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Full Length Research Paper

Harnessing genotype-by-environment interaction to determine adaptability of advanced cowpea lines to multiple environments in Uganda

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This study was conducted to determine the yield stability of advanced cowpea lines in diverse agroecological zones of Uganda in order to facilitate documentation requirements for national performance trials (NPT). Thirty cowpea genotypes were evaluated against six checks in three localities, over three growing seasons, making a total of 9 unique environments. The trials were laid in a 6x6 alpha lattice design with three replications and grain yield was the principal trait measured. Single-site and multilocation data were summarized using analysis of variance. Further analysis of stability was visualized using the genotype and genotype by environment interaction (GGE) biplot and the additive main effect and multiplicative interaction (AMMI) models. ANOVA depicted highly significant differences among the genotypes, locations, seasons and GEI for grain yield. Based on AMMI analysis, environmental effect accounted for the most variation (84.7%) in the phenotype followed by GE (9.45%) and genotypes (4.45%), alluding to the complex inheritance of grain yield in cowpea. The polygon view and the average environment coordination view of the GGE biplot revealed Ayiyi as the wining genotype in the major mega environment and the most stable and high yielding across environments respectively. The genotypes Ayiyi, WC64 and ALEGIxACC2 yielded higher than the checks and were very stable. The other genotypes G36 (WC 36), G3 (ACC12xSECOW3B), G32 (WC16), and G14 (MU9) did not outperform the checks but displayed high yield stability and the mean yields were above the overall average. These genotypes were considered desirable for advancement to National Performance Trial for potential release as new improved cowpea cultivars.

Key words: Cowpea (*Vigna unguiculata* L. Walp), additive main effect and multiplicative interaction (AMMI), genotype and genotype by environment interaction (GGE), stability, grain yield.

INTRODUCTION

Cowpea (*Vignaunguiculata* L. Walp) is an annual,herbaceous legume that belongs to the Fabaceae family. It ranks fourth among the most important legume crops after beans, groundnuts and soybean (Mwale et al.,

2017) and it is an important source of food for most people in the sub-Saharan region which is consumed in form of vegetable and grain. Farmers in eastern and northern Uganda start harvesting cowpea vegetables three weeks after planting, thus making it one of the best food security crops (Orawu et al., 2013). Cowpea provides high quality fodder for livestock and is a good protein supplement for small scale farming communities with high nutritive values of 24.8% protein, 1.9% fat, 6.3% fiber and 63.6% carbohydrate (Mwale et al., 2017). Unlike beans and other legumes, cowpea is a multi-purpose crop, providing the farmer with not only grains, but also a wide range of other products.

According to FAOSTAT (2015), the world production statistics of cowpea stands at 4.46 million metric tons with Sub-Saharan Africa producing over 95% of the world cowpea (4.24 million metric tons). Asia is the second largest producer with only 3% of the world production (0.13 million metric tons). Nigeria is the leading producer of cowpea in the world with 2.46 million metric tons. In the case of Uganda, production of cowpea stood at 12,929 tons from 26,354 hectares in 2016 with an average yield of 0.49 kg/ha (FAOSTAT, 2016), with the northern and eastern parts of the country accounting for most of the production.

The production of cowpea is greatly affected by both biotic and abiotic stresses (Mwale et al., 2017). Yield attained in farmer's field fluctuates and, in most cases, averages of less than 500 kg/ha can be attained compared to the yield potential of the crop estimated at 1,500 kg/ha. The development and deployment of improved varieties remains the ultimate strategy to curb these challenges. However, genetic improvement of traits quantitative is challenging because expressions are modified by the environment (Yan et al., 2010). Selection of complex traits like grain yield in a breeding program is effective at advanced generations when the lines have become homozygous and replicated trials are possible. At this stage, replicated and multilocation trials becomes handy in assessing consistency in performance of genetic materials that are destined for advanced testing and possible release. Yield stability studies provide useful information on the adaptability of potentially high yielding lines in vast agro-ecological zones and help breeders to make recommendations about genotypes that are widely or specifically adapted (Asio et al., 2005). The data for making such decisions are often complex and requires rigorous analysis with advanced statistical models, including AMMI and GGE to discover and summarize consistent patterns in the experimental trial data sets. The GGE biplot and the AMMI models have been widely applied in the analysis of GxE by several workers in a wide range of crops: Crossa et al. (1997) in wheat; Yan and Rajcan (2002) in soybean; Yan and Tinker (2005) in wheat; Yan and Tinker (2006) IN wheat; Ding and Tier (2008) in Pinus radiata; Yan et al. (2010) in oat; Farshadfar et al. (2013)

in chicken pea; Rad et al. (2013) in wheat. The present study utilized 36 cowpea lines, previously tested and selected in the breeding program for various attributes including yield potential, to assess their adaptation and stability to diverse agro-ecological zones in Uganda. The study utilized eight unique environments which involved a combination of three locations and three growing seasons, using grain yield measurement as a parameter to evaluate stability and adaptability of the 30 lines in comparison to six locally adapted check varieties. Specifically, this was meant to ascertain if any of the 30 lines were broadly adapted and outperformed the six local checks in terms of grain yield. The study identified potential cowpea lines for further test at NPT and release. and in addition, provided insights into how GxE can be exploited by breeders to identify high yielding, stable and adapted varieties.

MATERIALS AND METHODS

Experimental sites and their geographic characteristics

The study was conducted in three diverse regions of Uganda and these included Arua (Abi-ZARDI) in West Nile, Serere (NaSARRI) in Eastern and Makerere University Agricultural Research Institute, Kabanyolo (MUARIK) in Central for three consecutive seasons (2017A, 2017B and 2018A). The soil characteristics of the study sites are sandy clay loam for MUARK, sandy clay loam for Arua and black clay for Serere (Sserumaga et al., 2015). The first season trials (2017A and 2018A) were sown in the month of March of the respective years, while the 2017B season trials were sown in August 2017. Details of the experimental sites and their geographic characteristics are given in Table 1, while the seasonal rainfall data are provided in Table 2.

Experimental design, field management and data collection

The experimental trials were laid out in alpha-lattice design of six blocks with six genotypes per block and replicated three times. Each replication measured 30 m long and 27 m wide, thus totaling an area of 810 m². Plot dimension measured 3 m by 2 m. The seeds were sown at a spacing of 0.75 m between rows and 0.25 m within plants. This formed five rows and eight plants per row and resulted in a total of 40 plants per plot. Inter-plot distance was 1.5 m, while inter-replication distance was 2.0 m.

The plants were sprayed twice with chemicals, first at seedling stage to protect against aphids using cypermethrin (10% EC) at the rate of 2.5 g per hectare and the second application was at50% flowering stage with non-systemic insecticide; lambda-cyhalothrin (2.5 EC) at the rate of 2.5 g per hectare to protect against thrips and pod borers. No fertilizers were applied since the soils are generally fertile.

The following data were collected; Number of primary branches per plant (NB) estimated as an average from 5 plants per plot; days to 95% maturity (MAT95%) determined by counting the number of days from sowing to the date at which about 95% of the pods were mature.

Number of pods per plant (NPP) estimated as the average of

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Table 1. Experimental sites and their geographic and soil characteristics.

Location	Latitude	Longitude	Altitude (m.a.s.l)	Average annual temperature (°C)	Average annual rainfall (mm)	Soil type
MUARIK	0°28'N	32°37'E	1200	21.5	1150	Sandy clay loam
AbiZARDI	3°4.58'N	30°56'E,	1206	24	1250	Sandy clay loam
NaSARRI	1°35'N	33°35'E	1140	26.5	1415	Black clay

Source: Sserumaga et al. (2015).

Table 2. Seasonal rainfall data (mm) for 2017A, 2017B and 2018B collected from three agro ecological zones in Uganda.

Otation			201	17A		
Station	Mar	Apr	May	Jun	Jul	Mean
MUARIK	207.1	171	140	43.4	123	683.7
NaSARRI	44.5	181	195	81.2	98.8	600.6
AbiZARDI	71.1	69.7	128	147	243	658.6
			201	17B		
	Aug	Sep	Oct	Nov	Dec	Mean
MUARIK	50.7	147	88.4	204	27.4	517.2
NaSARRI	79.8	153	168	98	0	498.5
AbiZARDI	238.7	223	213	165	0	840.1
			201	I8A		
	Mar	April	May	June	Jul	Mean
MUARIK	133	204	147	77	69	630
NaSARRI	105	208	187	107	112	719
AbiZARDI	79	119	117	130	167	612

Source: Uganda Bureau of statistics (2018).

number of pods of five plants selected randomly in a given plot; number of seeds per pod (NSP) estimated as the average of the total number of seeds from five plants; hundred seed weight (100SW) determined as the weight in grams of 100 seeds randomly sampled from each plant and averaged for five plants; grain yield per plot (GY/PLOT) where all plants in a plot were harvested and bulked to determine the yield per plot in grams after drying the seeds to an estimated moisture content of 12%; grain yield per plant (GY/P) determined as the average weight of five randomly selected plants harvested from each plot expressed in grams and grain yield per hectare (GY/HA) determined as the total yield of a given genotype in kilograms per hectors.

Plant genetic materials

Thirty cowpea lines that included land races from local farmers in Uganda, breeding lines and released varieties from National Agricultural Research Organization (NARO) in Uganda and varieties from Ghana and International Institute for Tropical Agriculture (IITA) were used for this study. The details of the genotypes are provided in Table 3.

Statistical analysis

Analysis of variance

Analysis of variance (ANOVA) was performed for grain yield using statistical package, Genstat 18th edition to detect differences among

the genotypes and F-test at 0.05 and 0.001 probability levels to detect the significance of the differences among the genotype means (Moore et al., 2015a). Genotypes were considered as fixed factors while location, season and blocking were considered as random factors. The analysis process involved single site analysis to obtain single site means. The best linear unbiased predictors (BLUPS) were then used to obtain multi-location means and multilocation analysis of variance using general ANOVA. Pooled analysis of variance was then conducted across seasons to test for the effect of seasons. The stability of genotypes over time (across seasons) and over space (across locations) was determined from the analysis of variance by testing the level of significance of the mean square value of season (MS_Y) and location (MS_{L)} respectively (Beavis, 2015). MSY and MSL values enabled determination of temporary/spatial stability. Since the (MS_Y) and MS_L are often inflated by experimental error, the actual variance due to season/location was obtained by equating the MSY or MSL to the mean square error (MS_e) . In order to do this, GxE was decomposed into its components as presented in the model according to Moore et al. (2015b)

G x L (locations) + G x S (seasons) + G x SL (seasons x locations)

Linear model for single site analysis

$$\mathbf{Y_{ijk}} = \mu + G_i + R_j + B/R_{(k)} + e_{ijk}$$

Linear model for across location analysis:

Table 3. List of 36 Cowpea genotypes used in the study.

Genotype	Genotype code	Origin	Genotype type
ACC12 * SECOW 5T	G2	NARO, Uganda	Breeding line
ACC 2 * SECOW 2W	G3	NARO, Uganda	Breeding line
IT 889	G4	IITA	Breeding line
IT 2841 * BROWN	G5	IITA	Breeding line
ALEGI * SECOW 5T	G6	NARO, Uganda	Breeding line
EBELAT * NE 51	G8	NARO, Uganda	Breeding line
AYIYI	G10	Ghana	Breeding line
NAROCOWPEAS 3	G11	NARO, Uganda	Breeding line
F2588T2E	G12	Ghana	Breeding line
NE 39 * SECOW 4W	G13	NARO, Uganda	Breeding line
SECOW 4W * SECOW 5T	G18	NARO, Uganda	Breeding line
ACC12 X SECOW 3B	G23	NARO, Uganda	Breeding line
ALEGI X ACC2	G28	NARO, Uganda	Breeding line
Sunshine 2S	G9	Uganda	Land race
WC 68A	G19	West Central Uganda	Land race
WC 16	G20	West Central Uganda	Land race
WC 37	G21	West Central Uganda	Land race
NE 55	G22	North Eastern Uganda	Land race
NE 23	G25	North Eastern, Uganda	Land race
NE 37	G30	North Eastern, Uganda	Land race
CP 1	G31	Uganda	Land race
WC 36	G32	West Central, Uganda	Land race
NE 15	G33	North Eastern, Uganda	Land race
NE 20	G35	North Eastern, Uganda	Land race
NE 55	G36	North Eastern Uganda	Land race
NE 48	G1	North Eastern Uganda	Landrace
MU 9	G14	Unknown	Landrace
MU 9A	G15	Uganda	Landrace
WC 63	G24	West Central Uganda	Landrace
2392	G34	Uganda	Landrace
SECOW 5T	G16	NARO, Uganda	Released Variety
SECOW 4W	G17	NARO, Uganda	Released Variety
SECOW 1T	G26	NARO, Uganda	Released Variety
NAROCOWPEA1	G27	NARO, Uganda	Released variety
NAROCOWPEA4	G29	NARO, Uganda	Released variety
ASONTEM	G7	Ghana	Variety

$$Y_{ijkl} = \mu + L_i + Y_j + LY_{(ij)} + Rep(E)_k + B(Rep.L.Y) + G_l + GL_{(il)} + GY_{(lj)} + GLY_{(lij)} + e_{ijlk}$$

Where $:Y_{ijkl}=$ observation of ith genotype in Ith location, and season j, in replication k, $\mu=$ general mean, $G_l=$ effect of genotype I, $L_i=$ effect of location i, $Y_j=$ effect of season j, $LY_{(ij)}=$ interaction between location and season (effect of environment) $Rep(E)_k=$ effect of rep k in location i and season j, B(Rep.L.Y)= blocking effect, $GLY_{(lij)}=$ interaction of genotype I with location i and in season j, $e_{ijlk}=$ residual error of genotype I in environment (ij), replication k.

GGE biplot analysis

The linear model for the biplot analysis based on singular value

decomposition of the first two principal components described by Yan and Rajcan (2002) is presented thus;

$$Y_{ij} - \mu - \beta_j = \sum \lambda_j \, \varepsilon_{i(l)} \, \eta_{lj} + \epsilon_{ij} \tag{1}$$

Where: Y_{ij} = is the observed mean performance of genotype i in environment j, (i =1,2...n), (j=1,2...m), μ = grand mean, β_i = main effect of environment j (μ + β_i), \ddot{e}_i = SV of the $f^{\rm D}$ PC, the square of singular value is the sum of squares explained by PC_l where; I = 1,2...k. with $k \le \min$ (m, n) and for a two-dimensional biplot, k = 2. $\varepsilon_{i(l)}$ = eigen vector of genotype i for PC_l , η_{lj} = eigen vector for environment j for PC_l , ε_{ij} = residual associated with genotype i in environment j. PC1 and PC2 eigen vectors cannot be plotted

directly to construct a meaningful biplot before the singular values are partitioned into the genotype and environment eigenvectors (Yan and Tinker, 2006). In order to visualize the MET data, singular value partitioning (SVP) was partitioned into the genotype and environment eigen vectors as follows:

$$Y_{ij} - \mu - \beta_i = \sum G_{il} E_{jl} + \epsilon_{ij}$$

Where G_{il} and E_{jl} are the PC_l scores for genotype i and environment j respectively (Yan and Tinker, 2006). In a biplot, genotype i is displayed by a point defined by all the G_{il} values and environment j is displayed by a point defined by all the E_{jl} values where i = 1 and 2 for a two dimensional biplot (Yan and Tinker, 2006). Singular value was thus implemented by,

$$G_{il} = \lambda_l^{fl} \varepsilon_{il} \text{ and } E_{ij} = \lambda_l^{1-fl} \eta_{lj}$$
 (2)

Where; fl= partition factor for PC I and is usually between 0 and 1. The partition factor influences the kind of interpretation we can give to a biplot. To analyze the relationship between the trials, genotypes and the environments, the GGE biplot was generated using the formula presented as:

$$Y_{ij} - \mu - \beta_j = G_{i1}E_{j1} + G_{i2}E_{j2} + \epsilon_{ij}$$
(3)

The polygon view was constructed using the environment standardized GGE model presented as;

$$\frac{Y_{ij} - \mu - \beta_j}{sj} = \sum \lambda_l G_{il} E_{jl} + \epsilon_{ij}$$
(4)

The GGE biplot based on genotype scaling was used for the evaluation of genotypes because the relative importance of the PC₁ and PC₂ is fully reflected by the location of the genotypes in the GGE biplot (Yan and Tinker, 2006). Symmetrical scaling: $\mathit{fl}=0.5$. $\mathit{G}_{il}=\lambda_l^{0.5}\varepsilon_{il}$ and $\mathit{E}_{jl}=\lambda_l^{0.5}\eta_{ij}$ was used to visualize the relative importance of both the genotype variation and environment variation for both PC₁ and PC₂. The GGE biplots were generated using the R software version 3.5.0, while AMMI stability values were generated using Genstat 18th edition software.

AMMI analysis

The AMMI model as described by Akter et al. (2014) is presented below.

$$Y_{ijk} = \mu + G_i + E_j + \sum \lambda_k \alpha_{(ik)} \gamma_{jk} + d_{ij} + e_{ijk}$$

Where, μ = the grand mean. G_i = the genotype deviations from the grand mean. E_j = the environment deviations from the grand mean. $\lambda_k = k^{th}$ eigen value. $\alpha_{(ik)}$ = principal component score for the ith genotype for the kth principal component axis. γ_{jk} = principal component score for the jth environment for the kth PC axis. d_{ij} = residual GEI not explained by model. e_{ijk} = residual model. The AMMI stability values (ASV) were determined from the described expression below (Lin et al., 1986):

$$\mathsf{ASV} = \sqrt{\frac{IPCA1SS}{IPCA2SS}}(IPCA1SCORE)^2 + (IPCA2SCORE)^2$$

Where: ss = the sum of squares, IPCA1 and IPCA2 = the first and second interaction principal component axes respectively. The average stability value (ASV) could be considered as the distance from zero in a two-dimensional scatter plot of IPCA 1 scores against IPCA2 scores. The genotypes were evaluated for both cultivar superiority and static stability. The more the IPCA scores approximates zero, the more stable or adapted the genotype is over all environments tested. Genotypes with smaller stability values were considered to be more stable. The AMMI analysis of variance was generated using Genstat 18th edition software and the GxE effect was further partitioned into the first and second interaction principal component axis and GxE residual.

RESULTS

Agronomic attributes of the genotypes

The mean agronomic attributes of the 36 genotypes determined over two seasons (2017A and 2017B) in the three locations are presented in Table 4. The genotypes ACC2xSECOW2W, ALEGIxACC2, NAROCOWPEA1, SECOW2W, NAROCOWPEA3, Ayiyi, NAROCOWPEA4 and WC64 had higher 100 seed weight and superior grain yield per plant. These genotypes also exhibited higher number of pods per plant, number of seeds per plant and higher number of branches per plant.

Variances and summary statistics for phenological traits among 36 cowpea genotypes assessed across three locations in two seasons (2017A and 2017B) are presented in Table 5. All the traits were significantly influenced by the location effect at P<0.001 except the weight of 100 seeds that was not significantly affected at P< 0.05. The phenological traits exhibited moderate to high heritability (H) values ranging from 0.67 for MAT to 0.91 for GY/P (Table 5). The results for genotypic coefficient of variation (GCV) ranged from 3.38% to 13.33% with maturity date recording the lowest GCV and grain yield per plant recording the highest GCV at 13.33%. The number of pods per plant attained GCV of 13.21% followed by the weight of 100 seeds (11.9%) and number of seeds per pod (10.0%).

Multi-location analysis of variance

The results of the combined analysis of variance for grain yield among 36 cowpea genotypes evaluated across three locations in three seasons are presented in Table 6. There were highly significant differences (P<0.001) observed among genotypes, locations and seasons for grain yield and thus the three main sources of variation (G, E and GxE) greatly influenced grain yield in cowpea. The genotype x season, genotype x location and the genotype x location x season (GxE) interactions were highly significant (P<0.001). Grain yield in cowpea was greatly affected by the season and location effect and the season/location (GxE) interaction effect. Of the three main effects (genotype, location and season), the

Table 4. Mean phenological attributes of 36 cowpea lines determined for two seasons across three locations in 2017A and 2017B.

Genotype	Genotype code	MAT	NB	NPP	NSP	SW	GY/P
2392	G1	77	4.5	19.9	11.1	10.5	36.7
ACC 2 * SECOW 2W	G2	72.8	5.1	23.5	12.1	12	42.9
ACC12 x SECOW 3B	G3	71.7	5	27	12.6	12.9	47
ACC12 x SECOW 5T	G4	74.1	5	26.8	11.7	12	46.6
Alegi * SECOW 5T	G5	73.7	4.6	27.9	13.2	13	47.5
ALEGI x ACC2	G6	74.5	4.9	31.4	14.1	14.7	52.9
Asontem	G7	75.9	4.4	22.8	11	11.8	40.1
Ayiyi	G8	75.4	5.3	32.8	14.5	15.2	53.4
CP 1	G9	76.5	4.7	22	10	12.7	42.5
Ebelat * NE 51	G10	71.8	5	28.9	12.4	14.5	49.7
F2588T2E	G11	74.2	4.6	23	10.9	11.2	37.4
IT 2841 * BROWN	G12	77.5	4.7	26.6	11.1	12.9	44.1
IT 889	G13	72.2	4.7	28.5	12.6	14.5	49
MU 9	G14	75.5	4.8	29.5	12.5	14.6	49
MU 9A	G15	73.7	4.8	26.6	11.6	13.4	44.5
NAROCOWPEA1	G16	73.7	5.5	32.2	13.4	16.9	57
NAROCOWPEA3	G17	74.9	5.3	31.6	13.4	16.1	54.9
NAROCOWPEA4	G18	72.9	5.4	31.9	14.3	15.9	53.6
NE 15	G19	69.6	4.6	23.8	11.4	12.3	41.2
NE 20	G20	71.6	4.3	22.5	10.7	11	37.1
NE 23	G21	72.5	4.7	28.9	12.4	12.3	39.6
NE 37	G22	75.5	4.5	25.2	10.9	12	35.2
NE 39 * SECOW 4W	G23	80.0	4.5	24.7	12	13.4	40.2
NE 48	G24	73.7	4.4	26.2	13.3	13.9	44.8
NE 55	G25	75.3	4.3	22.8	11.2	12	38.2
Secow 1T	G26	72.7	4.5	24.2	12.6	12.5	41.9
Secow 4W	G27	74.7	5	30.9	13.7	14.6	52.6
SECOW 4W * SECOW 5T	G28	78	4.8	26.9	12.4	13	46.3
Secow 5T	G29	80.0	4.5	27.8	12	12.9	46
Sunshine 2S	G30	71.3	4.7	25.1	12.1	12.7	41
WC 16	G31	75	4.4	22.4	11.3	12	37.9
WC 36	G32	74.7	4.9	27.4	12	13.2	44.8
WC 37	G33	72.2	4.7	25.6	11.5	12.3	42.2
WC 63	G34	74.9	4.8	28.2	11.7	12.7	47.4
WC 68A	G35	80.1	4.8	29.7	12.7	12.3	52
WC64	G36	75.6	5	27.1	12.6	12.8	46.5

MAT=days to maturity, NB= number of branches, NPP= number of pods per plant, NSP=number of seeds per pod, SW= weight of 100 seeds, GY/P= grain yield per plant.

greatest contribution to the variation in cowpea yield was due to the seasonal effect (52.3%), followed by the locality (25.1%) and the genotype main effect had the lowest contribution to cowpea grain yield (8.5%).

AMMI analysis of variance

The additive main effect and multiplicative interaction (AMMI) analysis of variance for 36 cowpea lines

evaluated across three locations in three seasons is presented in Table 7. The results showed that there was highly significant (P<0.001) main effect of genotype, environment and GxE effect. The GxE interaction term was further partitioned into the first and second principal components which were both highly significant at P<0.001. The AMMI analysis showed that all the treatments (E+G+GE) accounted for 98.6% of the total variation in cowpea grain yield, while error only accounted for 1.24%. The total sum of squares was then

Table 5. Heritability, variances and summary statistics for major phenological traits among 36 cowpea genotypes assessed across three locations in two seasons (2017A and 2017B).

Statistics	MAT	NB	NPP	NSP	sw	GY/P
BSH (genotype mean basis)	0.90	0.67	0.86	0.76	0.85	0.91
σ2g	6.37	0.14	12.47	1.48	2.44	36.18
σ2GxL	2.55	0.29	8.15	1.86	1.64	12.89
σ2 L	6.47	0.06	8.66	1.62	0.02	13.76
σ2e	2.85	0.17	5.71	1.41	1.42	16.33
GM	74.6	4.77	26.7	12.2	13.1	45.11
LSD	1.75	0.43	2.79	1.22	1.19	3.94
CV	2.26	8.60	8.94	9.74	9.07	8.96
P (G)	0.00	0.00	0.00	0.00	0.00	0.00
P(GXL)	0.00	0.00	0.00	0.00	0.00	0.00
P(L)	0.00	0.00	0.00	0.00	0.67	0.00
GCV	3.38	7.79	13.21	10.00	11.9	13.33

BSH = Broad sense heritability, σ^2g =genotypic variance, σ^2GxL =genotype location variance, σ^2L = location variance, σ^2e =error variance, GM=grant mean, LSD =least significance difference, MAT = days to maturity, NB= number of branches, NPP= number of pods per plant, NSP=number of seeds per pod, SW= weight of 100 seeds, GY/P= grain yield per plant. GCV= genotypic coefficient of variation, P(G), P (GxE), and P(L) = significance of genotype, GxE, and location at P<0.05.

Table 6. ANOVA for multi-location evaluation of 36 cowpea genotypes for grain yield (kg/ha)

Source of variation	d.f	SS	MS	Explained SS
Total	863	748,091,291		100
Location	2	185,139,090	92,569,545***	24.7
Season	2	386,077,104	193,038,552***	51.6
Location x Season	3	63,041,021	21,013,674***	8.4
(Location/Season/Rep)	16	463,406	28,963*	0.1
Genotype	35	33,293,680	951,248***	4.5
Genotype x location	70	21,846,777	312,097***	2.9
Genotype x Season	70	26,146,239	373,518***	3.5
Genotype x location x Season	105	22,722,080	216,401***	3
Pooled error	560	9,361,894	16,718***	1.3

d.f = degrees of freedom, MS = mean square, SS= sum of squares, *, **, *** = significant at P<0.05, 0.01, 0.001 respectively.

Table 7. Additive Main effect and Multiplicative Interaction (AMMI) analysis of variance for yield of 36 cowpea genotypes across three locations for three seasons (kg/ha)

Source	d.f	S.S.	M.S.	Explained	%GxE
Total	863	748,091,291	866,850***		
Treatments (G+E+GE)	287	738,265,992	2,572,355***	98.6	
Genotypes	35	33,293,680	951,248***	4.45	
Environments (E)	7	634,257,215	90,608,174***	84.7	
Block	16	463,406	28,963ns	0.061	
Interactions (GxE)	245	70,715,096	288,633***	9.452	
IPCA 1	41	22,081,952	538,584***		31.2
IPCA 2	39	14,555,779	373,225***		20.58
Residuals	165	34,077,366	206,529		48.18
Error	560	9,361,894	16,718	1.25	

d.f = degrees of freedom, M.S = mean square, S.S= sum of squares, *, **, *** = significant at P<0.05, 0.01, 0.001.

Environment	Mean (kg/ha)	Variance	IPCAe1	IPCAe2
ARUA2017A	2671	175123	-18.2018	19.2375
ARUA2018A	1010	173490	13.75941	-29.1266
MUARIK 2017A	2483	247623	-38.6323	-8.946
MUARIK 2017B	2800	168864	6.09907	-17.2794
MUARIK2018A	871	66918	7.83788	0.68376
SERERE2017A	877	96922	-4.85107	4.64067
SERERE2017B	1651	83178	16.68372	7.9908
SERERE2018A	550	51751	17.30501	22.79924

Table 8. Environment means and IPCA Scores for grain yield for 36 cowpea genotypes in Uganda.

IPCAe1/IPCAe2 the first and second environment interaction principal components.

Table 9. Mean yield performance of 36 cowpea genotypes evaluated across locations in three seasons of 2017A, 2017B and 2018A.

Lasation	Sea	son		
Location	2017A	2017B	2018A	Total
ARUA	2670	-	1010	1840
MUARIK	2482	2800	870	2051
SERERE	876	1650	550	1025
Mean	2009	2225	810	1682

Yield data is not presented for the location ARUA in season 2017B as it was affected by combination of factors, especially dry spell and destruction by animals.

partitioned into the main effects where, the greatest contribution to the variation in cowpea grain yield was by the environment (E) which accounted for 84.7% of the total variation. This was followed by the interactions (GE), with 9.45% of the variation, while the genotypes only accounted for 4.45% of the total variation in cowpea grain yield. The blocking effect explained 0.061% of the total variation in cowpea yield and was barely significant. GxE was partitioned into its first and second interaction principal components (IPCA1 and IPCA2), where IPCA1 accounted for 31.2% of the total GxE, IPCA2 accounted for 20.58% and the residual accounted for 48.18% of the total GxE effect. The first two IPCAs were therefore sufficient to justify the AMMI model.

Environmental IPCA scores and variances for 36 cowpea genotypes evaluated in three seasons across three locations

The results for the environmental IPCA scores and variances for 36 cowpea genotypes evaluated over three seasons across three locations are presented in Table 8. The first environment linear interaction terms (IPCA1 scores) were able to discriminate between the

environments with Kabanyolo (MUARIK 2017A) having the highest IPCA1 score of -38.63, followed by ARUA 2017A, that recorded an IPCA1 score of -18.2 and the least interactive environment was observed with Serere 2017A (IPCA1 score of -4.85).

The environment variance ranged from 247,623 to 51,751, where Kabanyolo (MUARIK2017A) registered the highest and Serere 2018A recorded the least variation among the genotypes. MUARIK 2017A and ARUA 2017A contributed the greatest variation among cowpea genotypes and were the most favorable environments for testing the genotypes. According to the AMMI analysis, the order of discriminating ability of the environments based on their variances was MUARIK 2017A (247,623), ARUA2017A (175,123) and Serere 2018A (51,751). With respect to the mean yield of environments, the AMMI analysis showed that, MUARIK, season 2017B had an average mean yield of 2,800 kg/ha compared to ARUA, season 2017A which recorded an average mean yield of 2671 kg/ha. Serere, in season 2018A was the least representative and discriminatory environment since it had the lowest average mean yield of 550 kg/ha.

The results of the grand season/locality and overall grand mean for 36 cowpea genotypes are presented in Table 9. The overall mean yield of cowpea genotypes across localities and seasons was 1,682 kg/ha. With

respect to localities, the highest mean yield of cowpea genotypes was observed in Kabanyolo (MUARIK) with 2,051 kg/ha, followed by ARUA with 1,840 kg/ha and Serere had the least mean yield of 1,025 kg/ha. The estimates of the season mean yields revealed that, season 2017B registered the highest mean yield of cowpea at 2,225 kg/ha and the worst season was 2018A with a mean yield of 810 kg/ha across locations. The trials in season 2017B at Arua were completely destroyed by stray animals and therefore it was omitted in the analysis. The average yield for season 2017B was thus obtained from two localities.

Genotypic IPCA scores and variances for 36 cowpea genotypes evaluated in three seasons across three locations

The results for the genotype IPCA scores are presented in Table 10. Based on IPCA scores, the first linear interaction term (IPCA1 scores) were both negative and positive and ranged from -18.2 to 17.4 with WC68A registering the highest IPCA1 score and NE15 registering the lowest IPCA1 score. Since IPCA scores are absolute values, the lowest IPCA1 score was 0.8. Seventeen of the genotypes recorded negative IPCA1 scores, while 19 had positive IPCA1 scores. The genotypes with the negative IPCA1 scores were the higher yielders and included among others, WC64 (-13.8), NAROCOWPEA3 (-12.3), NAROCOWPEA4 (-11.6), NAROCOWPEA1 (-10.2), Ayiyi (-9.6), WC36 (-8.8) and ALEGIXACC2 (-3.4). The genotypes with positive IPCA1 scores were lower yielders and had the highest variation in yield and included 2392 (17.4), NE55 (14), Asontem (10.3), NE37 (9.7), CP1 (9.5) and F2588T2E (8.8). The most interactive and therefore unstable cowpea genotypes were WC68A (IPCA1 score = -18.2) followed by 2392 (IPCA1 = 17) and NE55 (IPCA1 score = 14). The least interactive and therefore, most stable genotype was NE15 (IPCA1 score = 0.8) followed by MU9 (IPCA1 score = 1.3) and SECOW 1T (2.0).

The ranking of genotypes based on cultivar superiority coefficients revealed that the genotypes with the lowest cultivar stability values were Ayiyi, WC64, ALEGIxACC2, NAROCOWPEA1, ACC12 SECOW 3B, ACC12XSECOW3B, NAROCOWPEA3, WC36 and were the most stable genotypes. The genotypes NE15, F2588T2E, CP1, SECOW 1T, NE55 and 2392 had the highest cultivar stability values and were the most unstable as well as low yielding. Based on the cultivar superiority coefficients, the genotype Ayiyi was ranked first in both stability and yield performance and this was followed by WC64, ALEGIXACC2, ACC12 x SECOW 3B, NAROCOWPEA1, ACC12XSECOW3B, NAROCOWPEA3 and WC36, while the genotype NE15 ranked least in both cultivar superiority and mean yield followed by F2588T2E, CP1, SECOW 1T, NE55 and 2392.

The genotypes Ayiyi, WC64 and ALEGIxACC2 also

ranked above the checks in both cultivar superiority coefficient and yield performance.

On the basis of mean yield of the genotypes across the three locations and three seasons, it was observed that the mean yield ranged from 1,206 to 2,069 kg/ha with an overall grand mean of 1,682 kg/ha. Fourteen of the thirtysix genotypes performed above the mean and among others included Ayiyi, WC64, ALEGIxACC2, ACC12 x SECOW 3B, NAROCOWPEA1, ACC12XSECOW3B, NAROCOWPEA3 and WC36. Twelve of the genotypes performed below average and among others including NE15, F2588T2E, CP1, SECOW 1T, NE55, and 2392. The AMMI analysis revealed that, the genotype Ayiyi had the highest mean yield (2,067 kg/ha) followed by WC64 (1,978 kg/ha) and ALEGIxACC2 (1,921 kg/ha), and the same genotypes had the lowest stability values. The genotypes G8 (Ayiyi), G36 (WC64) and (ALEGIXACC2) all ranked above the checks in both mean yield and stability. The general trend in IPCA scores, cultivar stability coefficients and mean yield of cowpea genotypes was that, where the genotype IPCA were negative, their cultivar superiority scores coefficients were very low but such genotypes registered the highest mean yields.

GGE biplot analysis

Best genotypes and cross over interactions

The 'which-won-where' pattern of the GGE biplot was constructed by joining the vertices of the genotypes that were furthest from the biplot origin and the results are presented in Figure 1. The genotypes G8, G36, G6, G1, G11, G19 and G35 were positioned on the vertices of the polygon and showed to have the longest vectors and being the most responsive genotypes. The line joining the vertices is a measure of the Euclidian distance between the genotypes when SVP = 1. The joining of these lines resulted into the formation of a polygon within which all the other 29 genotypes fell. The equality line was then drawn between the lines joining two genotypes from the origin of the biplot. This is a line on which the performance of two genotypes was the same in all environments. The equality line between the genotypes G36 (WC64) and G35 (WC68A) indicated that, genotype G36 was better in the environments MA and AA, and thus the ranking of the genotypes in this mega environment was as follows: G36 > G17 > G35; whereas genotype G8 was better in the environments MAA, MB, SA and AAA. The overall order of ranking of the best genotypes in all environments was as follows: G8 (Ayiyi) > G36 (WC64) > G6 (ALEGI*ACC2) > G16 (NAROCOWPEA1) > G3 (ACC12*SECOW3B) > G17 (NAROCOWPEA3). The genotypes G25, G9 and G11 were located on the line that connected G1 and G19. The ranking of the poorest genotypes in all environments was G1 > G25 > G26 > G9

Table 10. AMMI IPCA scores and genotype superiority for genotype mean yield (kg/ha).

Genotype	Superiority	Means	Rank	IPCAg1	IPCAg2
Ayiyi	61200	2069	1	-9.6	-17.9
WC64	85047	1980	2	-13.8	-8.4
ALEGI x ACC2	93253	1921	3	-3.4	-18.8
NAROCOWPEA1	110630	1891	4	-10.2	-0.4
ACC12 x SECOW 3B	121371	1863	5	3.1	-11.3
NAROCOWPEA3	141432	1871	6	-12.3	6.4
WC 36	164377	1767	7	-8.8	-5.9
SECOW 4W * SECOW 5T	181173	1773	8	4.5	1.1
NE 23	200636	1786	9	3.2	3.5
MU 9	202195	1741	10	1.3	-4.5
NAROCOWPEA4	203379	1735	11	-11.6	0.8
WC 16	225353	1703	12	8.2	-9.6
NE 37	248806	1731	13	9.7	3.1
Secow 4W	251711	1684	14	-12.3	9.5
MU 9A	252133	1675	15	2.9	7.1
IT 889	262172	1602	16	-4.9	3.1
WC 63	286872	1577	17	-4.7	-2.2
Ebalet * NE 51	308686	1574	18	-8.1	2.7
Alegi * SECOW 5T	309535	1518	19	-2.4	-5.8
Sunshine 2S	313475	1562	20	6.8	-7.0
ACC12 x SECOW 5T	324920	1564	21	12.7	-4.8
ACC 2 * SECOW 2W	327535	1521	22	-2.2	3.8
IT 2841 * BROWN	356400	1492	23	3.5	-1.1
WC 37	369051	1524	24	-6.5	-3.9
NE 48	373567	1470	25	-3.2	-4.6
NE 39 * SECOW 4W	393394	1484	26	7.2	3.6
Asontem	417392	1441	27	10.3	-4.8
WC 68A	422950	1496	28	-18.2	12.9
Secow 5T	431447	1448	29	3.6	11.9
NE 20	433986	1429	30	4.1	8.5
2392	453825	1498	31	17.4	-0.8
NE 55	491225	1409	32	14.0	1.0
Secow 1T	500809	1430	33	2.0	11.6
CP 1	534352	1327	34	9.5	-0.5
F2588T2E	560577	1342	35	8.8	13.0
NE 15	648444	1206	36	-0.8	8.7

> G11 > G19.

The equality line divided the polygon into four sectors. The first sector consisted of the environments MAA, AAA, MB and SA, while the second sector consisted of environments AA and MA, the third environment with SB and the fourth environment with SAA were categorized as minor environments. The genotype, G8 performed best in the first sector (MAA, AAA, MB and SA), while G16 was the best genotype in the environment sector formed by AA and MA, but genotype G31 was only best in the environment SB. The change in the ranking of the genotypes in each environment or group of environments depicted the presence of cross over interaction, suggesting that the genotype G16 was specifically

adapted to environments AA and MA, while genotype G31 was specifically adapted to environment SB. The genotype G16 could be thought of as being specifically adapted to season A, since MA and AA are 'season A' environments while the genotype G8 was widely adapted since it performed best in both seasons A and B. G19 was the poorest genotype in all environments followed by G1, G9 and G25 since they positioned on the vertices of the biplot on the negative side of the origin.

Mean yield performance and stability of genotypes

The average-environment coordination view (AECV)

Which Won Where/What

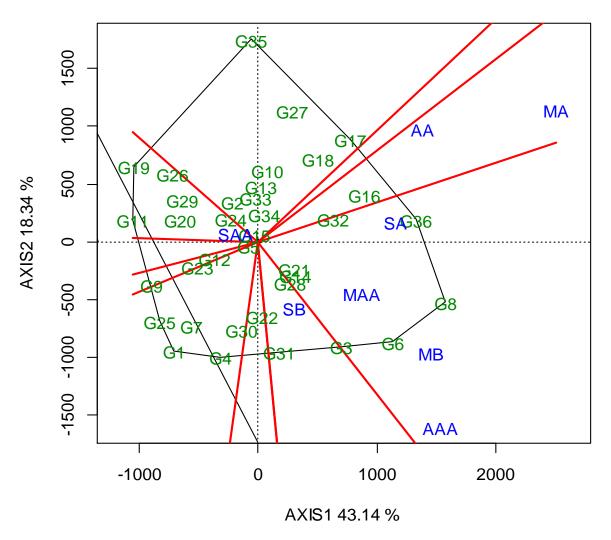


Figure 1. The "which-won-where" polygon view of the GGE biplot. PC1=43.14%, PC2=18.34% Total=61.5%, Scaling=0, Tester-centered G+GE, SVP=GH column-metric preserving. AA=Arua season 2017A, MA= MUARIK season 2017A, SA= Serere season 2017A, MB = MUARIK season 2017B, SB= Serere season 2017B, MAA= MUARIK season 2018A, SAA= Serere season 2018A, AAA= Arua season 2018A.

showing mean performance and stability of 36 genotypes across eight environments is presented in Figure 2. The AECV biplot was used to rank genotypes by their mean performance and stability. In this biplot, the x-axis is the performance line and it passes through the origin of the biplot with an arrow indicating the positive end of the axis and ranked genotypes according to their mean performance. The y-axis also passes through the origin of the biplot and is perpendicular to the x-axis and measured the stability of the genotypes. The projection of genotypes onto the AEC abscissa (x-axis) represented the main effect of the genotypes. The AEC_a ranked the genotypes according to their mean performance. The ranking of genotypes onto the AEC_a was highly correlated

to the genotype main effect. Therefore, the AEC_a approximated the contribution of each genotype to the main effect of the genotypes and the AEC ordinate (Y-axis) expressed the genotype's contribution to the GxE and thus, it represented genotypic stability.

Based on the magnitude of variation (GxE) across environments, the genotypes with longer markers had higher variation than those with shorter markers. Therefore, the genotype G35 had the longest projection to the AEC_a and the greatest contribution to the GxE. Based on the magnitude of the projections to the AEC_a, the genotypes ranked as; G35, G5, G4, G17 and G27 in order of their contribution to the interaction of yield with environments.

Mean vs. Stability

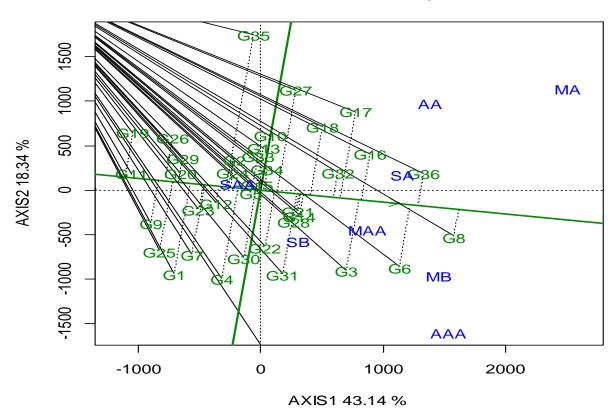


Figure 2.The average-environment-coordination view showing mean performance and stability of 36 genotypes across eight environments. AA=Arua season 2017A, MA= MUARIK season 2017A, SA= Serere season 2017A, MB = MUARIK season 2017B, SB= Serere season 2017B, MAA= MUARIK season 2018A, SAA= Serere season 2018A, AAA= Arua season 2018A.

The genotype G8 (Ayiyi) had a short projection to the AEC_a and thus contributed less to the GxE. However, the genotype G8 (Ayiyi) was the furthest from the origin of the biplot in the positive direction of the AEC_a and hence had the greatest contribution to the genotype main effect. On the other hand, the genotype G19 was the furthest from the origin of the biplot in the negative direction of the AEC_a , implying that it contributed least to the genotype main effect.

The most stable and high yielding genotype was one furthest to the positive side of the performance line and with the shortest marker. Based on both mean performance and stability, the genotype G8 (Ayiyi) was the most stable and high yielding. This was followed by the genotypes G36 (WC64), G6 (ALEGIXACC2), G16 (NAROCOWPEA1), G3 (ACC12xSECOW3B), G17 (NAROCOWPEA3), G32 (WC36), G14 (MU9) and G18 (NAROCOWPEA4). The genotypes G8 (Ayiyi), G36 (WC64), and G6 (ALEGIXACC2) were all ranked above the checks in both mean yield and stability. Genotypes G34, G15, G24, and G33 were considered as average yielders because the genotypes at the origin of the

biplothave average stability and performance. Genotypes close to the performance line were considered more stable than those furthest from it. The genotype G11 (F2588T2E) was on the AEC ordinate and very stable across localities but furthest from the ideal genotype or situated on the negative side of the AEC ordinate implying least mean performance. Such a genotype may therefore not be more desirable compared to, for example, genotype G5 (ALEGIxSECOW5T) which was off the AEC ordinate but close to the ideal genotype.

Ranking of genotypes relative to an ideal genotype

Figure 3 shows the GGE biplot that was used to rank genotypes by their mean performance and stability relative to an ideal genotype in a number of environments. In this biplot, the x-axis is referred to as the average tester coordinate (ATC) x-axis or the performance axis and the y- axis is the stability axis (ATC) y-axis. An ideal genotype is one that has both high yield capacity and high stability. Based on these principles,

Ranking Genotypes

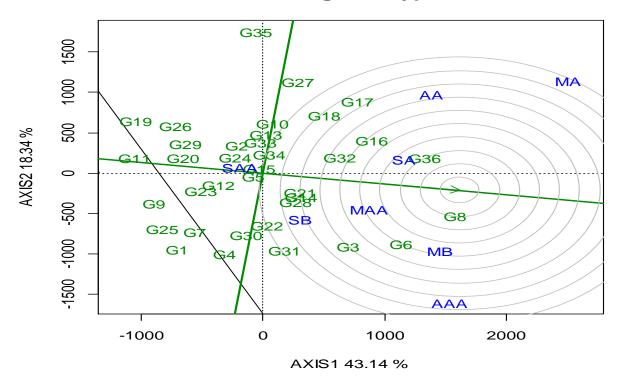


Figure 3. The comparison biplot (AEC) for ranking genotypes relative to an ideal genotype. AA=Arua season 2017A, MA= MUARIK season 2017A, SA= Serere season 2017A, MB = MUARIK season 2017B, SB= Serere season 2017B, MAA= MUARIK season 2018A, SAA= Serere season 2018A, AAA=Arua season 2018A.

there was no ideal genotype but the genotype G8 (Ayiyi) approximated the ideal genotype since it fell closest to the smallest inner circle, and the desirable genotypes were G36 (WC 36), G6 (ALEGXACC2), G16 (NARO COWPEA1), G3 (ACC12xSECOW3B), G17 (NAROCOWPEA 3), G32 (WC16), G18 (NAROCOWPEA4) and G14 (MU9).

DISCUSSION

In this study, the significant differences observed among the genotypes were expected since these were diverse collections from all parts of Uganda, International Institute Tropical Agriculture (IITA) Nigeria, National Agricultural Research Organization (NARO) and Ghana with diverse genetic backgrounds. Rubaihayo and Rusoke (1994) collected germplasm from all over Uganda, breeding lines from international programs, for instance the CGIAR centers and found highly significant differences among the lines. The presence of GxE in cowpea has also been reported by Asio et al. (2005) and Santos et al. (2015). From the present study, season effect contributed 52.3% of the total variation observed in cowpea yield, followed by localities that contributed

25.1%. Agbahoungba et al. (2016), in a trial involving 72 genotypes of cowpea tested in the same locations in the 2015/2016 seasons obtained similar results of the effect of GxE on cowpea grain yield. In this study, the season effect on grain yield was therefore, more profound than the location effect and this is contrary to the finding of Dehghani et al. (2008) and Agbahoungba et al. (2016) who observed a more profound effect of location than seasons. The AMMI analysis result showed that a large environmental sum of squares explained the diversity in the environmental conditions to which the genotypes were subjected as well as the inconsistent performance of the genotypes across those environments. This also explained the rank changes in the performance of the genotypes. The environmental effect was generally larger than the genotype main effect and the GxE effect but the most important sources of variations were those due to genotype and GxE. The trends observed in this study were very similar to the findings of other workers (Rad et al., 2013; Orawu et al., 2017), who observed higher contribution of environmental effect contribution of genotype effect to the total variation in yield.

A further understanding of the genotypes was enhanced with the construction of the polygon view of the

GGE biplot and was a useful tool for identifying the presence of cross over interaction, comparison of pairs of genotypes, identification of specifically genotypes and elucidation of the best or poorest in each environment or environments. In this biplot, genotypes G8, G36, G6, G1, G11, G19 and G35 were positioned on the vertices of the polygon and showed to have the longest vectors and being the most responsive genotypes. Some of the genotypes in this study responded well when grown in the first season and others in the second season of each year, with the overall performance of the genotypes being better in the second season. According to Orawu et al. (2017), mega-environment differentiation may be due to variations in weather pattern or soil types resulting in differences in the performances of crops. Yan and Tinker (2005) noted that test environments were dynamic factors that fluctuate considerably between years or seasons. The genotype cross-over interaction was also detected in this study because the ranking of the genotypes changed.

In this study, the AMMI analysis revealed that G8 (Ayiyi) had the highest mean yield (2,067 kg/ha) followed by G36 (WC64) (1,978 kg/ha) and G6 (ALEGIXACC2) (1,921 kg/ha) and the lowest stability values. These genotypes were considered to exhibit static stability or type I stability. Static stability is only useful to the breeder if it is associated with high yield. Accordingly, genotypes with the lowest stability values are the most stable.

In order to identify the most stable and high yielding genotype (widely adapted genotype), the average environment coordination view of the GGE biplot was used. The AEC was constructed using the mean performance of genotypes and their stability values. The AEC was genotype-metric preserving and consisted of both the stability and performance axes. In the biplot constructed, it showed that the genotype G11 (F2588T2E) was on the AEC ordinate and very stable across locations but furthest from the ideal genotype (from the center of the concentric circle or on the negative side of the AEC ordinate) implying least mean performance. Such a genotype might not be desirable compared to the genotype G5 (ALEGIxSECOW5T) which was off the AEC ordinate but closer to the ideal genotype. It was acknowledged that the genotype G11 (F2588T2E) was only consistent in its poor performance. Yan and Tinker (2006) used the average coordination view to evaluate Ontario winter wheat in Canada and were able to identify the most consistent genotypes, discriminatory and representative environments.

Conclusion

Overall, the analyses in this study found grain yield in cowpea to be greatly influenced by the main effects of genotypes, environment and the interaction between the genotype and the environment. The GGE biplot and the AMMI stability values were congruent in ranking the genotypes based on their mean yield and stability and complimented each other in determining the mean performance and stability of genotypes. The general trend in IPCA scores, cultivar stability coefficients and mean yield of cowpea genotypes was that, where the genotype IPCA scores were negative, their cultivar superiority coefficients were very low, but such genotypes registered the highest mean yields. The change in the ranking of the genotypes in each environment or group of environments depicted the presence of cross over interaction, suggesting specific adaptation of some genotypes to some environments.

The AMMI analysis also revealed that the genotype Ayiyi had the highest mean yield (2,067 kg/ha), contributed less to the GxE but had the greatest contribution to the genotype main effect. This was followed by WC64 (1,978 kg/ha) and ALEGIxACC2 (1,921 kg/ha) and the best stability values and ranked above the checks in both mean grain yield performance and stability and were superior to all local varieties.

The genotypes Ayiyi, WC64, ALEGIxACC2 ranked above the checks and other local varieties in both mean grain yield and stability. Therefore, they could be advanced to the national performance trials. The GGE and the AMMI biplots should be used concurrently to help understand the mean performance and stability of genotypes since the two complement each other. None of three locations showed mega environment associations. Genotype interactions showed differing responses to the two rainy seasons but additional years of data will be needed to determine if different genotypes should be recommended for the two different seasons.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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