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ADDITIVE MAIN EFFECTS AND MULTIPLICATIVE INTERACTION ANALYSIS FOR STORAGE ROOT YIELD OF CASSAVA GENOTYPES EVALUATED IN UGANDA

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ABSTRACT

Genotype by environment interaction (G x E) is a major problem in the study of quantitative traits as it complicates the interpretation of genotypes evaluation experiments and makes predications of performance difficult. In order to disentangle the genetic and GxE effects and get meaningful interpretation of the results, additive main effects and multiplicattive interaction (AMMI) were used to identify patterns in the data, estimate the genotype performance by removing G x E noise that are intrinsic in cassava genotypes and determine genotype performance in specific environments. The proportion of variation of treatment sum of squares (SST) due to genotypes(79.7%) was much larger than the proportion of SST due to environments (8.2%). Although the G x E interaction was significant ($P<0.05$), its contribution to the total variation was low, indicating that cassava genotypes were more closely related. The linear regression analysis indicated that the genotype TMS 81/01635 was more stable ($b=0.93$, $R^2= 0.48$) across environments. AMMI bi-plot revealed that genotypes Migyera and TMS 191/0057 and the group of environments (E1=Namulonge season 1, E3=Bulisa season 1, and E5=Kapchorwa season 1) were less interactive in season 1 than in season 2 suggesting that environments of the first season were better than the second season. Migyera had the best yield and was more stable. The results further revealed that the genotype TMS I 91/0067 was very interactive and was more specifically adapted to Kapchorwa season 2 environment.

Keys Words: Adaptation, AMMI, cassava genotype, genotype x environment interaction, stability

RÉSUMÉ

L'interaction entre génotype et environnement est un problème majeur dans l' étude des caractères quantitatifs puisqu'il complique l'interprétation de l'évaluation des génotypes et rend difficile la prediction de la performance du rendement. En vue de séparer la génétique des effects de l'interaction pour une bonne interpretation des résultats, l' analyse des effects additifs principaux et de l' interaction multiplicative (ou AMMI) a été utilisée pour identifier la tendance dans les données, estimer la performance des génotypes en séparant l'erreur de l'interaction intrinsique aux génotypes du manioc pour la détermination des performances des génotypes dans chaque environnement spécifique. La proportion de variation de la somme des carrés traitements due aux génotypes (79.7 %) était beacoup supérieur à celle due aux environnements (8.2%). Bien que l'interaction entre génotype et environnement était significatif ($P<0.05$), sa contribution à la variation totale était faible, signifiant que les variétés utilisées étaient relativement identiques. La régression linéaire a montré que le clone TMS81/01635 était stable ($b=0.93$, $R^2= 0.48$) à travers tous les environnements. AMMI a de sa part démontré que les génotypes Migyera

et TMS 191/0057 et les environnements suivants: E1=Namulonge saison1, E3=Bulisa saison 1 et E5=Kapchorwa saison 1) étaient moins interactifs en saison 1 que dans saison 2 suggérant que la saison de la première année était meilleure que celle de la deuxième année. Le clone Migyera était le meilleur productif et était plus stable. Les résults a ont plus révelé que le génotype TMS I 91/0067 était plus interactif et était plutot adapté specifiquement à l'environnement de la deuxième saison de Kapchorwa.

Mots Cles: Adaptation, AMMI, génotype de manioc, interaction entre génotype et l'environnement, stabilité

INTRODUCTION

Genotype x environment interaction (G x E) is the change in cultivars' relative performance over environments, resulting from differential response of the genotypes to various edaphic, climatic and biotic factors (Dixon *et al.*,1991). It is a major problem in the study of quantitative traits because it complicates the interpretation of genotypes evaluation and makes predications of genotype performance difficult. When G x E interactions are present, the breeder faces major problems in comparing the performance of cultivars across environments (Annicchiarico and Perenzin, 1994).

The analysis of G x E, therefore, becomes an important biometrical tool employed by the plant breeder not only for evaluating varietal adaptation but also in the selection of parents for base populations, in classifying environments, and in improving genotypes with desired adaptability (Lin and Binns, 1988). The statistical tools for assessing the stability of a genotype's performance in different environments have been reported to assist breeders in selecting superior cultivars. Many statistical methods have also been advocated for as a basis for the analysis of genotypes variation to accommodate interactions and provide guidance for exploiting positive interactions. The traditional Joint Linear Regression (JLR) (Yates and Cochran, 1938; Finlay and Willkinson, 1963; Eberhat and Russel, 1966) partition the G x E into components due to differences among regression slopes and deviation regressions. The R^2 or model fit methods are used to investigate the proportions of the total sum of squares (SST) attributable to predicted values from the fitted model. However, the JLR has not been successful and has been criticised because the predictive part due to regression does not explain enough of the genotype by environment interaction to be considered useful. A more fruitful approach has been to partition the interaction by pattern analysis methods (DeLacy *et al.*, 1996). Hill (1975) suggested that where the genotypes in an experiment differ in their physiological response to physical factors in the environment, the linear regression technique may over-simplify the true response pattern to an extent which could lead to erroneous conclusions.

An alternative powerful approach to the analysis of G x E is called the Additive Main Effects and Multiplicative Interaction Model or AMMI. It utilises the standard two analysis of variance (ANOVA) and Principal Component Analysis (PCA) to identify any pattern in the data (Gauch, 1992). The results of AMMI are generally presented both in the form of an ANOVA and a bi-plot which allows the visualisation of any relationship between the eigen values for PCA1 and the means of the genotypes and environments.

The AMMI model combines regular ANOVA for additive effects with PCA for multiplicative structure within the interaction. Gauch (1992) reported that AMMI is effective for several purposes such as understanding genotype-environment interaction, improving the accuracy of yield estimates, increasing the probability of successively selecting genotypes with the highest yields, imputing missing data, and increasing the flexibility and efficiency of experimental designs. Ultimately, these advantages imply larger selection gains in breeding research and more reliable recommendations in agronomy. A multi-dimensional analytical approach such as the AMMI is often required for effective description of adaptation patterns (Nachit *et al.*, 1992). With its bi-plots presentation of results, AMMI provides insights into experimental results for which it might require years of additional and complex experimentation to develop hypotheses. The biplot offers a powerful tool for perceiving and communicating the patterns in yield data because it shows both main effects and interaction for both

genotypes and environments. This eases interpretation and gives more rapid advancement of physiological genetic understanding of the quantitative effects of different genotype and environment and facilitates rapid development of hypotheses from normal field experiment (Zobel, 1990).

The study reported in this paper used AMMI to assess cassava genotypes yield, select stable genotypes, and to investigate the G x E effects.

MATERIALS AND METHODS

The experiments were conducted at Bulisa, low-altitude (650 m a.s.l), Sendusu farm at Namulonge Agriculture and Animal Research Institute, mid-altitude (1250 m a.s.l) and at Kapchorwa in high altitude (1750 m a.s.l) in Uganda. Three experiments were conducted during 1997/98 and 1998/99 crop seasons , one experiment at each location for each season giving a combination of six season-locations experiments. Bulisa is located at 31° 25' E latitude and at 02° 02' N longitude, Namulonge is located at 0° 32' N latitude, and at 32° 53' E longitude while Kapchorwa is at 34° 27' E latitude and 01° 24' N longitude. The combinations of location-seasons were considered as separate environments: N1 (Namulonge first season); N2 (Namulonge second season); B1 (Bulisa first season); B2 (Bulisa second season); K1 (Kapchorwa first season); and K2(Kapchorwa second season).

A randomised complete block design, with three replicates, was used for each trial. Each plot was 5 m x 16 m and the plants were planted at a spacing of 1 m x 1 m using a seed rate of 10,000 cuttings per hectare. Stem cuttings, each 25 cm long with at least four nodes, were planted horizontally. Six cassava genotypes originating from different sources: source 2 (Migyera, SS4); source 4 (TMS 81/ 01635, TMS I 92/ 0057) and source 5 (TMS I 92/0067 & TMSI 91/ 0397) were used. Source 2 is contained improved planting material from the International Institute of Tropical Agriculture (IITA) tested and evaluated in Uganda and found good performers in mid land; while sources 4 and 5 had improved material from IITA, adapted to low and mid land altitude in Nigeria, respectively. There was no fertiliser applied and only manual weedings were done whenever necessary. Some climatic characteristics of the locations, such as total rainfall, mean temperature and relative humidity, were collected from each location depending on the equipment available.

Tubers were harvested at 9 months after planting across locations. Cassava plants were uprooted, stems cut and tuberous root were removed, counted and weighed using a balance of 25 kg. Fresh tuberous root weights per hectare were then estimated and used for analysis. Yields were obtained for genotypes (G) grown in environments (E) (location-seasons). Each genotype and environment combination was termed a "treatment". Some climatic characteristics are summarised in Table 1.

The AMMI statistical model was used for data analysis according to Gaush and Zobel (1996). We adopted the AMMI statistical model equation:

$$Y_{ger} = \mu + \alpha_g + \beta_e + \Sigma \lambda_n y_{gn} \delta_{en} + \rho_{ge+Eger}$$

Where: Y_{ger} is the yield of genotype g in environment e for replicate r, μ is the grand mean, αg is the genotype *g* mean deviations (genotype means minus grand mean), βe is the environment *e* mean deviation, *n* is the number of PCA axes retained in the model, λn is the singular value for PCA axis n, y_{gn} is the genotype eigenvector value

TABLE 1. Meteorological characteristics of Namulonge, Bulisa and Kapchorwa during 1997/98 and 1998/99 seasons

Location	Season 1 (1997/98)		Season 2 (1998/99)	
	Rainfall (mm)	Mean temp. (°C)	Rainfall (mm)	Mean temp. (°C)
Namulonge	1569.9	21.6	772.1	21.5
Bulisa	1305.0	26.3	857.0	25.6
Kapchorwa	1168.6	18.4	1137.0	16.4

for PCA axis n, δ_{en} is the environment eigenvector values for PCA axis n, and ρ_{ge} is the residuals, and *E* ger is the error.

The eigenvectors are scaled as units of error and are unitless, whereas λ has the units of the yield.

A simple scaling for the multiplicative parameters $\lambda^{0.5} y_g$ and $\lambda^{0.5} \delta_e$ termed the "genotypes IPCA scores", and "environment IPCA scores" is used because their product gives the expected interaction value directly. Environment and genotype PCA scores were expressed as unit vector times the square root of λn (Zobel *et al.*, 1988). Analyses of variance for tuberous root yield were conducted with SAS software (SAS Institute, 1990).

RESULTS AND DISCUSSION

The correlation matrix analysis of genotypes mean yields across environments and environments mean yields across genotypes are presented in Table 2. The basic analysis of variance indicated that the treatments were highly significantly different (P<0.001), indicating that genotypes responded differently to the environments used.

The results of the analysis of variance of AMMI partitioned the main effect treatments into genotype, environments and genotype-environment interaction. All components were highly significantly different (P<0.001) except the genotype x environment interaction, which

TABLE 2. AMMI analysis of tuberous root yield of cassava genotypes mean scores for genotypes and environment

Source	df	Sum squares	Mean squares	Probability
(i) Analysis				
Treatment	35	6651.05	190.03	***
GEN	5	5303.05	1060.61	***
ENV	5	544.95	108.99	***
GXE	25	803.04	32.12	**
PCA 1	9	625.01	69.45	***
Residual	16	178.30	48.32	ns
Error	72	1117.24	15.52	-

(ii) Mean scores

Environment/genotype	Mean	Eigen-vector
E1	11.80	0.18
E2	12.04	2.35
E3	11.01	0.61
E4	12.60	-1.28
E5	12.75	0.67
E6	6.21	-2.53
G1	25.46	-0.32
G2	10.39	1.44
G3	11.80	1.76
G4	7.56	0.95
G5	8.28	-2.59
G6	2.93	-1.25

Grand mean of fresh storage root yield =11.07 t ha^{-1}
,* Significant at P<0.01, P<0.001, respectively
ns: not significant, P>0.05
E1 = Namulonge season 1, E2 = Namulonge season 2, E3 = Bulisa season 1, E4 = Bulisa season 2, E5 = Kapchorwa season 1, and E6 = Kapchorwa season 2

was significant at P<0.05. The results indicated that genotypes and environment effects accounted for 79.7 % and 8.2 % of the total sum of squares, respectively, while the interaction accounted only for 12.1% (Table 2). The same results also indicated that the first interaction principal component (IPCA 1) was highly important in explaining the interaction while the rest IPCA were not significant and remained in the residual component and constituted the noise.

The results of eigenvectors and eigenvalues for genotypes and environments of the 3 principal components are presented in Table 3. Prin1 explained 87.5 % of the genotype x interaction. The three principal components accounted for 99.0% of the total interaction of the data. The results also showed that the eigenvalues of the three principal components are positive, and again the first component had eigenvalue greater than one while the two others had eigenvalues less than one. The results within environments indicated that all eigen-vectors are positive for PCA1. Looking at weight, the results indicated that environment K2 (Kapchorwa second season) had a very high eigenvector of 5.027 meaning that it was more interactive. Genotype 1 (Migyera) showed a larger eigenvector of 5.498 followed by TMS 81/01635 with a small value of 0.428 while the other genotypes had negative values.

The results of AMMI are presented also by bi-plot (Fig. 1) which allows us to visualise any relationships between the eigenvalues for PCA_1 and the means of the genotypes and the environments. The biplots recovered 97.32 % of the sum of squares total. AMMI with its bi-plots which detected important sources of variation of G x E effects and summarised information on the main effects and the first principal component scores of the interaction (1PCA1) of both genotypes and environments simultaneously helped to diagnose the interpretation. Zobel *et al.* (1988) explained that displacement along the x-axis reflect differences in main effects, whereas displacement along y-axis exhibited differences in interaction effects. The present results (Fig.1) show how the different genotypes responded differently to different environments. The bi-plot figure revealed that genotypes Migyera and TMS I 92/0057 were the least interactive, indicating a broad adaptability, while the highest G x E was shown by genotype TMS I 92/0067 followed by TMS I 91/0397 showing specific adaptability to Kapchorwa. The same results indicated that environments N1, B1 and K1 were the best suggesting that environments of the first seasons were better than the second season. The second season rainfall was not well distributed and delayed in the early stages of plant growth. The

TABLE 3. Eigenvectors, eigenvalues and the proportions of the 3 first principal components for genotypes and environments

Environment/genotype	Prin1	Prin2	Prin3
E1	3.099	0.165	-0.339
E2	2.758	1.783	1.593
E3	2.633	0.220	0.737
E4	2.819	-0.430	-2.073
E5	2.479	1.035	-0.517
E6	5.027	-3.641	0.908
Migyera (G1)	5.498	0.339	1.079
SS4 (G2)	-1.128	2.456	-0.366
TMS 81/01635 (G3)	0.428	2.678	-0.265
TMS I 92/0057 (G4)	-1.211	1.920	0.301
TMS I 92/0067 (G5)	-1.041	-0.822	-2.341
TMS I 91/0397 (G6)	-3.060	0.408	-1.284
Eigenvalue	5.250	0.624	0.066
Percentage	87.5%	1 0.4%	1.1%
Cuumulative	87.5%	97.9%	99.0%

E1 = Namulonge season 1, E2 = Namulonge season 2, E3 = Bulisa season 1, E4 = Bulisa season 2, E5 = Kapchorwa season 1, and E6 = Kapchorwa season 2

environment 6 (Kapchorwa second season) received slightly less rainfall and was colder (Table 1). Low temperature was the main factor limiting cassava genotypes to fully express their potential in that location. The joint regression analysis (Table 4) indicated, however, that there was no statistical linear relationships between the G x E interactions with the environments suggesting that the heterogeneity was not significant and accounted only for a small part of the G x E interaction. The results of the joint regression model presented in Table 5 showed that TMS 81/01635 was more stable compared to the other genotypes (b=0.93, r^2=0.48). Eberhat and Russell (1966) and Lin *et al.* (1986) used the regression coefficient to select stable genotypes. A genotype is stable when it responds to environments as does the average. According to Lin *et al.* (1986), the stability of Migyera is the static concept which occurs when the yield of the genotype under consideration is constant across environments, i.e., stability in the sense of homeostasis.

Investigation of G x E interaction showed the proportion of sum of squares due to differences among sites ranging from 80 to 90 % and variation

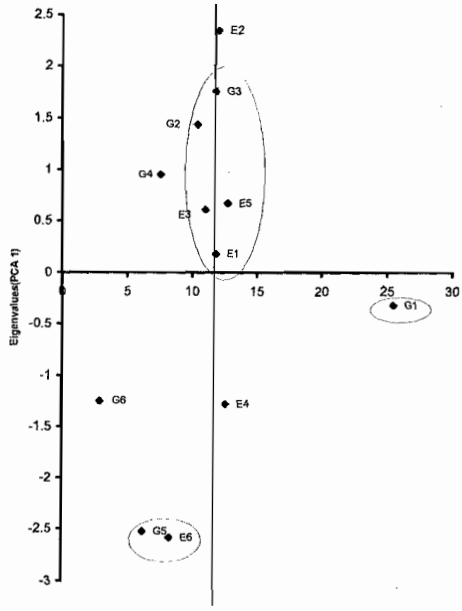


Figure 1. Bi-plot of AMMI model of the main effects on the abscica and the first IPCA axis on the ordinate for storage root yield (t ha^{-1}) of cassava genotypes.

TABLE 4. ANOVA table for joint regression analysis

Source	df	SS	MS	P
Total	107	7768.285	72.600	-
Treatment	35	6654.045	190.030	***
GEN	5	5303.052	1060.610	***
ENV	5	544.951	108.990	***
GXE	25	803.043	32.122	**
Joint Regr.	1	36.031	36.031	ns
GEN Regr.	4	216.322	65.330	**
ENV Regr.	4	34.261	8.565	ns
Residual	16	471.430	29.464	*
Error	72	1117.240	15.517	-

***: Significant at P<0.01
** : Significant at P<0.05

TABLE 5. Regressions parameters for the six cassava genotypes

Genotype	Mean	Slope	R^2	Index
Migyera	25.47	0.11	0.03	3
SS4	10.39	0.74	0.40	2
TMS 81/01635	11.80	0.93	0.48	1
TMS I 92/067	7.56	0.10	0.01	4
TMS I 92/0057	8.28	-1.11	0.38	6
TMS I 91/0397	2.93	-0.77	0.49	5

due to G x E was usually larger than genotypes variation, and interaction was frequently larger than the genotypes main effects. The results in the present study indicated that the proportion of genotypic variance was more important than environmental variance and the G x E interaction proportion was less than genotypes variation. This suggested that the genotypes used in this present study were not that different. The yield performance reported was from 9 months of growth, and may be if the results were for 12 or 15 months of growth the yield could have been higher. The first season received more rains than season 2 (Table 1). The genotypes responded by performing differently at different environments according to their genetic differences, but their physiological interaction with the physical factors of the environments were important as shown by AMMI analysis (Table 2). For the two seasons, Kapchorwa ranked the least in terms of yield performance. This could be attributed to the low temperature of 18.4 and 16.4 °C for season 1 and season 2, respectively. Leopold and Kriedmann (1975) reported that temperature as an environmental factor dictated developmental sequences, and regulated energy flow. At high temperature (24 to 30 ° C), the time from appearance to full expansion of a given leaf is about 2 weeks while expansion reduces greatly at lower temperatures. Cassava tolerates hot climate, but a critical point seems to exist between a daily average air temperature between 16 and 20°C below which the plant does not grow normally and yield decreases rapidly.

Cooper *et al.* (1996) and Fox *et al.* (1997) suggested that when the PCA1 values of genotypes and environments are close to zero, the entry having a small interaction effects has a general stability, its response pattern across the environments parallels the mean of all the genotypes in the trials. Our results showed that genotype 3 (TMS 81/01635) with PCA1 value of 0.4 was close to 0, indicating therefore that it was the genotype with small interaction among the group of genotypes tested. The entries with large positive or negative PCA1 values are largely responsible for G x E interaction and reflect more specific adaptation.

From the three statistics (ANOVA, Joint regression and AMMI) used to evaluate the accuracy of storage root yield, F-test and the percentage of the variance of the SST accounted for are in agreement that AMMI1 model was the most accurate and reliable technique.

In conclusion, AMMI model has been used successful to diagnose G x E interaction pattern of storage root of cassava. Genotype TMS 81/01635 had a low G x E interaction magnitude and thus performed well across environments. The stable locations (Namulonge season 1 and Bulisa season 1) could be considered as good sites for cassava evaluation in Uganda.

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