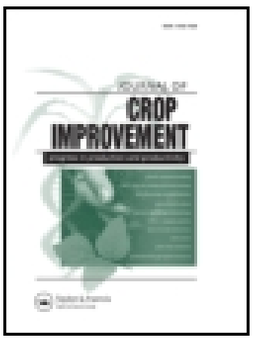

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Genetic parameter estimation and selection in advanced breeding population of white Guinea yam

Prince Emmanuel Norman [a,b,c], Pangirayi B. Tongoona[c], Agyemang Danquah[c], Eric Y. Danquah[c], Paterne A. Agre [b], Afolabi Agbona[b], Robert Asiedu[b], and Asrat Asfaw [b]

[a]Sierra Leone Agricultural Research Institute, Freetown, Sierra Leone; [b]International Institute of Tropical Agriculture, Ibadan, Nigeria; [c]West Africa Centre for Crop Improvement, College of Basic and Applied Sciences, University of Ghana, Accra, Ghana

ABSTRACT

White Guinea yam (*Dioscorea rotundata* Poir.) is an important tuber crop grown extensively in tropical regions of West African yam belt. Tuber yield, dry matter content, and tolerance to yam mosaic virus are key traits used for identification and selection of superior varieties for commercial deployment. In this study, we estimated genetic parameters for fresh tuber yield, tuber dry matter content, and quantitative field tolerance to yam mosaic virus in 49 clones grown in multi-environment trials (METs). We conducted genomic prediction involving 6337 single nucleotide polymorphisms (SNPs) and phenotypic field evaluation of data collected on the three traits from four sites. Additive genetic and non-genetic factors contributed significantly to phenotypic variation of studied yam traits in METs but to varying degrees. The non-genetic effects were relatively high for most of the measured traits. Narrow-sense heritability values were low (<0.30) for all studied traits. Further analysis of the performance of the clones at test sites with additive main effects and multiplicative interaction (AMMI) analysis exhibited significant genotype by environment interactions (GEI) for the three traits. The AMMI identified TDr10/00412, TDr11/00055, and TDr09/00135 clones with lowest mean trait stability index and outstanding performance for fresh tuber yield (t ha^{-1}), tuber dry matter, and mosaic virus resistance across sites. The elite clones identified could serve as useful source of alleles for the genetic improvement of the crop and possibly considered for release to farmers.

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AMMI stability; genotype by environment interaction; genotype by trait interaction; genetic parameter estimate; yam

1. Introduction

Yam (*Dioscorea* spp.) is a vegetatively propagated crop comprising >600 species (Burkill 1960), of which 11 are widely cultivated for food and industrial applications globally. White Guinea yam (*D. rotundata*) is among the widely cultivated species that serve as a valuable source of food and income to over 300 million people in Africa (Alabi et al. 2019). The global

CONTACT Prince Emmanuel Norman pnorman@wacci.ug.edu.gh

yam production is estimated at 73 million tons, with West Africa accounting for more than 93% of the total yam production (Aighewi et al. 2020).

Despite its importance, the average yield of most species of high economic value is low, estimated at approximately 20% of the attainable yield potential of 40 t ha^{-1} (Bassey and Akpan 2015). Although the average fresh tuber yield of yam reportedly increased from 7.8 to 8.8 t ha^{-1}, the production increment was attributable to corresponding increase in total production area from 1.2million ha in 1961 to 8.9million ha in 2019 (FAOSTAT 2020). This scenario is representative of the strong growth in sub-Saharan Africa (SSA) agricultural output that accrued mainly from area expansion and intensification of cropping systems relative to large-scale improvement in productivity (Brink and Eva 2009; NEPAD 2014). These efforts resulted in a slow-paced increase in yield per hectare that did not match the rapid global population growth (Heerink 2005). Moreover, biotic and abiotic stresses are noted to contribute to low yields and poor market-quality tubers of yams (Lebot 2009). Yam diseases, such as yam anthracnose and yam mosaic virus, cause severe yield losses and genetic erosion, and restrict international movement and exchange of germplasm (Egesi, Onyeka, and Asiedu 2007).

The potential of yams for sustainable food supply and wealth creation can be unlocked through a consolidated effort, including the development and deployment of robust varieties that maximize productivity (yield) and quality (nutritional and industrial quality) across various production environments. Yam varieties exhibit diverse attributes and performances across production environments. Tuber yield, dry matter content, and mosaic virus resistance are important selection criteria in yam breeding. Diverse breeding lines are extensively screened and tested across diverse environments (different sites and/or years) prior to choosing the best parents for crosses and the release of superior clones for commercial deployment. Not all genotypes perform consistently across environments (Kang 1998). The inconsistent performance between genotypes across environments, which is known as genotype by environment interaction (GEI), leads to either change in the ranking of genotypes (crossover GEI) or changes in trait values of genotypes without genotypic rank changes (non-crossover GEI) (Crossa 2012). The presence of GEI in breeding trials makes identification of superior genotypes based on mean performance across environments difficult, particularly when it is of crossover type (Kang 1998).

Several analytical techniques have been developed and utilized to assess the performances of genotypes in plant breeding experiments (Yan and Kang 2003; Smith, Cullis, and Thompson 2005; Malosetti, Ribaut, and van Eeuwijk 2013). The analytical techniques could involve univariate, bivariate and multivariate analyses, with and without accounting for genetic relationships among the test genotypes. Best linear unbiased predictor (BLUP) in mixed models using Residual Maximum Likelihood (REML) method, which

accounts for genetic relationship matrices, is among the advanced techniques utilized in many crop breeding trials to determine the breeding values and genetic parameters that guide the selection of elite genotypes in METs (Smith, Cullis, and Thompson 2005). The utilization of these analytical techniques for data exploration depends on the number of variables measured, how the variables are measured, explanation and contributions derived to enhance selection decisions.

The analytic techniques that incorporate relationship matrices dissect the genetic architecture of complex traits and aid in successful implementation of breeding strategies and designs (Muñoz et al. 2014). Relationship matrices are utilized for estimation of expected fraction of genes identical by state (genomic relationship matrix G), actual fraction of DNA shared by descent (additive genetic relationship matrix A), or fraction of alleles shared for loci affecting trait(s) of interest (relationship matrix T) (Wright 1922; vanRaden 2007). These matrices are useful for managing genetic diversity (Caballero and Toro 2002), genomic selection, and parentage testing (Dodds, Tate, and Sise 2005).

Models that utilize genomic data for determining genetic relationships predict genetic effects more accurately compared with those that utilize expected relationships from pedigrees (vanRaden 2007). Analytical models that incorporate relationship matrices have been effectively utilized in many crops to select subsets of promising genotypes as parents in crosses. These models have helped generate a new set of recombinant progenies or identify superior genotypes for further testing and/or possible release as new varieties. However, such models have seldom been used in analyzing data from yam breeding trials to select superior clones for commercial deployment or use as parents of crosses (Darkwa et al. 2020a). The objectives of this study were to: (1) estimate genetic parameters in white yam advanced breeding trials using molecular marker information; and (2) determine the magnitude of GEI and use it effectively to improve important traits in white yam.

2. Materials and methods

2.1 *Plant materials and trial design*

Plant materials included 49 white Guinea yam clones that were evaluated at four sites in Nigeria (Ibadan, Abuja, Ubiaja and Ikenne) in the 2017/2018 cropping season. Of the 49 clones, three were standard varieties and 46 elite breeding lines from the yam breeding program of the International Institute of Tropical Agriculture (IITA). The trial sites represented three agro-ecological zones for yam in Nigeria: forest, forest-savannah transition, and the southern Guinea savannah. The trial at each site was laid out in a 7 × 7 alpha lattice design with two replicates. Healthy tubers of each genotype were cut into setts

of 200 g each, pre-treated with a mixture of 70 g Macozeb, 75 mL Chlorpyrifos and 10 L tap water for 5 min and dried for 20 h under shade to heal wounds and prevent rotting of cut surfaces of setts caused by pathogenic organisms. The setts were planted in holes made on the crest of mounds at 1 m × 1 m spatial arrangement, giving a population of 10,000 plants ha^{-1}. The plants were raised without using stakes and external fertilizer. The trial plots were hand-weeded to keep the plots weed-free throughout the crop cycle.

2.2 *Phenotypic data collection*

The fresh tuber yield, tuber dry matter content, and yam mosaic virus were measured based on protocols in yam ontology (http://www.cropontology.org/ontology/CO_343/Yam). The data were collected with an Android Galaxy Tab A 2016 using the field book app (Rife and Poland 2014). The disease severity score values for yam mosaic virus (YMV) were converted to percentages and then used to estimate the area under the disease progress curve (AUDPC), as described by Forbes, Pérez, and Andrade Piedra (2014). The formula for computing AUDPC is shown below:

$$\mathrm{AUDPC} = \sum_{i=1}^{n-1} \left(\frac{y_i + y_{i+1}}{2} \right) (t_{i+1} - t_i)$$

where y_i = disease severity of the i^{th} observation, t_i = time (days) for the i^{th} observation, and n = total number of observations. The susceptibility scale values of YMV were estimated by first calculating the resistance-scale values, as described by Forbes, Pérez, and Andrade Piedra (2014) as follows:

$$S_x = S_y \left(\frac{D_x}{D_y} \right)$$

where S_x= estimated susceptibility-scale value, S_y = the assigned susceptibility scale value, D_x= observed disease score (AUDPC value) for the studied clones and D_y= observed disease score (AUDPC value) for the standard variety. The quotient of the assigned susceptibility value and the resistance measure of the standard variety (AUDPC value) was used to obtain a constant. The resistance value of each clone was then multiplied by the constant to obtain the susceptibility value of the clone.

2.3 *Molecular data*

Young fresh leaves were collected from three plants per clone and lyophilized before DNA extraction. Genomic DNA was extracted using a modified

CTAB protocol (Dellaporta, Wood, and Hicks 1983). DNA quality and concentration were assessed using both agarose gel and NanoDrop, following Aljanabi and Martinez (1997). Fifty micro liters (50 µL) of concentrated DNA from each sample was sent to Diversity Array Technology (DArT) Pty Ltd, Canberra, Australia, for sequencing. Raw HapMap file received was converted to a variant call format (VCF) for the analysis, using PERL programming language and Tassel (Bradbury et al. 2007; Elshire et al. 2011). The VCF file was filtered for missing values and polymorphic SNPs, with quality parameter and a call rate of >80%, depth >95%, and minor allele frequency of >5%. After filtering, 6337 polymorphic SNP markers were retained and used to construct genomic relationship matrix in the R (De Mendiburu 2019) package rrBLUP (Endelman 2011). The missing data for markers were imputed using beagle 4 (Browning and Browning 2007). SNP distribution and density along the different chromosomes were assessed using CMplot R package (Yin 2019). The VCF file with the final SNP markers was converted to the additive format in 0, 1, 2, where zero = genotype with no minor allele, 1 = heterozygote and 2 = homozygote minor allele count at each locus, using recodeA function implemented in plink (Purcell et al. 2007). The deviation of 1 from gene content or minor allele frequency (MAF) matrix was obtained to generate scores of −1, 0, 1 to be used in rrBLUP to construct the genomic relationship G-matrix.

2.4 *Data analysis*

Different analyses were employed to dissect the genetic and non-genetic factors influencing the performance of yam clones in the multi-environment trial dataset. The data collected were first subjected to a linear mixed model by residual maximum likelihood (REML) procedure (Patterson and Thompson 1971) to estimate the variance parameters and the empirical Best Linear Unbiased Predictions (E-BLUPs) for random effects using ASReml-R 4 (Butler et al. 2018). The univariate Genomic-BLUP model, including the random interaction term between the genomic effect of the i^{th} clone and the j^{th} site, is represented by the model described in Borgognone et al. (2016) and Smith and Cullis (2018), which is as follows:

$$y_{ij} = X_{\beta} + Z_p u_p + Z_g u_g + e_{ij}$$

where y_{ij} is the data vector of the response variable of the i^{th} clone in the j^{th} site (i =1,2, ...,I, j =1,2, ...,J), with Nj plots for site j; β is the vector of fixed effects associated with the corresponding design matrix (X), including the site main and site-specific design-based replication effects. The term u_p is a vector of random non-genetic (or peripheral) effects associated with site-

specific field-blocking structures (block within replication) used to capture extraneous variation, with the corresponding design matrix Zp; u_g is a vector of random genetic effect of each genotype in each trial site with associated design matrix Z_g, and **e** is the vector of combined residuals for individual trials. The vectors of random effects u_p, u_g and e are assumed pairwise independent with Gaussian distribution, with a mean of zero. The variance matrices for u_p, u_g and **e** were as described in Borgognone et al. (2016) and Smith and Cullis (2018). The random genotype effect (u_g) in the model comprised the clone effects nested within sites and hence referred to as clone by site effect. The random genetic effect was then partitioned into additive genetic component associated with the covariance structure proportional to genetic relationships derived from SNP markers and non-additive (or residual) genetic effect explained by individual identity following the approach described in Borgognone et al. (2016) and Ovenden et al. (2018), which is as follows:

$u_g = u_a + u_e$

with variance matrix var(u_g) = $G_a \otimes G + G_e \otimes Im$, where Ga and Ge are the additive and non-additive genetic variance matrices across sites, G is genomic relationship matrix, Im is identity matrix, u_a is the additive genetic component associated with the covariance structure proportional to genetic relationships derived from SNP markers, and $u_e$is the non-additive genetic effect explained by individual identity. The genetic relationship matrix G was calculated from SNP markers for the genotypes using the procedure described by vanRaden (2008). Accordingly, $G = \frac{MM'}{\sum^2 p_i q_i}$, where M is a n × m matrix (n = number of clones, m = number of marker loci), which specifies SNP genotype coefficients at each locus. The coefficients of the i^{th} column in the M matrix are $(0 - 2p_i)$ for A_1A_1, $(1 - 2p_i)$ for A_1A_2, and $(2 - 2p_i)$ for A_2A_2, where qi and pi are the frequencies of allele 1 (A_1) and allele 2 (A_2) at locus i, respectively.

From the variance component analysis, following genetic parameters were determined: additive genetic variance, non-additive genetic variance, non-genetic variance associated with among-plots and within-plot effects, proportion of total genetic variances that was additive, trait heritability ((both narrow-sense (h^2) and broad-sense (H^2)), genotypic coefficients of variation (GCV), phenotypic coefficient variation (PCV), expected genetic advance (GA), and genetic advance as percentage of mean (GAM). The GCV and PCV were determined using the following formulae described in Burton and Devane (1953):

$$GCV = \frac{\sqrt{\sigma^2 g}}{\bar{x}} \times 100$$

$$PCV = \frac{\sqrt{\sigma^2 p}}{\bar{x}} \times 100$$

where σ^2g is genetic variance and σ^2p is phenotypic variance for the trait from the final model in REML analysis, and $\bar{x}$ = trait mean. The GCV and PCV values were categorized using the technique proposed by Deshmukh, Basu, and Reddy (1986) as follows:

values <10% = low, values 10% to 20% = medium and values >20% = high.

Narrow-sense (h^2) and broad-sense (H^2) heritability values were determined using the following formulas used by Robinson, Comstock, and Harvey (1949):

$$h^2 = \frac{\sigma^2 \mathrm{a}}{\sigma^2 \mathrm{p}} \times 100$$

$$H^2 = \frac{\sigma^2 \mathrm{g}}{\sigma^2 \mathrm{p}} \times 100$$

where σ^2a, σ^2g, and σ^2p are the additive genetic, total genetic and phenotypic variances, respectively. The h^2 and H^2 values between 0% and 30% were regarded as low; those between 30% and 60% medium, and those >60% high. The expected genetic advance (GA) and the expected genetic advance as percent of population mean (GAM) were estimated for comparison of the extent of predicted genetic gain for traits considered for selection of superior clones based on the following equations given by Shukla et al. (2006):

$$\mathrm{GA} = \mathrm{K} \times \mathrm{H}^2 \times \sigma \mathrm{p}$$

$$\mathrm{GAM} = \frac{GA}{\bar{X}} \times 100$$

where K is the selection differential, which = 2.06 at 5% selection intensity; H^2 is broad-sense heritability; σp is the phenotypic standard deviation; and $\bar{X}$ is population mean. The GAM values <10% were classified as low, those between 10% and 20% as moderate and those >20% as high.

The three traits were further subjected to GEI analysis using AMMI and GGE-biplot techniques. The AMMI model stability statistics were computed using R (R Core Team 2019) package Agricolae (De Mendiburu 2019). The AMMI stability value (ASV) was estimated for each clone based on the contributions of the interaction principal component axis (IPCA1 and IPCA2) scores to the interaction sum of squares for the trait. The ASV was

estimated as follows using the procedure implemented in Purchase, Hatting, and van Deventer (2000):

$$\mathrm{ASV} = \sqrt{\left[\frac{\mathrm{IPCA1}_{\mathrm{sumofsquares}}}{\mathrm{IPCA2}_{\mathrm{sumofsquares}}}\ (\mathrm{IPCA1}_{\mathrm{score}})\right]^2 + \ (\mathrm{IPCA2}_{\mathrm{score}})^2}$$

where IPCA1 is the interaction principal component axis 1, IPCA2 is the interaction principal component axis 2, and $\frac{\mathrm{IPCA1}_{\mathrm{sumofsquares}}}{\mathrm{IPCA2}_{\mathrm{sumofsquares}}}$ is the weight given to the IPCA1 by dividing the IPCA1 sum of squares by the IPCA2 sum of squares (Farshadfar, Mahmodi, and Yaghotipoor 2011). The trait stability index (TSI) was estimated as the sum of the ranking based on genotype mean trait value and ranking based on the AMMI stability score (Bose et al. 2014; Tumuhimbise et al. 2014).

$$\mathrm{TSI} = \sum_{i=1}^{n}(\mathrm{RASV} + \mathrm{RY})$$

where RASV = rank of the genotypes based on the AMMI stability value; and RY = rank of the genotypes based on mean trait value across environments (ascending order for traits, with lower values considered superior and descending order for traits, with higher values considered superior); i is trait (i =1,2, … .,n) and n is the total number of traits or observations.

The GEI analysis was further extended to GGE biplot model that dissects simultaneously the genotype main (G) and genotype × environment (GE) effects in the MET dataset, following the procedure described in Yan et al. (2000) and Yan and Kang (2003). The "which won-where" polygon representation of GGE biplot was explored for identification of best and worst genotypes in a specific environment or a mega-environment (Yan et al. 2000; Yan and Kang 2003). The discriminating power of the test environments was determined using GGE biplots based on average environment coordinate (AEC) (Yan and Kang 2003). The genotype-by-trait biplot was generated with GGE biplot analysis according to Yan and Kang (2003).

3. Results

3.1 *Quantitative genetic parameter estimates for measured traits in dataset*

The mean values, ranges and associated genetic parameter estimates for the measured traits are presented in Table 1. The genetic and non-genetic effects contributed substantially to the trait variation in the current set of materials but to varied degrees. The variation attributable to non-genetic (environmental) was

Table 1. Estimated genetic and non-genetic parameters[†] of agronomic and quality traits from multi-environment trials of white Guinea yam elite clones.

Trait[‡]	Mean± SD[§]	Range	σ^2_a	σ^2_{rg}	σ^2_{ng}	% σ^2_a	σ^2_g/σ^2_{ng}	h^2	H^2	GCV	PCV	GA	GAM
YMV	2.86 ± 0.19	2.16–3.64	0.03	0.09	0.09	25	1.33	0.15	0.58	12.1	16.0	0.5	17.5
TBRYLD	10.33 ± 1.96	6.14–15.61	1.73	3.53	8.52	33	0.62	0.13	0.38	22.2	35.9	2.9	28.1
DMC (%)	31.96 ± 1.47	27.61–35.96	0.05	4.22	7.61	1	0.56	0.004	0.36	6.5	10.8	2.6	8.1

[†]σ^2_a, additive genetic variance; σ^2_{rg}, residual or non-additive genetic variance; σ^2_{ng}, non-genetic variance; %σ^2_a, percent of total genetic variance that is additive; σ^2_g/σ^2_{ng}, ratio of total genetic variance to non-genetic variance; h^2, narrow-sense heritability; H^2, broad sense heritability; GCV, genotypic coefficient of variation; PCV, phenotypic coefficient of variation; GA, genetic advance; and GAM, genetic advance as percentage of mean.

[‡]YMV: yam mosaic virus; TBRYLD: fresh tuber yield; and DMC: dry matter content.

[§]SD, Standard deviation.

higher than the genetic variation for all traits, except yam mosaic virus. The percentage of total genetic variance (that is, additive and non-additive (dominance, epistatic)) varied across the measured traits. The non-additive genetic variance component was highest for fresh tuber yield, tuber dry matter content and yam mosaic virus. The additive genetic variance was negligible for tuber dry matter content and yam mosaic virus compared to that for fresh tuber yield. The narrow-sense heritability estimates were low (<0.30), whereas the broad-sense heritability estimates were intermediate (0.36–0.58) for all traits. Phenotypic coefficient of variation (PCV) was slightly higher than the genotypic coefficient of variation (GCV) for all the traits. Fresh tuber yield (22.2%) had high GCV, whereas yam mosaic virus (12.1%) had medium and dry matter content (6.5%) had low GCVs. The PVC for fresh tuber yield was 35.9% (high), whereas that for yam mosaic virus was 16.0% and for dry matter content 10.8%, both considered medium PCV values. Genetic advance as percent of the mean (GAM) ranged from 8.1% to 28.1%. Fresh tuber yield (28.1%) exhibited high GAM value, whereas yam mosaic virus susceptibility scale (17.5%) and dry matter content (8.1%) had medium and low GAM values, respectively.

3.2 *Unraveling GEI of key traits for yam breeding*

Tuber dry matter, yam mosaic virus susceptibility and fresh tuber yield were used to further assess the response of clones at test environments using AMMI and GGE biplot techniques. The AMMI analysis of variance exhibited highly significant ($P = 0.001$) main effects of clones and environments for all three key traits. The GEI was statistically significant for tuber dry matter ($P < 0.05$), for fresh tuber yield ($P < 0.01$) and reaction to yam mosaic virus infestation ($P < 0.001$) (Table 2). The test environments accounted for the highest proportion of the total sum of squares for fresh tuber yield, whereas main effect of clones accounted for the highest proportion of the total sum of squares for dry matter content and reaction to yam mosaic virus. For fresh tuber yield, the environment contributed 46.14%, compared to 29.32% and 24.54% contributions by genotype and GEI, respectively. The IPC1 accounted for 49.98% of the interaction sum of squares, with IPC2 accounting for 35.00%. For dry matter content, genotypic effect accounted for 39.44% of the variation, whereas the environment accounted for 25.95% and the GEI accounted for 34.61%. The IPC1 accounted for 42.03% of the interaction sum of squares, with IPC2 accounting for 35.32%. For yam mosaic virus severity, the main effect of clone accounted for 48.60%, whereas the environmental effect was 26.76% and the GEI was 24.64%. The IPC1 accounted for 43.09% of the interaction sum of squares, with IPC2 accounting for 30.10%.

Based on the AMMI stability index, TDr09/00135, TDr10/00310, TDr11/00055, and TDr10/00412 were identified as the best clones expressing high and stable genotypic values for fresh tuber yields (Table 3). Clones TDr11/

Table 2. Additive main effects and multiplicative interaction (AMMI) analysis of variance for fresh tuber yield, dry matter content, and yam mosaic virus severity.

		Fresh tuber yield		Dry matter content		Yam mosaic virus	
Source[†]	Degrees of freedom	Sum of squares	Mean squares	Sum of squares	Mean squares	Sum of squares	Mean squares
IPC1	50	5976.86	119.54***	4149.06	82.98***	67.01	1.34***
IPC2	48	4184.85	87.18***	3486.86	72.64***	46.81	0.97***
Genotype(G)	48	1760.83	36.68***	1568.46	32.68***	36.62	0.763***
Environment(E)	3	2770.54	923.51***	1032.13	344.04***	20.16	6.72***
REP(ENV)	52	1019.46	19.60***	723.97	13.92***	10.80	0.21***
G × E	141	1473.39	10.45**	1376.65	9.76*	18.57	0.13***
Residuals	141	980.54	6.95	956.54	6.78	9.58	0.07

*, **, *** = significant at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively.
[†]IPC1 = interactive principal component 1; IPC2 = interactive principal component 2; REP(ENV) = replications within environments; G × E = genotype by environment interaction.

01408, TDr10/00913, TDr11/00291, TDr10/00282, and TDr09/00135 demonstrated high and stable tuber dry matter content, whereas TDr89/02665, TDr10/00412, TDr09/00122, TDr09/00052 and TDr11/00055 showed stable yam mosaic virus resistance across the test environments. The correlation of stability indices between fresh tuber yield and tuber dry matter was r = −0.171 (p =0.24), and that between tuber dry matter and yam mosaic virus susceptibility scale was r = −0.174 (p =0.10), whereas the correlation was positive and significant (r = 0.27, p =0.05) between fresh tuber yield and mosaic virus susceptibility scale. Despite the pattern of correlations between stability indices, clone TDr10/00412 expressed relatively superior and stable performance for fresh tuber yield, tuber dry matter, and yam mosaic virus field resistance, whereas TDr09/00135 combined superior AMMI stability indices for fresh tuber yield and dry matter. TDr11/00055, on the other hand, combined best performance and stability for fresh tuber yield and yam mosaic virus field resistance. Rankings and simultaneous selection for the three traits identified TDr10/00412, TDr89/00983, TDr10/01012, TDr11/000291, and TDr09/00135 as the top five genotypes combining superior performance and stability for growing in various environments.

Further extension of the GEI analysis with GGE biplot model dissected different responses of yam clones across test sites for the traits (Figures 1–4). For the fresh tuber yield, the PC1 and PC2 collectively explained 78.1% of the total variation attributable to genotype and the GEI (Figure 1(a)). The polygon view of the GGE biplot revealed nine sectors where the test sites occupied two sectors making two environment clusters: one consisted of Ikenne, Ubiaja and Ibadan test sites in the forest to forest-savannah transition ecologies; and the other consisted of a sole test site in southern Guinea savannah ecology with respect to fresh tuber yield potential. Clones TDr09/00263 and TDr10/00605 (G5 and G20) were the highest yielders in environment cluster 1 that represented the forest to forest-savannah transition ecologies, whereas clones TDr11/

Table 3. Additive main effects and multiplicative interaction (AMMI) stability statistics dissecting the performance stability for fresh tuber yield (t ha^{-1}), tuber dry matter content (%), and mosaic virus susceptibility scale for 49 elite clones of white Guinea yam evaluated at four sites in Nigeria in 2017/2018.

	Fresh tuber yield (tha^{-1})			Tuber dry matter (%)			Yam mosaic virus susceptibility scale			
Clones	Mean	ASV[†]	TSI[‡]	Mean	ASV	TSI	Mean	ASV	TSI	Mean trait stability index
TDr09/00135	13.231	0.358	**14**	32.961	0.469	**27**	2.870	0.657	74	**38.3 (5)**
TDr10/00310	11.563	0.153	**17**	27.608	0.545	70	2.904	0.172	42	43.0 (16)
TDr11/00055	14.261	0.579	**18**	30.166	1.016	82	2.231	0.204	**21**	40.3 (8)
TDr10/00412	10.669	0.156	**25**	32.451	0.406	31	2.561	0.062	**10**	**22.0 (1)**
TDr00/00001	12.280	0.537	**25**	28.398	0.754	73	2.368	0.341	39	45.7 (20)
TDr10/01012	10.705	0.256	26	32.400	1.505	68	2.970	0.469	73	55.7 (34)
TDr09/00052	12.069	0.489	27	32.749	0.917	53	2.608	0.108	**18**	**32.7 (3)**
TDr09/00220	10.834	0.407	29	33.793	0.942	44	3.086	0.141	48	40.3 (8)
TDr11/01272	12.206	0.656	32	27.656	0.328	54	2.796	0.208	40	42.0 (13)
TDr89/00983	13.070	0.955	35	34.863	0.619	**28**	2.430	0.259	33	**32.0 (2)**
TDr11/00128	10.233	0.452	37	32.916	0.962	52	3.111	0.224	58	49.0 (24)
TDr10/00600	10.693	0.603	37.5	34.546	1.326	52	2.793	0.185	35	41.5 (10)
TDr10/00605	15.621	1.222	38	30.314	0.219	45	2.626	0.290	42	41.7 (11)
TDr11/00291	8.344	0.089	39	32.970	0.439	**24**	3.229	0.060	48	**37.0 (4)**
TDr10/00052	13.271	1.246	42	31.244	0.874	65	2.686	0.241	40	49.0 (24)
TDr10/00021	13.765	1.278	43	30.414	0.876	72	2.843	0.518	69	61.3 (41)
TDr09/00267	9.150	0.437	44	31.149	0.456	48	3.641	0.570	96	62.7 (42)
TDr09/00122	12.990	1.200	44	31.506	0.875	63	2.424	0.094	**11**	39.3 (6)
TDr09/00121	12.133	1.142	46	33.331	0.960	47	2.703	0.260	43	45.3 (19)
TDr11/00734	10.693	0.847	46.5	32.924	1.526	61	3.199	0.451	86	64.5 (46)
TDr10/00563	8.326	0.256	47	35.585	1.119	44	2.573	0.484	52	47.7 (22)
TDr09/00013	9.865	0.641	48	32.859	0.721	42	3.103	0.228	58	49.3 (26)
TDr09/00404	9.711	0.635	49	31.877	0.497	43	2.648	0.319	45	45.7 (20)
TDr10/00248	8.043	0.217	49	30.124	0.516	61	2.765	0.288	46	52.0 (28)
TDr10/00228	7.981	0.162	49	31.052	1.943	85	2.968	0.113	39	57.7 (37)
TDr09/00263	13.045	1.497	51	34.688	1.915	54	2.159	0.407	39	48.0 (23)
TDr11/01408	10.103	0.801	52	33.841	0.391	**16**	3.158	0.236	66	44.7 (17)
TDr11/01142	6.950	0.204	52	32.474	0.397	29	3.121	0.445	78	53.0 (29)
TDr10/00149	9.509	0.658	53	30.321	0.504	56	2.898	0.269	55	54.7 (31)

(*Continued*)

Table 3. (Continued).

	Fresh tuber yield (tha^{-1})			Tuber dry matter (%)			Yam mosaic virus susceptibility scale			
Clones	Mean	ASV[†]	TSI[‡]	Mean	ASV	TSI	Mean	ASV	TSI	Mean trait stability index
TDr11/00629	11.868	1.402	55	30.701	0.801	66	3.135	0.121	51	57.3 (36)
TDr11/00015	11.474	1.263	55	28.875	0.861	73	2.821	0.190	38	55.3 (32)
TDr10/00060	7.064	0.401	56	35.075	0.968	41	2.821	0.102	28	41.7 (11)
TDr11/00180	12.939	1.692	57	30.768	1.077	78	2.356	0.493	48	61.0 (40)
TDr09/02079	8.309	0.622	58	34.766	1.013	44	2.623	0.183	26	42.7 (14)
TDr10/00913	8.911	0.874	62	32.883	0.211	**19**	2.786	0.380	54	45.0 (18)
Danacha	8.709	0.938	65	32.220	0.409	35	3.015	0.589	81	60.3 (39)
TDr11/00008	8.970	1.028	65	31.488	0.323	37	2.656	0.125	26	42.7 (14)
TDr09/00408	11.081	2.078	66	31.665	0.062	30	3.308	0.120	58	51.3 (27)
TDr89/02665	8.118	0.767	66	35.966	1.215	45	2.351	0.100	**9**	40.0 (7)
TDr09/00295	10.575	1.476	66	32.051	0.530	45	2.959	0.337	62	57.7 (37)
Oju-iyawo	8.780	0.980	67	31.395	0.741	59	2.844	0.412	63	63.0 (43)
TDr09/00134	6.831	0.693	71	31.977	0.551	49	3.133	0.354	74	64.7 (47)
TDr10/00245	10.210	1.518	71	33.703	1.132	53	3.061	0.091	37	53.7 (30)
TDr09/00341	10.169	1.663	73	27.871	0.187	49	2.979	0.399	69	63.7 (44)
TDr10/00144	9.805	1.511	74	32.161	0.580	48	2.871	0.194	44	55.3 (32)
TDr10/00282	8.163	1.185	76	32.773	0.386	**25**	3.195	0.233	67	56.0 (35)
TDr11/00228	8.920	1.417	76	28.704	0.863	75	3.163	0.093	47	66.0 (48)
TDr09/00152	8.018	1.037	77	32.290	0.536	43	3.155	0.306	72	64.0 (45)
TDr11/01701	6.133	0.964	79	31.526	0.506	47	3.224	0.507	91	72.3 (49)

[†]ASV: AMMI stability value.

[‡]TSI: AMMI stability index; bolded values indicate the five top-ranking genotypes combining superior respective trait value with performance stability across different sites. Mean stability index refers to the average stability index value for simultaneous selection for fresh tuber yield, tuber dry matter, and yam mosaic virus severity while the number in parenthesis is ranking based on mean stability index.

00055, TDr10/00052, TDr09/00122, TDr09/00408 and TDr10/00245 (G13, G43, G33, G40, and G2, respectively) were the highest yielders in environment cluster 2 that represented the southern Guinea savannah ecology for yam cultivation in Nigeria (Figure 1(a)).

The graphical display in the GGE biplot for the tuber dry matter content depicted the existence of mega-environments, where the outermost 11 clones in the biplot formed an 11-sided polygon with "winner" clone at the vertex. The four test sites were delineated into three out of the 11 sectors forming three environment clusters, where the first cluster comprised Ibadan site, the second cluster constituted Ikenne and Ubiaja sites, and the third cluster represented the Abuja site. Clone TDr10/00563 in the environment cluster one represented by Ibadan site, TDr89/02665 in the environment cluster two represented by Ikenne and Ubiaja sites and TDr09/02079 in the third environment cluster represented by Abuja site were winning yam clones for the tuber dry matter content (Figure 1(b)). Figure 2(a,b) represents the discriminating ability and representativeness of test sites for fresh tuber yield and tuber dry matter. Based on the GGE biplots average environment coordination (AEC), Ikenne for fresh tuber yield and Ibadan for tuber dry matter content had the longest vectors and large PC1 values with wider angles from AEC compared to the other sites, hence, were the most discriminating sites for these traits (Figure 2(a,b)). The more representative site for expression of fresh tuber yield was Ubiaja, whereas Ikenne and Ubiaja seemed to be more representative for tuber dry matter content, as it had small absolute PC2

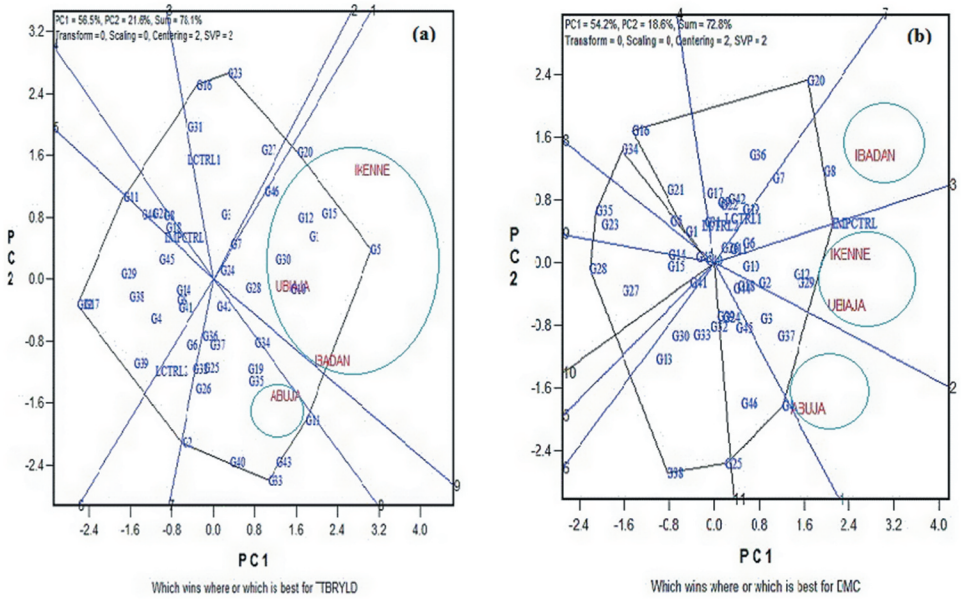

Figure 1. Polygon representation of GGE biplot based on total fresh tuber yield (a) and dry matter content (b), of 49 yam genotypes grown at Abuja, Ibadan, Ikenne and Ubiaja in Nigeria.

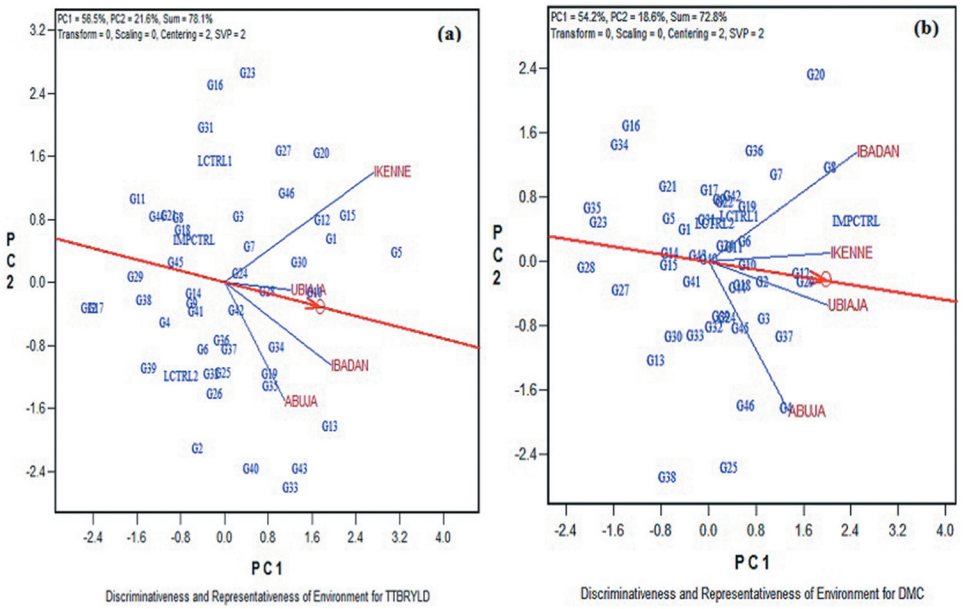

Figure 2. Discriminating power and representativeness of the test environments for total fresh tuber yield (a) and dry matter content (b), of 49 yam genotypes.

score with longest vector and very narrow angle from AEC for respective traits. Figures 3 and 4 display "which-won-where" pattern of the yam clones and the discrimination ability and representativeness properties of test sites for resistance to yam mosaic virus field infection. The PC1 and PC2 for reaction to yam mosaic virus natural field infection collectively explained about 80% of the total variation attributable to genotype main and the GEI effects. The polygon view of biplot for reaction to yam mosaic virus formed six sectors, with four test sites occupying two of the six sectors, suggesting two environment clusters: one consisted of Abuja and Ibadan, and the other comprised Ubiaja and Ikenne. Clones TDr09/00408, TDr09/00267 and TDr09/00135 (G40, G41, and G10) were the most susceptible to yam mosaic virus in environment cluster 1, whereas TDr11/00734 and Oju-iyawo (G25 and LCTR1) were the most susceptible clones in environment cluster 2 (Figure 3). The assessment of test site quality for yam mosaic virus resistance identified Abuja, Ibadan and Ikenne as the sites with relatively more discriminating power than Ubiaja (Figure 4).

The genotype-by-trait (GT) biplot (Figure 5) identified yam clones with the highest values for the three traits assessed in our study. The GT biplot also depicted how the clones performed with regard to particular traits. The variation attributable to PC1 and PC2 of GT biplot was 85.9%. Nine clones were associated with fresh tuber yield (Figure 5; Table 4). Clone TDr10/00605 (G31) out-yielded the eight clones. Thirteen clones were associated

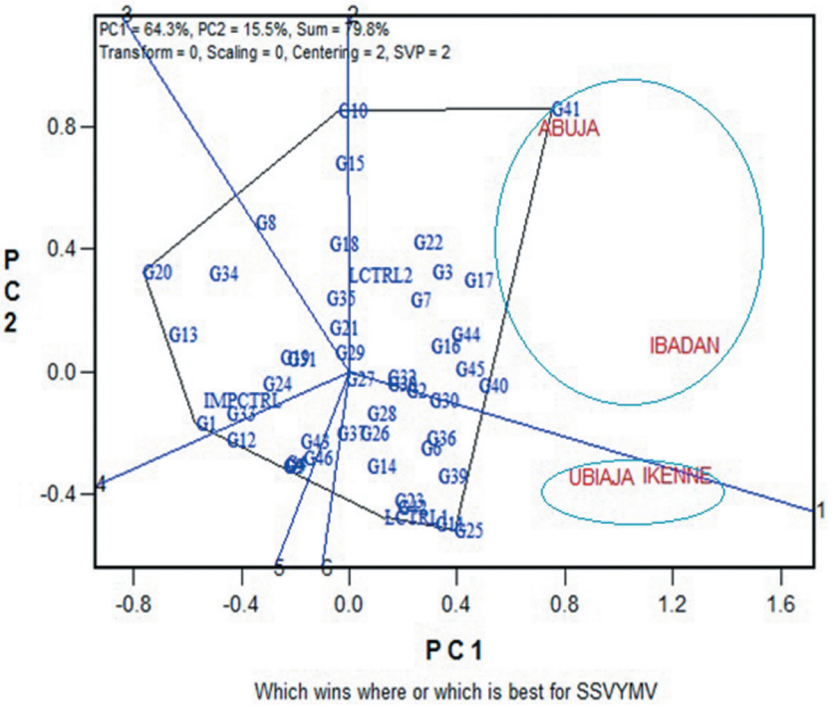

Figure 3. Polygon representation of GGE biplot based on susceptibility scale values of yam mosaic virus of 49 yam genotypes grown at Abuja, Ibadan, Ikenne, and Ubiaja in Nigeria.

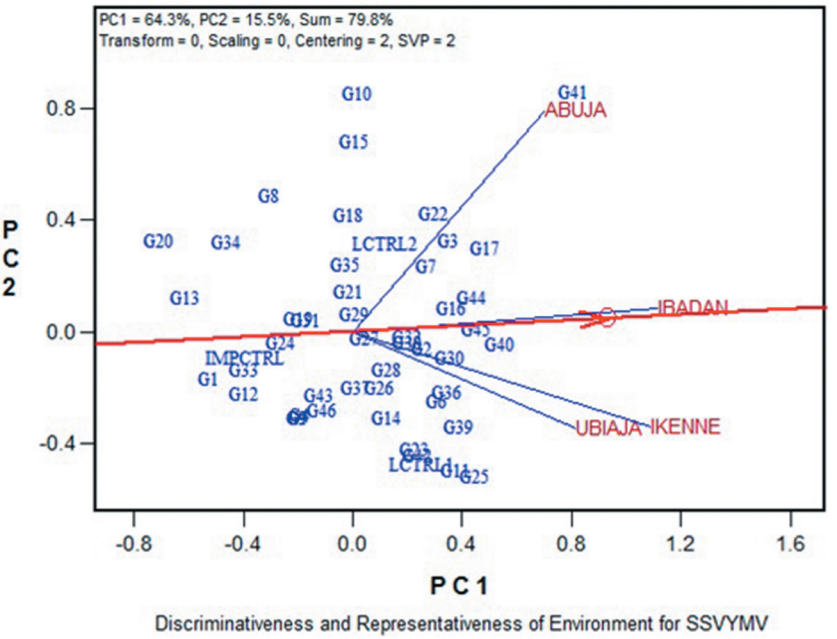

Figure 4. Discriminating power and representativeness of the test environments for susceptibility scale values of yam mosaic virus of 49 yam genotypes.

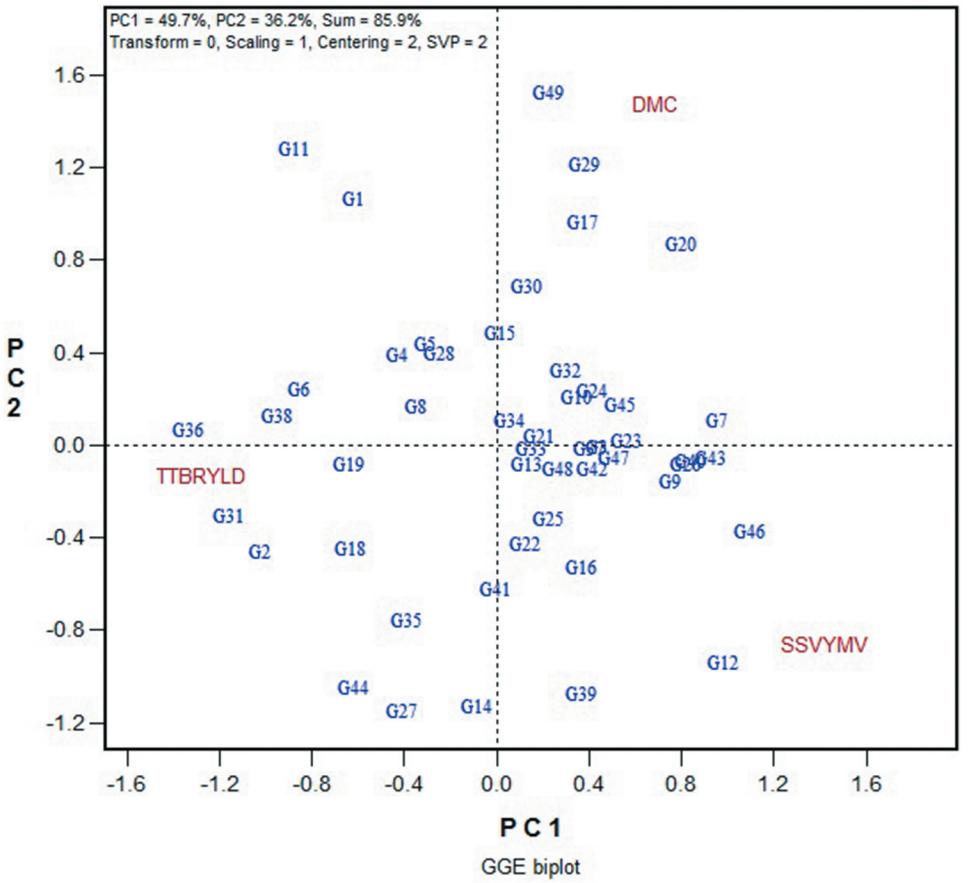

Figure 5. Genotype by trait biplot of 49 clones of white Guinea yams grown at Abuja, Ibadan, Ikenne, and Ubiaja in Nigeria.

with tuber dry matter content. Among these 13 clones, TDr89/02665 (G49) had the highest value for tuber dry matter content. For the yam mosaic virus, 17 clones exhibited susceptible reaction. Of the 17 clones, the three most susceptible genotypes were TDr09/00267 (G12), TDr09/00408 (G16) and TDr11/00291 (G40).

4. Discussion

In the present study, we dissected the nature and extent of genetic and non-genetic factors, explaining the variation among yam genotypes in an MET using phenotypic and molecular marker information. The magnitude of phenotypic variance attributable to the genetic and non-genetic factors matters in determining the most likely means to exploit the heritable variation for the trait in a breeding population via selection or recombination breeding. The total genetic variance was smaller for fresh tuber yield and dry

Table 4. Names, codes and trait values of yam clones studied in the genotype-by-trait biplot analysis.

Clones	Codes	Fresh tuber yield (tha^{-1})	Tuber dry matter (%)	Yam mosaic virus susceptibility scale
TDr09/00135	G8	13.231	32.961	2.87
TDr10/00310	G27	11.563	27.608	2.904
TDr11/00055	G36	14.261	30.166	2.231
TDr10/00412	G28	10.669	32.451	2.561
TDr00/00001	G2	12.28	28.398	2.368
TDr10/01012	G33	10.705	32.4	2.97
TDr09/00052	G4	12.069	32.749	2.608
TDr09/00220	G10	10.834	33.793	3.086
TDr11/01272	G44	12.206	27.656	2.796
TDr89/00983	G1	13.07	34.863	2.43
TDr11/00128	G37	10.233	32.916	3.111
TDr10/00600	G30	10.693	34.546	2.793
TDr10/00605	G31	15.621	30.314	2.626
TDr11/00291	G40	8.344	32.97	3.229
TDr10/00052	G19	13.271	31.244	2.686
TDr10/00021	G18	13.765	30.414	2.843
TDr09/00267	G12	9.15	31.149	3.641
TDr09/00122	G6	12.99	31.506	2.424
TDr09/00121	G5	12.133	33.331	2.703
TDr11/00734	G42	10.693	32.924	3.199
TDr10/00563	G29	8.326	35.585	2.573
TDr09/00013	G3	9.865	32.859	3.103
TDr09/00404	G15	9.711	31.877	2.648
TDr10/00248	G25	8.043	30.124	2.765
TDr10/00228	G23	7.981	31.052	2.968
TDr09/00263	G11	13.045	34.688	2.159
TDr11/01408	G45	10.103	33.841	3.158
TDr11/01142	G43	6.95	32.474	3.121
TDr10/00149	G22	9.509	30.321	2.898
TDr11/00629	G41	11.868	30.701	3.135
TDr11/00015	G35	11.474	28.875	2.821
TDr10/00060	G20	7.064	35.075	2.821
TDr11/00180	G38	12.939	30.768	2.356
TDr09/02079	G17	8.309	34.766	2.623
TDr10/00913	G32	8.911	32.883	2.786
Danacha	G47	8.709	32.22	3.015
TDr11/00008	G34	8.97	31.488	2.656
TDr09/00408	G16	11.081	31.665	3.308
TDr89/02665	G49	8.118	35.966	2.351
TDr09/00295	G13	10.575	32.051	2.959
Oju-iyawo	G48	8.78	31.395	2.844
TDr09/00134	G7	6.831	31.977	3.133
TDr10/00245	G24	10.21	33.703	3.061
TDr09/00341	G14	10.169	27.871	2.979
TDr10/00144	G21	9.805	32.161	2.871
TDr10/00282	G26	8.163	32.773	3.195
TDr11/00228	G39	8.92	28.704	3.163
TDr09/00152	G9	8.018	32.29	3.155
TDr11/01701	G46	6.133	31.526	3.224

matter content than the non-genetic variance, indicating that a large proportion of the total variation was non-heritable or environmental. The smaller genetic variance relative to non-genetic variance also implied that selection progress for fresh tuber yield and dry matter content would be slow. The substantial non-genetic effect on a trait among yam clones highlights the potential to improve these traits through the use of selection methods that are not influenced by environment, such as use of molecular markers (Evans et al. 2018). Unlike fresh tuber yield and dry matter content, YMV had a larger proportion of the phenotypic variation attributed to genetic factors than to non-genetic factors. This suggests that selection progress for YMV could be achieved faster compared to the fresh tuber yield and dry matter in the current set of yam genotypes.

Traits that had high broad-sense heritability ($H^2 \geq 0.60$) captured higher total genetic variance attributable to both additive and the non-additive (the dominance and epistasis) effects. The broad-sense heritability is more important in clonally propagated crops than in non-clonally propagated crops, as clonal propagation captures all genetic effects: additive, dominance and epistasis, and can pass the genotype intact on to the next generation. Traits that exhibited high heritability and a high genetic advance as percentage of mean indicated that progress can be made for those traits through selective breeding. Johnson, Robinson, and Comstock (1955) suggested the relevance of combining heritability with genetic advance for efficient predictability of response to selection. Generally, both the non-genetic (environmental) and non-additive (dominance and epistasis) variances contributed more to total phenotypic variance than the additive genetic variance, leading to low narrow-sense heritability estimates for the three traits studied.

The current study also revealed the potential of genomic best linear unbiased prediction (gBLUP) for assessing the genetic merits of yam clones in multi-environment trials and choosing superior parents for crosses. Besides, gBLUP analysis could be used to reduce the stages of field evaluation in yams to save resources and increase the pace of cultivar release. The merits of genomic prediction in reducing cycle time and evaluation stages in crop breeding programs have been extensively explained (Muranty et al. 2015; Resende et al. 2017, 2012; Burgueño et al. 2007; Bradbury et al. 2007; Garcia, Carbonell, and Asíns 2000), including root and tuber crops (Friedmann et al. 2018; Norman et al. 2018). Genomic prediction contributes to efficient parental identification for crossing (Heffner, Sorrells, and Jannink 2009).

The GEI analysis of the three traits using AMMI model indicated the possibility of identification and selection of widely adapted and/or specifically adapted genotypes for target environments. Both the main genetic effect and the GEI effects were important in controlling these traits. However, the environmental (site) effect alone exhibited the greatest influence relative to the main

genetic and GEI effects, indicating much benefit would be achieved from improved agronomic management (Xu 2016). Such a strong environmental influence on variation among clones for fresh tuber yield (t ha^{-1}) has been previously reported by Egesi and Asiedu (2002) for yam and by Ntawuruhunga and Dixon (2010) for cassava. The presence of strong environmental effects should not be ignored, but rather exploited by breeding programs using stability analysis, such as AMMI and GGE, which identify genotypes with general adaptation across environments and specific adaptation to particular environments (Farshadfar, Mahmodi, and Yaghotipoor 2011).

The AMMI stability indices dissected the performance stability of yam clones across environments. The AMMI stability indices effectively identified the top-ranking five clones that integrated performance superiority with stability for the measured traits. However, none of the clones appeared in common in the top five list for all three traits, possibly because different traits are controlled by different genes and each trait exhibits differential response to different environments. The stability indices for fresh tuber yield and tuber dry matter had a weak and negative correlation. Likewise, stability indices for tuber dry matter and yam mosaic virus susceptibility had a weak and negative correlation. However, the association between fresh tuber yield and mosaic virus susceptibility scale was positive and significant. Detailed assessment at the individual clone level identified negative correlation-breaker individuals. Clone TDr09/00135 was among the negative correlation-breaker clones that were in the top-ranking five genotypes for fresh tuber yield and tuber dry matter. Clone TDr11/00055 and TDr10/00412 simultaneously exhibited superior and stable performance for fresh tuber yield and yam mosaic virus resistance. Considering the relevance of the key traits in discriminating the yam clones, a multiple trait selection index that takes into account each of these traits simultaneously would identify superior and stable clones for commercial deployment. The multiple trait selection technique helps breeders to take balanced selection decisions that include relevant traits of interest to producers, marketers and consumers. Accordingly, TDr10/00412, TDr11/00055, and TDr09/00135 were the best clones that combined relatively superior mean values with stable performance for fresh tuber yield, tuber dry matter content, and mosaic virus resistance at different sites. An agronomically superior variety possesses a range of traits but superiority and stability for all traits are rarely combined within a single variety. Instead, a range of trait superiority and stability are found in different genotypes. Thus, use of index selection facilitates identification of desirable genotypes integrating high and stable trait performance across environments and simultaneous selection of promising genotypes (Baker 1986; Yan and Kang 2003).

Further dissecting the adaptation and stability of the clones with GGE biplot analysis assisted in clustering the test environments into distinct

mega-environments, with each environment comprising sites sharing consistently best-performing clones. A site in each mega-environment represents the target environment with the power of differentiating clones (Yan and Tinker 2006). According to Yan et al. (2007) test environments are classified into three main groups. The first group has short vectors and lacks sufficient information about variability in the genotypes. The second group with long vectors, small angles, and the average environment coordination (AEC) abscissa possesses an ideal environment quality for identification of superior genotypes. The third group that is characterized by large angles and AEC abscissa, is useful for culling of unstable genotypes. Yan and Kang (2003, 91) noted that the angle between the vector of an environment and the AEC axis is a measure of representativeness of that environment. Abuja, Ibadan and Ikenne had a relatively longer vector than Ubiaja did. The vectors of Abuja, Ikenne and Ubiaja, each forming a wide angle with AEC, showed relatively weak representativeness, whereas Ibadan, with a narrow angle, showed relatively strong representativeness of a test site for screening white yam clones with mosaic virus resistance.

The GT biplots revealed best-performing clones that were associated with fresh tuber yields and tuber dry matter content, whereas those that were associated with YMV, especially the vertex clones, were the worst performers or most susceptible ones. These findings are substantiated by the mean performance data for the clones across METs (Table 3). The biplot of the grand mean showed clone TDr10/00605 (G31) to be the best genotype for fresh tuber yield and clone TDr89/02665 (G49) for tuber dry matter content. Our results suggest the relevance of assessing multiple traits across diverse environments in yam breeding trials to ensure that the selected genotype(s) have acceptable performance in target environments and meet the demands of the producers, processors and the consumers. These findings concur with the suggestion that putative white yam clones should be selected on the basis of desired high fresh tuber yield, acceptable tuber dry matter content, and field tolerance to YMV (Darkwa et al. 2020b). Our findings also established the relevance of GT biplot in unraveling vital information that could be useful for parental selection aimed at improving key traits, as reported by Yan and Frégeau-Reid (2008). Thus, the clones that exhibited good attributes would be useful as parents in a hybridization program aimed at generating improved clones with high fresh tuber yields, tuber dry matter content, and resistance to YMV.

5. Conclusions

Application of various analyses in the current study helped to assess the data generated from breeding trials to derive useful genetic information and determine the nature of GEI in yam. Complementation of mixed model with genomic relationship matrix improved understanding of the genetic

merits and genetic architecture of tuber yield, dry matter content, and yam mosaic virus infection in white yams. Moreover, the useful genetic values of superior yam clones, identified for target environments in this study, present an opportunity for the genetic improvement of the crop.

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Authors' contributions

PEN and AA designed the experiment. AA, PBT, EYD, AD and RA supervised the work. PEN, AA, AA and PA performed the data analysis. AA and PEN wrote the manuscript. All the authors contributed to writing the article, read and approved its submission.

Disclosure statement

The authors declare no conflict of interest.

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ORCID

Prince Emmanuel Norman http://orcid.org/0000-0002-0150-8610
Paterne A. Agre http://orcid.org/0000-0003-1231-2530
Asrat Asfaw http://orcid.org/0000-0002-4859-0631

References

Aighewi, B., N. Maroya, R. Asiedu, D. Aihebhoria, M. Balogun, and D. Mignouna. 2020. "Seed yam production from whole tubers versus minisetts." Journal of Crop Improvement 34(6): 858–874. doi:10.1080/15427528.2020.1779157

Alabi, T. R., P. O. Adebola, A. Asfaw, D. De Koeyer, A. Lopez-Montes, and R. Asiedu. 2019. "Spatial Multivariate Cluster Analysis for Defining Target Population of Environments in

West Africa for Yam Breeding." *International Journal of Applied Geospatial Research* 10 (3): 1–30. doi:10.4018/IJAGR.2019070104.

Aljanabi, S. M., and I. Martinez. 1997. "Universal and Rapid Salt-extraction of High-quality High Quality Genomic DNA for PCR-Based Techniques." *Nucleic Acids Research* 25 (22): 4692–4693. doi:10.1093/nar/25.22.4692.

Baker, R. 1986. *Selection Indices in Plant Breeding*. Boca Raton, FL, USA: CRC Press.

Bassey, E. E., and U. S. Akpan. 2015. "Evaluation of Guinea White Yam (*Dioscorea Rotundata* Poir) for Yield and Yield Components in Nigeria." *American Journal of Experimental Agriculture* 8 (4): 216–223.

Borgognone, M. G., D. G. Butler, F. C. Ogbonnaya, and M. F. Dreccer. 2016. "Molecular Marker Information in the Analysis of Multi-environment Trials Helps Differentiate Superior Genotypes from Promising Parents." *Crop Science* 56: 2612–2628.

Bose, L. K., N. N. Jambhulkar, K. Pande, and O. N. Singh. 2014. "Use of AMMI and Other Stability Statistics in the Simultaneous Selection of Rice Genotypes for Yield and Stability under Direct Seeded Conditions." *Chilean Journal of Agricultural Research* 74: 1–9.

Bradbury, P. J., Z. Zhang, D. E. Kroon, T. M. Casstevens, Y. Ramdoss, and E. S. Buckler. 2007. "TASSEL: Software for Association Mapping of Complex Traits in Diverse Samples." *Bioinformatics* 23: 2633–2635.

Brink, A. B., and H. D. Eva. 2009. "Monitoring 25 Years of Land Cover Change Dynamics in Africa: A Sample Based Remote Sensing Approach." *Applied Geography* 29 (4): 501–512.

Browning, S. R., and B. L. Browning. 2007. "Rapid and Accurate Haplotype Phasing and Missing Data Inference for Whole Genome Association Studies by Use of Localized Haplotype Clustering." *American Journal of Human Genetics* 81: 1084–1097.

Burgueño, J., J. Crossa, P. L. Cornelius, R. Trethowan, G. McLaren, and A. Krishnamachari. 2007. "Modeling Additive × Environment and Additive × Additive × Environment Using Genetic Covariances of Relatives of Wheat Genotypes." *Crop Science* 47: 311–320.

Burkill, I. H. 1960. "The Organography and the Evolution of Dioscoreaceae, the Family of the Yams." *Journal of Linnean Society London, Botany* 56: 319–412.

Burton, W. G., and E. H. Devane. 1953. "Estimating Heritability in Tall Fescue (*Festuca Arundinacea*) from Replicated Clonal Material." *Agronomy Journal* 45: 478–481.

Butler, D. G., B. R. Cullis, A. A. Gilmour, B. J. Gogel, and R. Thome. 2018. *ASReml-R Reference Manual Version 4*. HP1IES, UK: VSNi Ltd, Hemel Hempstead.

Caballero, A., and M. A. Toro. 2002. "Analysis of Genetic Diversity for the Management of Conserved Subdivided Populations." *Conservation Genetics* 3: 289–299.

Crossa, J. 2012. "From Genotype × Environment Interaction to Gene × Environment Interaction." *Current Genomics* 13: 225–244.

Darkwa, K., B. Olasanmi, R. Asiedu, and A. Asfaw. 2020b. "Review of Empirical and Emerging Methods and Tools for Yam (*Dioscorea* Spp.) Improvement: Status and Prospects." *Plant Breeding* 1–24. doi:10.1111/PBR.12783.

Darkwa, K., P. Agre, B. Olasanmi, K. Iseki, R. Matsumoto, A. Powell, G. Bauchet, et al. 2020a. "Comparative Assessment of Genetic Diversity Matrices and Clustering Methods in White Guinea Yam (*Dioscorea Rotundata*) Based on Morphological and Molecular Markers." *Scientific Reports* 10: 13191. doi:10.1038/s41598-020-69925-9.

De Mendiburu, F. 2019. "*Agricolae-Statistical Procedure for Agricultural Research*. R-package Version 1.3.0."

Dellaporta, S. L., J. Wood, and J. B. Hicks. 1983. "A Plant DNA Mini Preparation Version II." *Plant Molecular Biology Reporter* 1: 19–21.

Deshmukh, S. N. N., M. S. Basu, and P. S. Reddy. 1986. "Genetic Variability, Character Association and Path Coefficients of Quantitative Traits in Virginia Bunch Varieties of Groundnut." *Indian Journal of Agricultural Science* 56: 816–821.

Dodds, K. G., M. L. Tate, and J. A. Sise. 2005. "Genetic Evaluation Using Parentage Information from Genetic Markers." *Journal of Animal Science* 83: 2271–2279.

Egesi, C. N., and R. Asiedu. 2002. "Analysis of Yam Yields Using the Additive Main Effects and Multiplicative Interaction (AMMI) Model." *African Crop Science Journal* 10: 195–201.

Egesi, C. N., T. J. Onyeka, and R. Asiedu. 2007. "Severity of Anthracnose and Virus Diseases of Water Yam (*Dioscorea Alata* L.) In Nigeria I: Effect of Yam Genotype and Date of Planting. Crop." *Protection* 26 (8): 1259–1265.

Elshire, R. J., J. C. Glaubitz, Q. Sun, J. A. Poland, K. Kawamoto, E. S. Buckler, and S. E. Mitchell. 2011. "A Robust, Simple Genotyping-by-sequencing (GBS) Approach for High Diversity Species." *PloS One* 6: e19379.

Endelman, J. B. 2011. "Ridge Regression and Other Kernels for Genomic Selection with R Package rrBLUP." *The Plant Genome* 4: 250–255.

Evans, L. M., R. Tahmasbi, M. Jones, S. I. Vrieze, G. R. Abecasis, S. Das, D. W. Bjelland, et al. 2018. "Narrow-sense Heritability Estimation of Complex Traits Using Identity-by-descent Information." *Heredity* 121: 616–630. doi:10.1038/s41437-018-0067-0.

FAOSTAT Food and Agriculture Organization Statistical Databases. 2020. Food and Agriculture Organization of the United Nations. Accessed March 19, 2017. https://www.fao.org/faostat/en/#home

Farshadfar, E., N. Mahmodi, and A. Yaghotipoor. 2011. "AMMI Stability Value and Simultaneous Estimation of Yield and Yield Stability in Bread Wheat (*Triticum Aestivum* L.)." *Australian Journal of Crop Science* 5: 1837–1844.

Forbes, G., W. Pérez, and J. Andrade Piedra. 2014. *Field Assessment of Resistance in Potato to Phytophthora Infestans*, 35. Lima (Peru): International Potato Center (CIP).

Friedmann, M., A. Asfaw, N. Anglin, L. A. B. Lopez-Lavalle, R. Bhattacharjee, A. Brown, E. E. Carey, et al. 2018. "Genomics-assisted Breeding in the CGIAR Research Program on Roots, Tubers and Bananas (RTB)." *Agriculture* 8: 89.

Garcia, M. R., E. A. Carbonell, and M. J. Asíns. 2000. "QTL Analysis of Yield and Seed Number in Citrus." *Theoretical and Applied Genetics* 101: 487–493.

Heerink, N. 2005. "Soil Fertility Decline and Economic Policy Reform in Sub-Saharan." *Land Use Policy* 22 (1): 67–74.

Heffner, E. L., M. E. Sorrells, and J.-L. Jannink. 2009. "Genomic Selection for Crop Improvement." *Crop Science* 49 (1): 1–12.

Johnson, H. W., H. F. Robinson, and R. S. Comstock. 1955. "Estimates of Genetic and Environmental Variability in Soybeans." *Agronomy Journal* 47 (7): 314–318.

Kang, M. 1998. "Using Genotype-by-Environment Interaction for Crop Cultivar Development." *Advances in Agronomy* 62: 199–252. doi:10.1016/S0065-2113(08)60569-6.

Lebot, V. 2009. *Tropical Root and Tuber Crops: Cassava, Sweet Potato, Yams and Aroids*, XIX 413. Wallingford: CABI.

Malosetti, M., J. M. Ribaut, and F. A. van Eeuwijk. 2013. "The Statistical Analysis of Multi-environment Data: Modeling Genotype-by-environment Interaction and Its Genetic Basis." *Frontier Physiology* 4: 1–17.

Muñoz, P. R., M. F. R. Resende Jr., S. V. Gezan, M. D. V. Resende, G. de Los Campos, M. Kirst, D. Huber, and G. F. Peter. 2014. "Unraveling Additive from Nonadditive Effects Using Genomic Relationship Matrices." *Genetics* 198: 1759–1768.

Muranty, H., M. Troggio, I. B. Sadok, M. A. Rifaï, A. Auwerkerken, E. Banchi, R. Velasco, et al. 2015. "Accuracy and Responses of Genomic Selection on Key Traits in Apple Breeding." *Horticulture Research* 2: 15060.

NEPAD New Partnership for Africa's Development. 2014. *Agriculture in Africa: Transformation and Outlook*. www.nepad.org/system/files/Agriculture%20in%20Africa.pdf

Norman, P. E., A. Asfaw, P. B. Tongoona, A. Danquah, E. Y. Danquah, D. D. Koeyer, and R. Asiedu. 2018. "Can Parentage Analysis Facilitate Breeding Activities in Root and Tuber Crops?" *Agriculture* 8: 1–24.

Ntawuruhunga, P., and A. G. O. Dixon. 2010. "Quantitative Variation and Interrelationship between Factors Influencing Cassava Yield." *Journal of Applied Bioscience* 26: 1594–1602.

Ovenden, B., A. Milgate l, J. Wade, G. J. Rebetzke, and J. B. Holland. 2018. "Accounting for Genotype-by-environment Interactions and Residual Genetic Variation in Genomic Selection for Water Soluble Carbohydrate Concentration in Wheat." *G3 Genes Genome Genetics* 8: 1909–1919.

Patterson, H. D., and R. Thompson. 1971. "Recovery of Inter-block Information When Block Sizes are Unequal." *Biometrika* 58: 545–554.

Purcell, S., B. Neale, K. Todd-Brown, L. Thomas, M. A. R. Ferreira, D. Bender, J. Maller, et al. 2007. "PLINK: A Tool Set for Whole-genome Association and Population-based Linkage Analyses." *American Journal of Human Genetics* 81: 559–575.

Purchase, J. L., H. Hatting, and C. S. van Deventer. 2000. "Genotype × Environment Interaction of Wheat in South Africa: Stability Analysis of Yield Performance." *South African Journal of Plant and Soil* 17: 101–107.

R Core Team. 2019. *R: A Language and Environment for Statistical Computing*. Vienna, AU: R Foundation for Statistical Computing.

Resende, M. F., Jr., P. Muñoz, J. J. Acosta, G. F. Peter, J. M. Davis, D. Grattapaglia, M. D. Resende, and M. Kirst. 2012. "Accelerating the Domestication of Trees Using Genomic Selection: Accuracy of Prediction Models across Ages and Environments." *New Phytologist* 193: 617–624.

Resende, R. T., M. D. V. Resende, F. F. Silva, C. F. Azevedo, E. K. Takahashi, O. B. Silva-Junior, and D. Grattapaglia. 2017. "Assessing the Expected Response to Genomic Selection of Individuals and Families in Eucalyptus Breeding with an Additive-dominant Model." *Heredity* 119: 245–255.

Rife, T. W., and J. A. Poland. 2014. "Field Book: An Open-source Application for Field Data Collection on Android." *Crop Science* 54: 1624–1627.

Robinson, H. F., R. E. Comstock, and P. H. Harvey. 1949. "Estimates of Heritability and the Degree of Dominance in Corn." *Agronomy Journal* 41: 353–359.

Shukla, S., A. Bhargava, A. Chatterjee, J. Srivastava, N. Singh, and S. P. Singh. 2006. "Mineral Profile and Variability in Vegetable Amaranth (*Amaranthus Tricolor*)." *Plant Foods for Human Nutrition* 61: 21–26.

Smith, A. B., and B. R. Cullis. 2018. "Plant Breeding Selection Tools Built on Factor Analytic Mixed Models for Multi-environment Trial Data." *Euphytica* 214: 143.

Smith, A. B., B. R. Cullis, and R. Thompson. 2005. "The Analysis of Crop Cultivar Breeding and Evaluation Trials: An Overview of Current Mixed Model Approaches." *Journal of Agricultural Science* 143: 449–462.

Tumuhimbise, R., R. Melis, P. Shanahan, and R. Kawuki. 2014. "Genotype × Environment Interaction Effects on Early Fresh Storage Root Yield and Related Traits in Cassava." *The Crop Journal* 2: 329–337.

vanRaden, P. M. 2007. "Genomic Measures of Relationship and Inbreeding. Animal Improvement." *Interbull Bulletin* 37: 33–36. http://journal.interbull.org/index.php/ib/issue56

vanRaden, P. M. 2008. "Efficient Methods to Compute Genomic Predictions." *Journal of Dairy Science* 91: 4414–4423.

Wright, S. 1922. "Coefficients of Inbreeding and Relationship." *American Naturalist* 56: 330–338.

Xu, Y. 2016. "Envirotyping for Deciphering Environmental Impacts on Crop Plants." *Theoretical and Applied Genetics* 129: 653–673.

Yan, W., and J. Frégeau-Reid. 2008. "Breeding Line Selection Based on Multiple Traits." *Crop Science* 48: 417–423. doi:10.2135/cropsci2007.05.0254.

Yan, W., L. A. Hunt, Q. Sheng, and Z. Szlavnics. 2000. "Cultivar Evaluation and Mega-environment Investigation Based on the GGE Biplot." *Crop Science* 40: 597–605.

Yan, W., and M. S. Kang. 2003. *GGE Biplot Analysis: A Graphical Tool for Breeders, Geneticists, and Agronomists (P. 271)*. Boca Raton, FL, USA: CRC Press.

Yan, W., M. S. Kang, B. Ma, S. Woods, and P. L. Cornelius. 2007. "GGE Biplot Vs. AMMI Analysis of Genotype-by-environment Data." *Crop Science* 47: 643–655.

Yan, W., and N. A. Tinker. 2006. "Biplot Analysis of Multi-environment Trial Data: Principles and Applications." *Canadian Journal of Plant Science* 86: 623–645.

Yin, L. 2019. *Package "CMplot"*. https://github.com/YinLiLin/R-CMplot/blob/master/CMplot.r