle length was governed by dominance, additive x additive and additive x dominance interactions it had both fixable and non-fixable genetic components in their inheritance. 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 this trait. 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, reduced ovule viability, anomaly in stigmatic and style positions, reduced number of pollen grains retained by the stigma, disturbed fertilization processes, obstacle in growth of the endosperm, proembryo and unfertilized embryo. The cross exhibited pronounced additive x dominance and dominance x dominance type of interactions. In those crosses, internating or multiple crossing among the selected segregants would increase the spikelet fertility. 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) and Raikwar and Mishra (2012).

Salinity is detrimental to the various processes of crops such as seed germination, flowering and fruit set and ultimately it causes diminished economic yield and also quality of produce (Sairam and Tyagi, 2004). The interaction effect (j) was found to be prevalent. Hence, non-fixable type of gene interaction was governing the expression of this trait intermating programme with selected segregants would help in realization of superior genotypes with improved single plant yield. Senthilkumar (2012) reported additive x dominance epistatic interaction for plant yield. Additive and non-additive gene actions in governing



the inheritance of yield in barely under problematic soils were also reported by Raikwar and Mishra (2012). The increase in Na⁺ ion content and decrease in K⁺ ion uptake disturbs ionic imbalance as observed in most species exposed to salt stress. Due to high uptake and accumulation of Na⁺ and antagonistically low uptake, translocation and accumulation of K⁺ and also enhanced K⁺ efflux under salt stress could suppress growth by decreasing the capacity of osmotic adjustment and turgor maintenance or by inhibiting metabolic activities. The diminution of K⁺ concentration in tissue may also be due to direct competition between K⁺ and Na⁺ at plasma membrane, inhibition of Na⁺ on K⁺ transport process in xylem tissues and/or Na⁺ induced K⁺ efflux from the roots. 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; Shabala and Cuin, 2008). The cross, ASD 18 / TRY (R) 2 exhibited pronounced additive x dominance type of gene interactions. Hence, the trait was under the control of fixable genetic effects simple selection might reduce Na⁺: K⁺ ratio. Dashti et al., (2010) reported additive x additive and additive x dominance interactions governing the inheritance of Na+: K⁺ ratio.

Proline is a known osmo-protectant, and plays an important role in osmotic balancing, protection of sub-cellular structures, enzymes and in increasing cellular osmolarity (turgor pressure) that provide the turgor necessary for cell expansion under salt stress conditions (Kumar, 2010). Additive x dominance type of epistatic interactions was found to be involved in governing the inheritance of this trait. Hence, for realizing superior segregants to this trait, selection had to be postponed to advanced generations. Chlorophyll a: b ratio increased under salinity stress suggesting more damage to chlorophyll b than chlorophyll a under salt stress (Sabir et al., 2009). The additive x dominance interaction was present in cross ASD 18 / TRY (R) 2, where dominance x dominance interaction was also present. Since, predominance of dominant gene effects governing the expression of this trait in all crosses, selection in early segregating generations might not yield desirable results. Hence, delaying selection to later generations might be advocated. Similar results were reported by Farshadfar et al., (2008).

Table 2: Generation means, scaling tests and genetic effects for different physiological traits

| Generations | PC | CABR | CSI | | | |
|-----------------|-----------------------|----------------------|----------------------|--|--|--|
| P ₁ | 529.15 ± 1.05 | 1.83 ± 0.005 | 65.25 ± 0.28 | | | |
| P ₂ | 734.25 ± 1.24 | 1.67 ± 0.004 | 71.25 ± 0.28 | | | |
| F ₁ | 769.97 ± 0.95 | 1.69 ± 0.003 | 77.53 ± 0.23 | | | |
| F ₂ | 717.57 ± 4.40 | 1.68 ± 0.002 | 74.61 ± 0.26 | | | |
| B ₁ | 655.53 ± 0.69 | 1.74 ± 0.003 | 72.20 ± 0.22 | | | |
| B ₂ | 753.87 ± 0.75 | 1.69 ± 0.003 | 75.33 ± 0.20 | | | |
| Scales | | | | | | |
| А | $11.95^* \pm 1.98$ | $-0.03^* \pm 0.01$ | $1.62^*\pm0.56$ | | | |
| В | 3.52 ± 2.16 | $0.03^*\pm0.01$ | $1.88^*\pm0.55$ | | | |
| С | $66.96^{*} \pm 17.78$ | $-0.17* \pm 0.01$ | $6.86^{*} \pm 1.20$ | | | |
| D | $25.74* \pm 8.86$ | $-0.08* \pm 0.01$ | $1.68^*\pm0.60$ | | | |
| Genetic effects | | | | | | |
| m | $683.19* \pm 17.74$ | $1.58^*\pm0.01$ | $71.61^* \pm 1.22$ | | | |
| (d) | $-102.55^* \pm 0.81$ | $0.08^{*} \pm 0.003$ | $-3.00^{*} \pm 0.20$ | | | |
| (h) | 50.76 ± 35.84 | $0.26^*\pm0.04$ | 6.05 ± 2.82 | | | |
| (i) | $-51.49* \pm 17.72$ | $0.17^*\pm0.01$ | $-3.36^{*} \pm 1.20$ | | | |
| (j) | $4.22^{*} \pm 1.30$ | $-0.03* \pm 0.01$ | -0.13 ± 0.36 | | | |
| (1) | 36.02 ± 18.24 | $-0.16^* \pm 0.02$ | -0.13 ± 1.70 | | | |

Conclusion

Predominance of dominance and non-additive gene action was observed for most of the traits. Therefore, 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. Hence, selection in early segregating generations might not yield desirable results so delaying selection to later generations when dominance gene effects disappear as well as resorting to intermating of segregants in F_2 generation might be advocated not only to harness dominant type of gene action but also to break any undesirable linkage.

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