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Genotype and genotype x environment interaction effects on the rice grain yield performance in different agro-ecologies in Tanzania

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This study aimed to assess the potential of elite rice lines to perform consistently and provide a high yield in several testing environments in Tanzania. A total of eleven rice genotypes were assessed for their yield performance and stability during two consecutive cropping seasons at three different environments. The assessment of grain yield stability was conducted using the Additive Main effect and Multiplicative Interaction (AMMI) and genotype by environment (GGE) biplot statistical models. These models are widely used to identify superior rice cultivars and ideal testing environments. The combined analysis of variance revealed statistically significant ($p < 0.05$) effects of genotypes, environments, and their interaction on grain yield. Genotypic performance was greatly affected by seasonal variability. The AMMI analysis revealed that the contributions of genetic (G), environmental (E), and genotype-environment interaction (GE) impacts to the overall variation in grain yield were 11.73%, 31.92%, and 1.90%, respectively. The study highlights the considerable challenge posed by genotype-by-environment interactions in crop breeding and the need to comprehend the genetic pathways that underlie environmental adaptability. It is essential to identify rice cultivars that are both stable and adaptable, and to determine highly discriminative testing conditions, to generate elite rice cultivars in Tanzania. The research findings offer useful insights for rice breeding programs to improve the selection of superior genotypes and optimize testing environments to maximize grain yield.

Key words: Rice genotypes, genotype x environment interaction, yield stability.

INTRODUCTION

Rice (*Oryza sativa* L.) is one of the most important staple crops that feed approximately half of the population in the world (Fukagawa and Ziska, 2019). It is one of the most important cereal crops that are grown for its diverse uses in Asia, Africa, and Australia (Qui et al., 2017; Wing et al., 2018; Vigueira et al., 2019). Rice is cultivated under a wide range of agro-climatic conditions including dryland farming systems, which contribute to 38% of the total

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cultivated area, followed by rain-fed wetland (33%), irrigated wetland (20%) and deep water and mangrove swamps (9%) production systems (Balamurugan and Balasubramanian, 2017).

Most breeding programs use multi-location trials to select high-yield stability and broad adaptation at the final stage of the cultivar development pipeline (Djurovic et al. 2014). However, multi-location trials are frequently expensive and lead to a reduction in selection (Gerrano et al., 2020). Yet, multi-environment trials are important as they are used to predict and estimate yield potential and identify stable and most adapted genotypes for a particular environment (Aly et al. 2011). The performance of a candidate is influenced by its genetic composition, environmental effects, and the interaction of these two components (Alberts, 2004). The interactions are important in conferring adaptation, but their inconsistencies and unpredictability complicate the selection process (Akcura et al., 2011).

Genotype x environment (G x E) interaction and yield-stability analysis have continued to be important in verifying the stability of genotypes. The G X E interactions cause genotypes to perform differently in diverse environments (Crossa 1990). The environment can influence the expression of a cultivar and lead to the selection or non-selection of such a genotype (Hallauer and Miranda, 1988). This complicates the selection of traits since they have inconstant expression under different environments (Zaidi et al., 2007). G X E interactions also reduce the heritability of quantitative traits (Nzuve et al., 2013). It is, therefore, important to carry out multi-environment trials to quantify G X E interactions to accurately account for the interactions before any effective selection can be carried out (Aly et al. 2011; Babic et al. 2011).

To obtain consistent yield across diverse environments, a variety should have adaptability and stability to fit into various growing conditions. Homogenous environments are expected to have similar G X E coefficients, but this is not easily attainable in practice, especially in sub-Saharan Africa, where environments vary in soil properties and microbes, rainfall, and agronomic management practices (Alberts 2004). G X E interactions result in variable performance of a genotype over time and space. Their interactions are treated as undesirable and confounding effects (Yan and Tinker 2006), although they can provide breeding opportunities. The main concern for breeders is not only to quantify G X E interactions but also to tie genotypes to their most suitable environments.

A comprehensive evaluation of GXE interaction needs more advanced statistical methods to be applied than the standard analysis of variance (ANOVA) because it assumes homogeneity across the different sites. Moreover, ANOVA does not account for non-additive terms (Mitrovia et al., 2012). The additive main effects and multiplicative interactions (AMMI) (Gauch et al., 2008) and genotype (G) and genotype-by-environment interaction biplot analysis (GGE-biplots) (Yan and Tinker 2006) methods have been consistently used to assess G X E interaction effects. The AMMI model is a powerful tool that uniquely estimates genotype, environments, and GXE interaction components (Babic et al., 2011).

The model involves both additive and multiplicative components of a two-way data structure which enabled a breeder to get precise predictions on genotypic potentiality and environmental influences on it. In addition, AMMI is a powerful tool for the evaluation of G × E interaction with a high degree of accuracy. In addition, it breaks down the interaction into separate components for each environment (Bose et al., 2014). The AMMI compresses the interactions into principal components depending on the number of significant interactions (Kandus et al., 2010). However, despite such usefulness, the AMMI also has its shortcomings such as failure to identify superior genotypes or suitable environments. This can be accounted for by incorporating the GGE biplot analysis.

Nonetheless, the relative versatility of the GGE, especially in mega-environment delineation and genotype selection, is worthy of being exploited for the selection of genotypes for a specific location and stability of crop genotypes. More importantly, it would assist in guiding the direction of varietal development for stable ecology-based selections. Additionally, GGE biplots can be used to support the superiority and stability indices in identifying both broad and specific adaptations (Kaya et al., 2006). In GGE biplots, grain yield potential and stability is evaluated using an average environment coordination (AEC), which is defined by the average principal component scores for all the environments (Dehghani et al., 2009). The main objectives of the present study are to identify higher-yielding promising rice genotypes having a wide environment and environment interaction for their yield stability and adaptability across diverse environments.

MATERIALS AND METHODS

Planting materials

In this study, a total of eleven rice genotypes including three commercial varieties (checks) were used. The complete set and details of genotypes used in the study are summarized in Table 1.

Description of experimental areas

Eleven rice genotypes were evaluated at the Mombo, Dakawa, and Kyela sites of the Tanga, Morogoro, and Mbeya regions, respectively. The field experiments were implemented in three different sites to maximize the influence of the interaction of phenotypic values with environments. The districts were purposely selected based on their high potential for rice production. The field trials were conducted in 2021 and 2022 the main cropping seasons and three locations making a total of six environments. The climatic conditions of the study sites are summarized in Table 2.

Table 1. List of rice genotypes used in the study and their sources.

Genotypes	Source
SR33705F2-64-3-3-HV-1	KAFACI
SR23364-133-35-1-HV-1	KAFACI
SR35262-HB3414-34-1	KAFACI
SR34599-HB3440-246-1	KAFACI
SR34599-HB343440-188-1	KAFACI
SR33705F2-76-1-1-HV-1	KAFACI
SR34590-HBND-1-HV-1	KAFACI
SR33705F2-59-3-1-HV-1-1	KAFACI
TXD 306	TARI
Komboka	IRRI
TXD 88	TARI

KAFACI = Korea Africa Food and Agriculture Cooperative Initiative; IRRI = International Rice Research Institute; TARI = Tanzania Agricultural Research Institute.

Experimental design and plant management

The experiments at all sites were laid out in randomized complete block design in triplicates. The plot sizes where 2 m x 5 m in which plants were spaced 20 cm between rows. Experimental units in all sites were established using seedling transplants. Seedlings were transplanted 21 days after nursery establishment, with one seedling per hill. Gap filling was done as necessary within two weeks after transplanting to ensure uniform crop stands. Fertilizer was applied at a rate of recommendation (two instalments as a top dressing). The first and second applications were done at the tillering and booting stages, respectively. Weed, pests, and disease control were carried out as recommended for the crop using a combination of chemical and cultural practices. After crop establishment, sufficient soil moisture was maintained in each plot using supplemental irrigation.

Data analysis

Data were pooled across seasons and locations and subjected to an analysis of variance for randomized complete block design in Genstat 24th edition (Payne et al. 2017). Genotype was set as a fixed factor, while location and genotype by location interaction, replication, and block were treated as random factors. Subsequently, AMMI model was performed to deduce stable and high-yielding genotypes, and specific and broad adaptation (Finlay and Wilkinson 1963; Gauch, 1993). The AMMI analysis was performed in Genstat version 18th (Payne et al. 2017). The stability analysis among genotypes over environments was done using GGE biplot multivariate analysis methods as described in Equation 1:

$$Y_{ij} = \mu + g_i + e_j + \sum_{k=1}^{t} \lambda_k \alpha_{ik} \gamma_{jk} + \varepsilon_{ij} \tag{1}$$

where Y_{ij}, is the yield of genotype i^{th} in the j^{th} environment, μ is the grand mean, g_i is the mean of ith genotype minus the grand mean, e_j is the mean of j^{th} environment minus the grand mean, λ_k is the square root of the eigenvalue of the principal component analysis (PCA) axis, α_{ik} and λ_{jk} are the principal component scores for PCA*k* of the ith genotype and jth environment respectively and eij is the residual error. The data was subjected to genotype, genotype x environment (GGE) biplot analysis (Yan and Tinker, 2006). The biplots visually depict genotypic performance over multiple environments based on principal components. The bi-plots were formatted to compare environments to a hypothetical ideal environment and compare the genotypes to an ideal genotype. The GGE-bi-plots were constructed using Genstat version 18 (Payne et al. 2017).

RESULTS

Genotype and environmental variance

The combined analysis of variance revealed significant *($P<0.05$)* variations for location, genotype, and season on grain yield (Table 3). The genotype x location interaction effects *($P<0.001$)* were observed for grain yield among the rice genotypes studied. Similarly, the combined (three-way) interaction involving genotype, location, and season differed significantly ($P<0.001$) with rice grain yield among genotypes.

Identifying high-yielding rice cultivars

The results (Table 4) indicated that rice genotype SR34590-HBND-1-HV-1 achieved the highest yield followed by SR33705F2-76-1-1-HV-1 while genotype SR34599-HB3440-188-1, SR35262-HB3414-34-1, and SR23364-133-35-1-HV-1 had the least yield (4 t ha^{-1}) among all the genotypes evaluated across the locations and seasons (Table 3).

The highest-yielding genotype observed in the Dakawa site was SR34590-HBND-1-HV-1. In comparison, genotype SR34599-HB3440-188-1 was the poorest performer in that location. At Mombo, genotypes Komboka and SR23364-133-35-1-HV-1 were the best and worst performing genotypes in terms of yield, respectively. When comparing genotype yield at Kyela, genotype SR33705F2-76-1-1-HV-1 had the highest yield, while genotype SR35262-HB3414-34-1 attained the lowest yield (3 t ha^{-1}) in that environment.

Additive main effect and multiplicative interaction

The AMMI analysis revealed that environment, genotype, and their genotype by environment interaction effects were highly significant ($p < 0.001$) for grain yield (Table 5). The environment contributed to 31.92% of the total variation in yield performance. In comparison, genotyping variations accounted for only 11.73%, while 1.9% of the variance was accounted for by interactions.

The AMMI model further partitioned the interaction sum of the square into interaction principal component axes 1

Table 2. Locations, season, altitude, latitude, and longitude of evaluating locations.

Code	Location	Season	Altitude (m)	Latitude (S)	Longitude (E)	Temp (Max) ºC	Temp (Min) ºC
E1	Mombo	2021	474	4° 53' 0"	38° 17' 0"	29.49	22.61
E2	Mombo	2022	474	4° 53' 0"	38° 17' 0"	28.13	21.53
E3	Dakawa	2021	361	06°24"	37°33 "	30.93	19.84
E4	Dakawa	2022	361	6° 24"	37°33"	31.6	20.4
E5	Kyela	2021	488	9°34'59.99"	33°51'0"	27.2	21.3
E6	Kyela	2022	488	9°34'59.99"	33°51'0"	26.6	20.6

Table 3. Mean squares and degrees of freedom for grain yield evaluated at three locations.

Source of variation	DF	MS
Replication	2	0.60ns
Location	3	0.30***
Genotype	10	0.80***
Year	1	0.20*
Genotype x Location	30	0.42***
Genotype x Year	10	0.12*
Location x Year	3	1.40*
Genotype x Location x Year	30	5.45***
Residual	173	0.06ns

*, ** and *** = significance at level 0.05, 0.01 and 0.001 respectively; ns = non-significant; df = degree of freedom and MS = mean square.

Table 4. Mean performance of rice genotypes for grain yield (tonne ha^{-1}) across locations.

Genotype	Yield in t/ha		
	Dakawa	Mombo	Kyela
SR34590-HBND-1-HV-1	6.7^{a}	4.4^{ab}	7.2^{ab}
SR33705F2-76-1-1-HV-1	6.4^{ab}	3.6^{bc}	7.7^{a}
Komboka	6.3^{ab}	5.6^{a}	4.8^{abc}
SR34599-HB3440-246-1	6.2^{ab}	4.6^{ab}	5.3^{abc}
TXD 88	6.0^{abc}	4.6^{ab}	4.5^{bc}
TXD 306	5.9^{abc}	3.2^{bc}	4.9^{abc}
SR23364-133-35-1-HV-1	5.8^{abc}	2.0^{c}	4.5^{bc}
SR35262-HB3414-34-1	5.7^{abc}	3.5^{bc}	3.0^{c}
SR33705F2-59-3-1-HV-1-1	5.3^{bcd}	3.5^{bc}	6.6^{ab}
SR33705F2-64-3-3-HV-1	5.0^{cd}	3.3^{bc}	4.5^{bc}
SR34599-HB3440-188-1	4.3^{d}	3.7^{bc}	4.2^{bc}
Mean	5.80	3.80	5.20
LSD	1.15	1.70	3.18
CV (%)	11.70	18.23	15.34

LSD = Least significance difference; CV = Coefficient of variations.

and 2 (IPCA1 and IPCA2, respectively) and residual term. Both IPCA1 and IPCA2 were significant and accounted for 42.63% and 27.92% of the observed variation due to the genotype x environment interaction.

Table 5. AMMI analysis of variance for rice grain yield (tonne ha^{-1}) evaluated at Mbeya, Dakawa, Ifakara, and Mombo during the 2021 and 2022 cropping seasons.

Source of variation	Df	SS	MS	Total variation (%)	G X E (%)
Total	197	1698.40	8.62		
Treatments	65	1412.60	21.73***		
Genotypes	10	212.70	21.27***	11.73	
Environments	5	1028.20	205.63***	31.92	
Block	12	77.30	6.44***	3.55	
Interactions	50	171.80	3.44***	1.90	
IPCA 1	14	73.20	5.23***		42.63
IPCA 2	12	48.00	4.00*		27.92
Residuals	24	50.60	2.11		

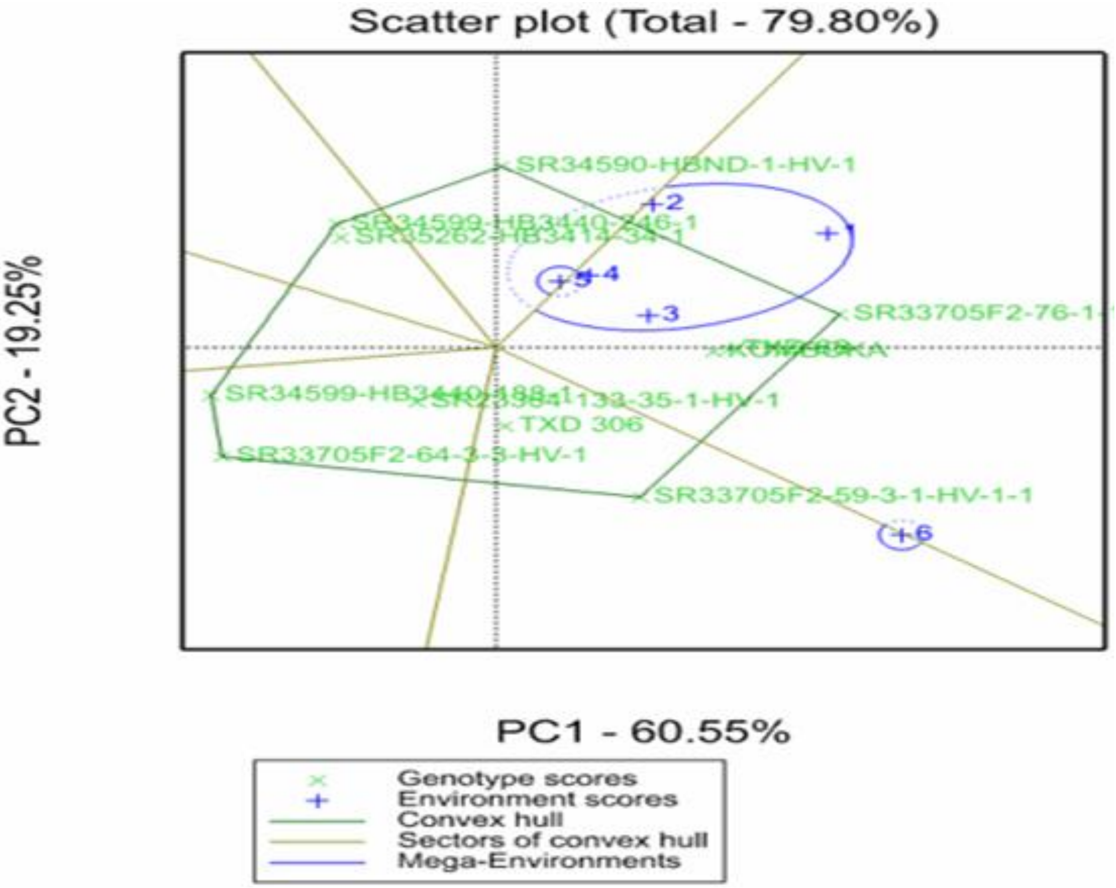

Figure 1. Polygon views of the GGE-biplot based on symmetrical scaling for ‘‘which-won-where’’ and mega-environment delineation. +1 = Mombo 2021; +2 = Mombo 2022; +3 = Dakawa 2021; +4 = Dakawa 2022; +5 = Mbeya 2021; +6 = Mbeya 2022.

Delineation of mega-environments and superior cultivars

The environments were grouped into three of the six sectors depicted by the GGE biplot (Figure 1). Environments 1, 2, 3, 4, and 5 were clustered into one sector and formed one mega-environment, while one environment was considered as a separate individual environment. Environments 1 and 2; 3 and 4; and 5 represent plantings at Mombo and Dakawa in the 2021 and 2022 cropping seasons, respectively. In addition, environment 5 was a planting that took place at Mbeya in

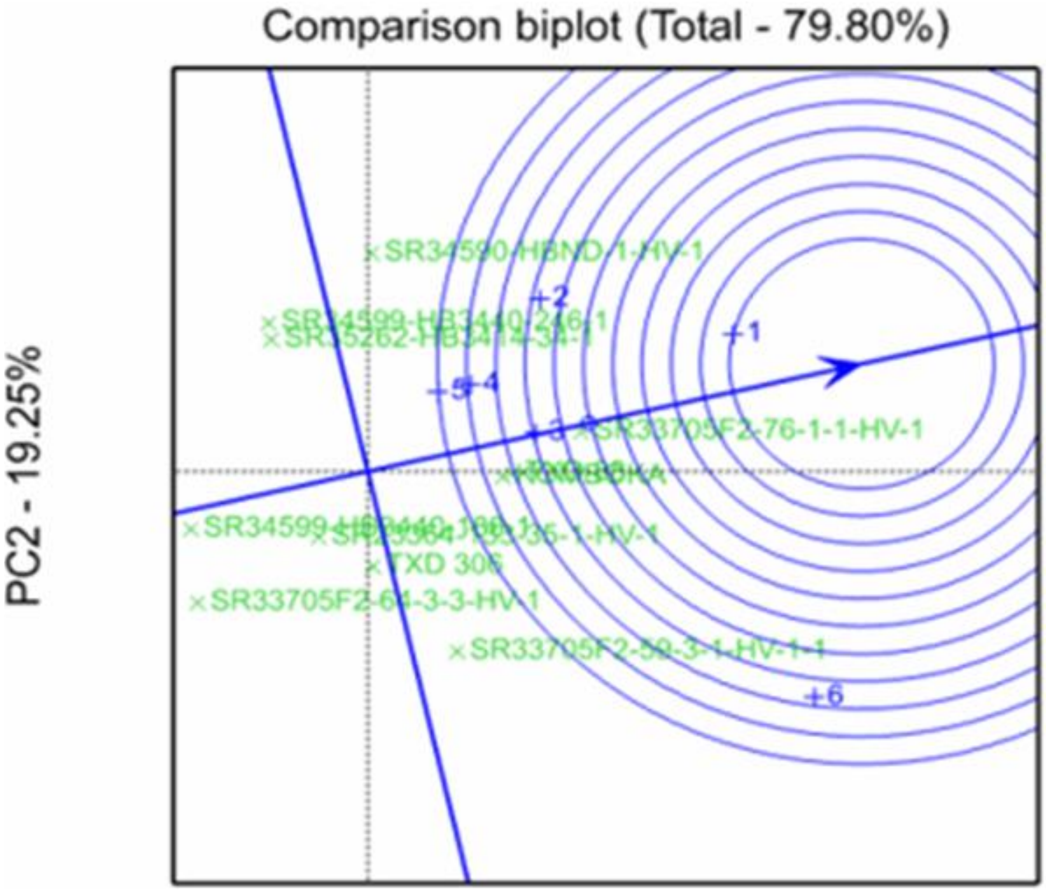

Figure 2. GGE-biplot showing the best rice genotypes based on mean grain yield performance and stability across six environments. +1 = Mombo 2021; +2 = Mombo 2022; +3 = Dakawa 2021; +4 = Dakawa 2022; +5 = Mbeya 2021; +6 = Mbeya 2022.

2021 and environment 6 was also Mbeya planting in 2022. The GGE biplot also identified genotypes that had specific adaptations and high yields in the respective environments. The genotypes located at the vertices of the polygon were SR33705F2-76-1-1-HV-1, SR33705F2-76-1-1-HV-1, SR33705F2-59-3-1-HV-1-1, SR33705F2-64-3-3-HV-1, SR34599-HB3440-188-1 and SR34599-HB3440-246-1. The genotype SR34599-HB3440-246-1 was the best performing and most adapted genotype for the mega-environment comprised of environments 1, 2, 3, 4, and 5, while the rest cultivars exhibited no specific adaptation to any environment.

Ideal genotype

The two principal components accounted for 79.8% of the variation among the cultivars (Figure 2). The GGE biplot compares the cultivars with the ideal genotype located at the epicenter of the concentric circles. Genotypes that are plotted close to the epicenter are close to the ideal genotype in terms of yield production and stability averaged across environments and seasons. The ideal cultivar is a hypothetical genotype generated by the algorithms. Cultivars with performance close to the ideal genotype at the epicenter were SR33705F2-59-3-1-HV-1-1, TXD 88, and Komboka. Cultivars SR33705F2-64-3-3-HV-1 and SR34599-HB343440-188-1 were the farthest from the ideal genotype, signifying their low yield and poor stability.

Ideal environment

An ideal environment is one which highly discriminating the tested varieties and at the same time be representative of the target locations (Yan and Kang, 2003) and desirable environments are close to the ideal environment. The planting in Mombo in 2021 and 2022 provided the most ideal conditions (Figure 3). This environment was closest to the epicenter, which represents the ideal environment. The ideal environment offers the highest discriminatory ability. The environment 3 (Dakawa, 2021) was the next most suitable

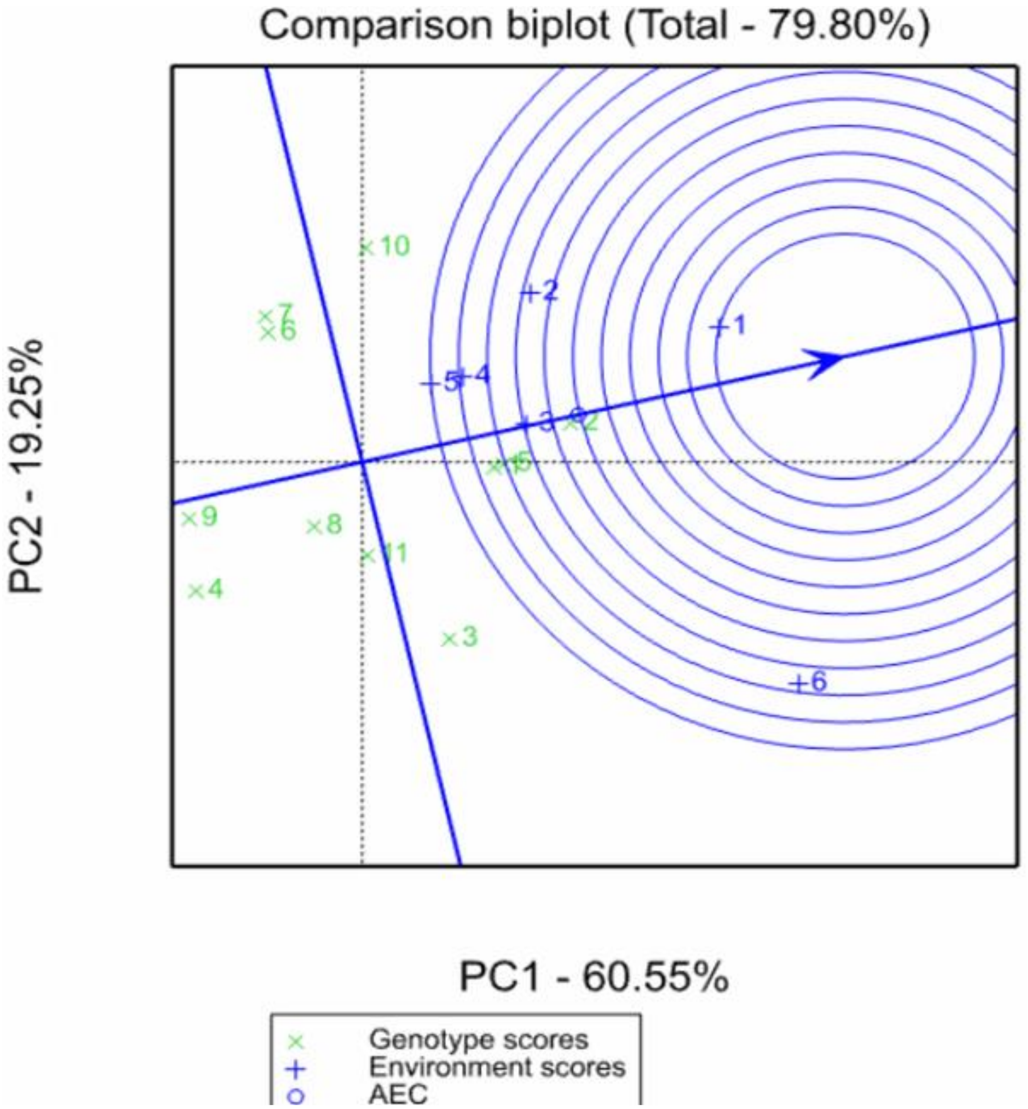

Figure 3. GGE-biplot showing the ideal environment. +1 = Mombo 2021; +2 = Mombo 2022; +3 = Dakawa 2021; +4 = Dakawa 2022; +5 = Mbeya 2021; +6 = Mbeya 2022.

environment.

Genotype stability

The GGE biplot (Figure 3) explains 79.80% of the total yield variation, composed of PC1 (60.55%) and PC2 (19.25%). The PC1 scores indicate the yield performance of the tested genotypes while the PC2 scores obtained from the Multi-environment tests indicate the genotypes' stability. The biplot exhibited the genotypes SR33705F2-76-1-1-HV-1(2) followed by KOMBOKA (5) and TXD 88(1) were the best-performing genotypes in terms of yield and yield stability across the environments. However, genotype SR33705F2-64-3-3-HV (9) revealed high yield stability across the environments, but its yield performance was poor. The genotypes SR34590-HBND-1-HV-1(10) and SR33705F2-59-3-1-HV-1-1 (3) exhibited low yield stability, but their yield performance was fairly above the mean.

DISCUSSION

Crop development initiatives take into account the simultaneous consideration of a wide range of agronomic and economically significant features (Cooper et al., 2021). Enhancing the desired traits would lead to the enhancement of additional traits (Begna, 2021). The rice genotypes had substantial diversity in grain yield, suggesting that there were differences in their genetic potential for this trait or the impact of the environment, as yield is inherited quantitatively. The grain yield was significantly affected by the interaction between season and genotype, indicating that different varieties respond differently to diverse seasons. These findings are consistent with the results reported by Silva et al. (2020). The variance in the mean square for genotype × site for grain yield indicates that certain genotypes had distinct performances across various locations.

Furthermore, the notable correlation identified between genotype and environment on grain yield indicates that the various locations had varying influences on the performance of the genotype. The variability demonstrated by the genotypes in this study is valuable for the identification of accessions for breeding programs and the subsequent improvement of rice varieties. The variation in genotype performance across various environments diminishes the correlation between genotypes. The genotypes in this study will require multiple cycles of evaluation to discover superior genotypes, as the environmental influence has a significant impact. However, the GXE interaction requires the identification of genotypes that are both adaptive and stable in each environment.

Additive main effect and multiplicative interaction

The environment accounts for 31.92% of the overall variation, indicating that a significant portion of the observed variations in rice genotypes can be attributed to environmental factors. This suggests that variances in environmental conditions are mostly attributed to variations in location rather than seasonal changes, which aligns with the findings of Osman et al. (2022). The genotype's sum of squares had a higher magnitude than that for G × E interaction, suggesting significant variations in genotypic response across locations. This finding aligns with prior results by Vaezi et al. (2017). The cultivars contributed a lesser amount of the variance, complicating the selection process that relies on phenotypic observation. The interaction had a comparable impact on the observed variances, indicating that it would be challenging to align genotype with phenotypic performance. The substantial importance and contribution of IPCA1 to the overall variation suggests that all of the variation observed across the five settings can be accounted for by a single IPCA, which aligns with the recommendation made by Osman et al. (2022). The significance of IPCA1 is further enhanced when a substantial portion of the variation is attributed to a single source, such as the environment in this particular study. In their study, Balcha et al. (2022) found that the quantity of IPCAs rises in correlation with the intricacy of the model and the augmentation in the number of sources of variation. In their study, Yan et al. (2000) found that 80% of the variation observed was attributed to environmental factors. In contrast, genotype and the interaction between genotype and environment accounted for 20% of the total variation.

Delineation of mega-environments an ideal environment

The cultivars SR33705F2-76-1-1-HV-1, SR34590-HBND-1-1-HV-1, SR33705F2-59-3-1-HV-1-1, SR33705F2-64-3-3-HV-1, SR34599-HB3440-188-1, and SR34599-HB3440-246-1 are linked together in a polygon (Figure 1), suggesting that these genotypes are the most distant from the original and well-suited to certain locations. The remaining rice cultivars were limited to the polygon due to their shorter vectors compared to the vertex genotypes, which made them less susceptible to the influence of a specific environment. According to Yan and Rajcan (2002), genotypes with shorter vectors have a lower level of responsiveness to the genotype x environment interaction in a certain context.

The environments were categorized into three out of the six segments identified by the biplot, suggesting that certain environments were correlated and formed mega-environments. The genotypes SR33705F2-64-3-3-HV-1, SR34599-HB3440-188-1, and SR34599-HB3440-246-1 were located at the vertices of unclustered habitats, indicating that these genotypes did not exhibit any special adaptation or performed poorly across different environments. Santos et al. (2017) found that genotypes situated on the vertices of the polygon, but without a clustered environment, exhibit poor yield and are not suitable for selection to enhance yield. The aggregation of habitats into a unified mega-environment is crucial because it allows for the concurrent selection of genotypes across the environments within the same mega-environment.

Simultaneous selection is allowed because settings within the same mega-environment exhibit a positive correlation (Yan et al. 2000), hence decreasing expenses in breeding programs. In this study, habitats 1, 3, 4, 5, and 5 were grouped and showed a positive association. This suggests that breeders can choose a testing location for evaluating a single season. These settings were categorized based on the dominant environmental parameters under which they were planted during the same cropping season. The variation in rainfall and temperature significantly influenced the demarcation of the mega-environments. The other two habitats that were considered to be distinct were further characterized by other factors.

Adaptability and stability across environments

The selection of genotypes depends on finding a balance between their adaptation to the environment and their stability (Mukherjee et al., 2013). An ideal genotype should exhibit high performance in specified target contexts while signifying consistent performance across a wide range of situations (Bhakta and Das, 2008). Based on the data presented in Figure 3, cultivar SR33705F2-76-1-1-HV-1 has shown adaptability to a wider range of conditions and consistent performance across different contexts. Therefore, it is recommended to consider this cultivar along with the improved varieties TXD 88 and KOMBOKA for selection. Cultivar SR34590-HBND-1-HV-1(10) and SR33705F2-59-3-1-HV-1-1(3) exhibited above-average yield performance but lacked consistency across different locations. This indicates that these cultivars are only suitable for specific locations and cannot be universally recommended until agronomic methods are implemented to maximize their potential yield output (Das et al., 2010).

Conclusion

The AMMI analysis was able to separate and quantify the components of the genotype-by-environment interaction (G x E) in the studied genotype. Moreover, the analysis was able to display G x E interaction, identify stable genotypes s and assess their adaptability across environments, and guide the decision on the best-performing genotype for recommendation in the studied environment.

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CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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