Analysis of Stability and G × E Interaction of Rice Genotypes across Saline and Alkaline Environments in India


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(Received 3 June 2015; Accepted 13 October 2015; Communicated by J. Zhang)

Genotype × environment (G×E) interaction effects are of special interest for identifying the most suitable genotypes with respect to target environments, representative locations and other specific stresses. Twenty-two advanced breeding lines contributed by the national partners of the Salinity Tolerance Breeding Network (STBN) along with four checks were evaluated across 12 different salt affected sites comprising five coastal saline and seven alkaline environments in India. The study was conducted to assess the G × E interaction and stability of advanced breeding lines for yield and yield components using additive main effects and multiplicative interaction (AMMI) model. In the AMMI1 biplot, there were two mega-environments (ME) includes ME-A as CARI, KARAIKAL, TRICHY and NDUAT with winning genotype CSR 2K 262; and ME-B as KARSO, LUCKN, KARSA, GOA, CRRI, DRR, BIHAR and PANVE with winning genotypes CSR 36. Genotypes CSR 2K 262, CSR 27, NDRK 11-4, NDRK 11-3, NDRK 11-2, CSR 2K 255 and PNL 1-1-1-6-7-1 were identified as specifically adapted to favorable locations. The stability and adaptability of AMMI indicated that the best yielding genotypes were CSR 2K 262 for both coastal saline and alkaline environments and CSR 36 for alkaline environment. CARI and PANVEL were found as the most discernible environments for genotypic performance because of the greatest GE interaction. The genotype CSR 36 is specifically adapted to coastal saline environments GOA, KARSO, DRR, CRRI and BIHAR and while genotype CSR 2K 262 adapted to

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0133-3720/$20.00 © 2016 Akadémiai Kiadó, Budapest
alkaline environments LUCKN, NDUAT, TRICH and KARAI. Use of most adapted lines could be used directly as varieties. Using them as donors for wide or specific adaptability with selection in the target environment offers the best opportunity for widening the genetic base of coastal salinity and alkalinity stress tolerance and development of adapted genotypes. Highly stable genotypes can improve the rice productivity in salt-affected areas and ensure livelihood of the resource poor farming communities.

**Keywords:** AMMI, G×E interaction, rice, salinity, alkalinity

**Introduction**

Rice is the staple food and most important cereal crop in Asia. In India, it accounts for about 43% of the total food grain production. The world cereal production is about 2500 million tones (mt) with rice production of 675 million tones accounting for about 27 per cent of total food grain production in world (FAO 2013). At the current rate (1.8%) of population growth, the country’s rice requirement by the year 2020 would be around 125 million tons (Mishra 2005). Approximately, 900 million hectares of soil are affected by salinity which includes both sodic and saline soils (OECD/FAO 2012). Rice is considered highly sensitive to salinity (Maas and Hoffman 1977) and cultivars adapted to the salt-affected areas are generally poor yielding. Salt-tolerant landraces such as Pokkali, Cheriviruppu and Nonabokra are tall and photosensitive, with low yield potential and poor grain quality (Gregorio et al. 2002). The breeding programs were initiated in India, Philippines and other rice-growing countries to develop high-yielding saline tolerant cultivars having adaptability to a wide range of target environments. The high population growth rate and conversion of productive agricultural lands for industrial and residential purposes have pushed rice cultivation to less productive areas that are prone to abiotic stresses such as salinity, alkalinity, drought and flood. Salt stress reduces the crop yield due to alterations in plant metabolism, reduced water potential, ion imbalances and toxicity. Sometimes, severe salt stress may lead to total crop failure (Jagadish et al. 2012). The effects of salinity depend on the stage of plant development when salinity occurs, concentration and nature of salts present and duration of salinization (Zeng et al. 2001; Krishnamurthy et al. 2014). Considering the genetic background and unpredictable environmental factors which prevail at different locations and over time, differential responses are observed from the improved genotypes when tested across different environments. The variable genotypic responses in different environments are called genotype × environment (G×E) interaction, which goes back to the classical work of Allard and Bradshaw (1964). The G×E interactions that result in inconsistent genotype ranking across the test environments are usually too large to be ignored. The remarkable G×E interactions for the most quantitative traits such as grain yield can limit the genetic gain under selection and cultivar recommendation in salt stress environments. In every plant breeding program, the G×E interaction effects are of special interest for identifying the most desirable genotypes, mega-environments, representative locations and other adaptation targets.
Several procedures of yield stability analysis differing in the concepts of stability or statistical principles according to the basis of G×E interaction are known. The linear regression (Finlay and Wilkinson 1963) has been the most commonly used method for studying phenotypic stability. The use of multivariate statistical procedures to study the G×E interaction has been proposed to eliminate the problems of univariate methods. Introduction of the additive main effects and multiplicative interaction (AMMI) model by Zobel et al. (1988) has increased the interest on the principal component analysis (PCA) method to explore the G×E interaction. The AMMI model uses an additive linear model to analyze multivariate datasets and combines the additive analysis of variance for main effects with the multiplicative PCA for the G×E interaction. According to Gauch and Zobel (1996), the first interaction PCA (IPCA1) is superior to linear regression in accounting for the G×E variations. Yield stability estimated by the AMMI model seems to be more repeatable than the other stability statistics because the AMMI is more effective and useful in exploring complex G×E interaction patterns. Gauch (2006) and Gauch et al. (2008) claimed that the AMMI model always did well, and was often better than the conventional univariate stability methods like linear regression model and also some multivariate procedures like genotype plus G×E interaction (GGE) biplot (Yan et al. 2000) in the sum of square recovery. The objectives of this study were to evaluate the performance of rice genotypes across different coastal saline and alkaline environments developed at various national research centres, to assess the G×E interactions and identify most suitable genotype(s) for each mega-environment through the yield stability and adaptability analysis by using the AMMI model.

Materials and Methods

Experimental layout, genotypes and management practices

A set of 22 advanced breeding lines selected on the basis their performance at station trials for at least two seasons of respective national partner and contributed to the Salinity Tolerance Breeding Network (STBN) along with four checks (Table S1*). This set was evaluated across 12 different salt-affected (five coastal saline and seven alkaline) sites spread throughout India during the wet season, 2011 using a randomized complete block design (RCBD) with three replications. In each replication, the genotypes were transplanted in 5.0 m² plots with a spacing of 20 cm × 15 cm using 35-day-old seedlings at all the sites, except at CSSRI, Karnal, where smaller plots of 1.0 m² were used because of the limited space available in the artificial controlled micro-plot facility. The set of genotypes tested and three tolerant checks (CST 7-1, CSR 27 and CSR 36) were common across the sites, while a popular cultivar of individual areas was used as the local check. The recommended packages of practice were followed to get a normal healthy crop.

*Further details about the Electronic Supplementary Material (ESM) can be found at the end of the article.
Site characterization

The experiment was conducted across five coastal saline and seven alkaline environments well distributed throughout the country. Detail characterization of the individual locations (geographical position, rainfall, elevation and soil texture) is presented in Table S2. Soils in coastal saline locations varied from sandy loam to clay loam in texture, with the ECe (saturation extract) of 3.0–14.2 dS/m and pH of 5.0–7.0 (where pH2 measurement was of 1 part soil and 2 parts distilled water and herein after will be denoted as pH). Similarly, soils in alkaline locations varied from sandy loam to clay loam, with the ECe of 0.4–3.2 dS/m and pH of 8.8–9.9 (Table S2). The salinity and alkalinity were measured before transplanting and at the time of transplanting, flowering and maturity.

Field observations and measurements

Rice genotypes were sown in different sites between the last week of May and first fortnight of June. The evaluation of the genotypes was carried out in salt-affected environments during 2011. The data on different weather parameters during the cropping period (June–Nov) were obtained from the meteorological unit of the respective research station and are presented in Table S2. In each site, data on days to 50% flowering (days), plant height (cm), panicle length (cm), number of filled grains/panicle, 1000-grain weight (g) and grain yield (Kg/ha) were recorded. Data on flowering were recorded when 50% of the panicles in a plot emerged. Plant height from the ground level to the panicle tip was measured at maturity on 10 plants from three middle rows. Grain yield was determined from the whole plot and expressed in tons/hectare.

Statistical analysis

To analyze the G×E interactions, the AMMI model was used (Gauch 1988). This model is a combination of customary analysis of variance (ANOVA) and principal component analysis (PCA). The equation of the model is:

\[ Y_{ge} = \mu + \alpha_g + \beta_e + \sum \lambda_n \gamma_{gn} \delta_{en} + \rho_{ge} + \varepsilon_{ger} \]

where, \( Y_{ge} \) is the trait value of genotype \( g \) in environment \( e \); \( \mu \) is the grand mean, \( \alpha_g \) is the genotypes deviation from grand mean and the environment deviation \( \beta_e \), \( \lambda_n \) is the eigen value of PCA axis \( n \); \( \gamma_{gn} \) and \( \delta_{en} \) are the genotype and environment PCA scores for PCA axis \( n \); \( \rho_{ge} \) is the residual of AMMI model and \( \varepsilon_{ger} \) is the random error. AMMI’s stability value (ASV) was calculated by using following formula.

\[ \text{ASV} = \sqrt{((\text{SSIPCA1}/\text{SSIPCA2}) (\text{IPCA1}^\text{*SCORE1})^2 + (\text{IPCA1}^\text{*SCORE2})^2} \]

where SSIPCA1/SSIPCA2 is the weight given to the IPCA1 value by dividing the IPCA1 SS by the IPCA2 SS; and the IPCA1 and IPCA2 scores are the genotypic scores in the AMMI model.
The effects of genotype (G) and genotype by environment (G×E) interactions were considered as random in the model. In this case, the best linear unbiased prediction (BLUP) of G and G×E effects was calculated (Piepho et al. 2008). The components of genotypic variance (σ²_g), variance of G×E interaction (σ²_i) and residual (σ²_e) were estimated by the method of restricted maximum likelihood.

Results

Performances of genotypes for grain yield and yield component traits across coastal saline and alkaline locations

The genotype STBN 22 (CSR 2K 262) gave the highest mean grain yield of 2649 kg/ha among the 26 genotypes across the coastal saline and alkaline environments. It was followed by STBN 25 (CSR 36) with a grain yield of 2477 kg/ha, while STBN 5 (CR 2461-1-122-2-1) recorded the lowest yield of 1092 kg/ha (Table S2). Days to 50% flowering ranged from 92 for STBN 21 (CSR 2K 255) to 116 for STBN 5 (CR 2461-1-122-2-1), with an average value of 102. Plant height ranged from 78 cm for STBN 2 (RAU-1-16-48) to 116 cm for STBN 7 (CR 2219-44-2). Highly sensitive genotypes do not come up to flowering stage while medium tolerant and tolerant reduce the days to flower. The number of filled grains per panicle ranged from 65 for STBN 21 (CSR 2K 255) to 119 for STBN 16 (RP 4631-146-19-1-1-2-3), 1000-grain weight ranged from 18 g for STBN 8 (CARI Dhan 2) to 25 g for STBN 22 (CSR 2K 262) and panicle length ranged from 20.0 cm for STBN 3 (CR 2218-64-1-327-4-1) to 25.6 cm for STBN 16 (RP 4631-146-19-1-1-2-3).

Stability and adaptability analysis using AMMI model

The AMMI ANOVA (Table S3) shows that genotypes, environments, and the G×E interactions were highly significant (P < 0.01). The G×E effects were further partitioned into ten principal component (PC) axes and most of them (PC 1–PC 9) were found significant at the 0.01 probability level for all the observed traits. The PC 1 and PC 2 cumulatively contributed 59% of the total G×E interaction for grain yield while the first four principal components (PC 1–PC 4) together explained more than 90% of the variation, which was sufficient to consider a completely reliable interpretation for the behavior of G×E interaction (Table S3). The phenotypic mean values and BLUP estimates of grain yield of 26 rice genotypes are given in Table 1. Both the phenotypic and BLUP means showed that the genotype STBN 22 (CSR 2K 262) was the most productive, followed by STBN 24 (CSR 27). As expected, the genotype ranking in the two approaches did not differ, since the data were balanced. The results of ANOVA showed that all the sources of variation (genotypes, environments and G×E interactions) differed significantly at 1% probability level. The AMMI model PC1 and PC2 scores of grain yield predictions in terms of balanced linear unbiased predictions (BLUP) and the yield stability index (YSI) for 26 rice genotypes are presented in Table 1. According to the YSI ranking, genotypes STBN 22 (CSR 2K 262) and STBN 24 (CSR 27) have the highest mean grain yield but lower yield stability index (YSI).
The AMMI1 biplot for grain yield clearly indicated that the 12 environments had differed in both main and interaction effects (Fig. 1). Genotypes STBN 22 (CSR 2K 262), STBN 24 (CSR 27), STBN 26, STBN 13 (NDRK 11-4), STBN 12 (NDRK 11-3), STBN 11 (NDRK 11-2), STBN 18 (PNL 1-1-1-6-7-1) and STBN 21 (CSR 2K 255) exhibited high main effects with positive PC 1 score and, hence, were identified as specifically adapted to favorable locations. Since the environments of CARI, KARAI, TRICH and NDUAT had positive PC 1 scores, these had positive interactions with the above geno-
Figure 1: Biplot AMMI1 and AMMI2 with the first principal axis of interaction for grain yield (kg/ha) of 26 rice genotypes across 5 coastal saline and 7 alkaline locations (PANVE, KARSA, GOA, KARSRO, DRR, BIHAR, CRRI, LUCKN, NDUAT, TRICH, KARAI, CAR) in India.
types and were considered as the favorable environments for these genotypes, which produced more than average grain yield (Fig. 1 and Table 1). However, these genotypes had negative interactions with the other eight environments and possessed negative PC 1 scores or produced less than mean grain yield. On the other hand, the genotypes STBN 25 (CSR 36), STBN 10 (NDRK 11-1) and STBN 19 (CSR 2K 219) had negative PC 1 scores with high main effects. The environments of BIHAR and PANVE had negative PC 1 scores and are considered as favorable for the above-mentioned genotypes. The biplot clearly indicates that the genotypes STBN 15 (RP 4353-MSC-38-43-6-2-4-3), STBN 17 (PNL 9-1-2-7-4-6-1), STBN 26 and STBN 14 (NDRK 11-5) are stable, possessing general adaptability at all the locations. In the AMMI2 biplot (Fig. 1), some corner genotypes that can be visually determined as STBN 22 (CSR 2K 262), STBN 11 (NDRK 11-2), STBN 21 (CSR 2K 255), STBN 23 (CST 7-1), STBN 16 (RP 4631-146-19-1-1-2-3), STBN 19 (CSR 2K 219), STBN 25 (CSR 36) and STBN 14 (NDRK 11-5) are the most responsive ones. These were either the best or the poorest genotypes at some or all the test environments and could be utilized to determine the mega-environments. The first mega-environment contains the test location CARI with genotype STBN 11 (NDRK 11-2) as the winner (Fig. 1). The second mega-environment contains the test locations KARAI and NDUAT with genotype STBN 21 (CSR 2K 255) as the winner. The third mega-environment contains the test locations CRRI, DRR, LUCKO, KARSA, BIHAR, KARSO and GOA with genotype STBN 16 (RP 4631-146-19-1-1-2-3) as the winner. The fourth mega-environment contains the test location PANVE with genotype STBN 19 (CSR 2K 219) as the winner. The fifth mega-environment contains the test location TRICHI with genotype STBN 24 (CSR 2K 262) as the winner.

The genotypes STBN 22 (CSR 2K 262), STBN 24 (CSR 27), STBN 26, STBN 13 (NDRK 11-4), STBN 12 (NDRK 11-3), STBN 14 (NDRK 11-5), STBN 11 (NDRK 11-2), STBN 21 (CSR 2K 255), STBN 18 (PNL 1-1-1-6-7-1), STBN 17 (PNL 9-1-2-7-4-6-1) and STBN 15 (RP 4353-MSC-38-43-6-2-4-3) had more than the average grain yield (Fig. 1 and Table 1), but only three of them, i.e. STBN 26, STBN 17 (PNL 9-1-2-7-4-6-1) and STBN 15 (RP 4353-MSC-38-43-6-2-4-3) had above-average yield with low instability (Fig. 1 and Fig. S1). In general, the most stable genotypes were STBN 2 (RAU-1-16-48), STBN 3 (CR 2218-64-1-327-4-1), STBN 7 (CR 2219-44-2) and STBN 5 (CR 2461-1-122-2-1) because the GE interaction scores were lowest and positions closest to the center of the AMMI2 biplot, although the average yield was much lower than the mean of all genotypes and the yield of other genotypes (Fig. 1 and Table 1). Genotype STBN 22 (CSR 2K 262) was one of the most productive and specifically adaptable to less restrictive environments. Its yield was higher in environments with coastal saline soils, while genotype STBN 14 (NDRK 11-5) recorded higher yield in alkaline soils. Genotype STBN 22 (CSR 2K 262) had expressed the highest grain yield across the 12 environments (both coastal salinity and alkalinity). For genotype STBN 17 (PNL 9-1-2-7-4-6-1), high stability but low yield was observed (Figs 1 and 2). The environments of CARI and PAVNE contributed most to the G×E interaction that means the instability was greatest, since the scores were the highest on the axes of interaction (Fig. 1). In turn, the more stable environments of LUCKNOW, NDUAT and TRICHI had lower PC1 scores (Fig. 1). The envi-
environments of GOA, KARSO, DRR, CRRI and BIHAR lie very close to each other within the same group (Fig. S1) and indicate that locations were saline locations. The proximity of genotype STBN 25 (CSR 36) to these environments indicates its specific adaptability to coastal saline environments. The variety CSR 36 was expressed the adaption to 5 locations of saline. Similarly, the proximity of genotype STBN 22 (CSR 2K 262) to environments of LUCKN, NDUAT, TRICH and KARAI indicates its adaptability to alkaline environments (Fig. S1).

Discussion

Performances of genotypes for grain yield and yield component traits

The mean grain yield of the genotypes was generally higher under moderate salt stress than under high salt stress. The trend of grain yield reduction across different levels of salt stress indicated that the yield reduction increased with increasing stress level and duration of crop exposure to stress. The reduced performance of the traits may be due to the genotypes being exposed to strong salt stress for longer duration. The yield and its contributing traits are affected drastically by the presence of salts in the soil (Ali et al. 2013; Krishnamurthy et al. 2014). The grain yield in salt stress environments depends on many factors and more on salt stress and rain fall (Tack et al. 2015). The mean grain yield is less in the environments, where salt stress and rainfall were more and vice versa (shown in Table S2). The mean yield of genotypes at Karnal was very less as compare to other environments due to the artificial controlled screening was facilities by rain out shelter.

Stability and adaptability analysis using AMMI model

Determination of appropriate and significant number of interaction PCs in the AMMI model is important for exploring the nature of $G \times E$ interaction. Due to the essence of AMMI model, the conventional F-test is not correct for testing of PCs. Using AMMI1 and AMMI2 biplots, test environments are grouped into mega-environments and the winning genotype for each environment can be identified. Biplots of AMMI model are effective at identifying cultivars and testing locations that are major sources of $G \times E$ interaction. Biplots and best linear unbiased predictions (BLUPs) are the best tool to compare cultivar performance across environments (Thomason and Phillips 2006). The high accumulated per cent value of explanation of the sum of squares on the first two axes of interaction, the adaptability and stability of rice genotypes can be graphically interpreted, considering only biplots with the first two axes of the GE interaction. This value was relatively higher than that reported for rice by Anandan et al. (2009) in coastal saline environments and Balestre et al. (2010) in upland environments and Kumar et al. (2011) in rice who also applied the AMMI analysis. The use of phenotypic means is widespread in stability and adaptability studies on different crops, but it should not be seen as an optimal procedure to predict the genotypic values, due to the strong influence of the “noise” or interferences (block, plot, location, year, etc.), which are confounded in the means, masking the real
genotypic values. The future performance of genotypes can be predicted and to quantify
the G×E as well as stability and adaptability, considering the effect of genotypes as ran-
dom in the model (BLUP) will most likely lead to the realistic estimations. Stability per
se should not be the only parameter for selection, because the most stable genotypes
would not necessarily give the best yield performance. Hence, there is need for approach-
es that incorporate both the mean yield and stability in a single index. Various authors
have introduced different selection criteria for simultaneous selection for yield and stabil-
ity (Eskridge 1990; Bajpai and Prabhakaran 2000). As ASV takes into account both
IPCA1 and IPCA2 that justify most of the variation in the G×E interaction, the ranks of
ASV and yield mean are decided in such a way that the lowest ASV takes the rank one,
while the highest yield mean takes the rank one. Then, the two ranks are summed in a
single simultaneous selection index of yield and yield stability named as the yield stabil-
ity index (YSI). The genotype with the lowest YSI is considered the most stable with high
grain yield.

In AMMI1 biplot, the usual interpretation of a biplot is that the displacements along
the abscissa indicate differences in main (additive) effects, whereas displacements along
the ordinate indicate differences in interaction effects. Genotypes that group together
have similar adaptation while environments which group together influence the geno-
types in the same way. However, proximity of genotype points to environment points
does not always indicate a high level of adaptation. The best adapted genotype can plot
far from the environment. The AMMI2 biplot presents the spatial pattern of the first two
PC axes of the interaction effects corresponding to the genotypes and helps in visual in-
terpretation of the G×E interaction patterns and identification of the genotypes or loca-
tions that exhibit low, medium or high level of interaction effects. Genotypes near the
origin are non-sensitive to environmental interactive forces and those distant from the
origin are sensitive to salt stress and have large interactions. The points of either geno-
types or environments which are close to each other have similar interaction patterns,
while those that are distant from each other have different interaction patterns (Muthura-
mu et al. 2011). The CARI and TRICHY are the two sites which exhibit enough pressure
on the genotypes to express their differences, while the locations clustered with red out-
line are almost similar and do not exert enough environmental push to discriminate the
genotypes. Based on this definition, the greater stability of LUCKN, NDUAT and TRICHI
locations compared to CARI and PANVEL suggests that the genotype classification of the
former group should have lower standard deviation of genotype performances than the
classification in other production environments. Genotypes and environments with the
same sign in the AMMI2 biplot must interact positively and, if the signs are opposite, they
must interact negatively. Kumar et al. (2010) identified genotypes and environments with
same-sign PCI scores, having positive specific interactions.

The genotypes CSR 2K 262 was expressed the adaption to 4 locations of alkaline.
Hence, the genotypes could be used in breeding program to combine the alkaline as well
as saline tolerance. Results of the production environments with low G×E interaction can
be extrapolated to other environments and used to increase rice productivity in salt-affect-
ed areas. Conversely, highly instable production environments with high G×E interac-

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tion, for example CARI and PANVEL should be used in genotype competition trials, for facilitating the selection of superior genotypes.

The stability and adaptability analysis using AMMI indicated the rice genotypes CSR 2K 262 in both coastal saline and alkaline environments and CSR 36 in alkaline environment as the most productive in terms of grain yield. The genotype CSR 36 is specifically adapted to coastal saline environments while CSR 2K 262 is adapted to alkaline environments. The CARI and PANVEL locations had the greatest effect of G×E interaction. Several genotypes produced grain yields higher than the average yield, but only two genotypes, namely PNL 9-1-2-7-4-6-1 and RP 4353-MSC-38-43-6-2-4-3 had the above-average yield with low instability. These genotypes could be used directly as varieties or as donors in future breeding programmes for improving the rice productivity in salt-affected areas and ensuring livelihood of the resource poor farming communities.

Acknowledgements

Authors sincerely thank the Bill and Melinda Gates Foundation for funding support under the STRASA project (IRRI-ICAR collaborative project) the Directors of all the partner Institutes for encouragement and CRIL, IRRI for helping in data analysis.

References


Electronic Supplementary Material (ESM)

Electronic Supplementary Material (ESM) associated with this article can be found at the website of CRC at http://www.akademiai.com/content/120427/

Electronic Supplementary Table S1. List of 26 rice genotypes and their pedigree and sources

Electronic Supplementary Table S2. Description and characterization of the locations used in the evaluation of 26 rice genotypes in the wet season (kharif) 2011

Electronic Supplementary Table S3. Combined analysis of variance for yield and its components traits and proportion of the sum of squares of genotype–environment interaction for each axis of the main components of the AMMI analyses for 26 rice genotypes in five coastal and seven alkaline environments in the India