Genetic Analysis of Agronomic and Quality Traits from Multi-Location white Yam Trials using Mixed Model with Genomic Relationship Matrix

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Abstract: Traits that define the suitability of a crop for production and consumption are often assessed and predicted to identify superior genotypes for commercial deployment. This study assessed genetic parameter estimates and prediction for 25 agronomic and quality traits in 49 white yam clones. It employed best linear unbiased prediction (BLUP) in a mixed model analysis using genomic relationship matrix derived from 6337 Diversity Array Technology (DArT) molecular markers, multivariate technique of the principal component and canonical discriminant analysis with BLUP predicted values to select key traits for yam breeding. Findings revealed that additive genetic, non-additive genetic and non-genetic factors contributed substantially to phenotypic variation of the studied yam traits. The non-genetic effects accounted for higher variation than the total genetic effects for majority of the traits except yam mosaic virus (YMV), tuber number per plant, ash content, flour yield, peel loss, and protein content. The narrow sense heritability was generally low (<0.30) for all traits except yam anthracnose (0.31), ash content (0.30) and peel loss (0.89). Trait selection with multivariate analysis identified 15 from the 25 traits with fresh tuber yield, tuber dry matter content (DMC), YMV, root-knot and *Scutellonema bradys* nematode susceptibility as the most important traits for white yam variety testing. This paper presents the importance of complementing BLUP prediction that accounts for the relationship among the genotypes with multivariate analysis for genetic parameter estimation, prediction and selection in yam breeding trials to accelerate the genetic gains.

Keywords: Dioscorea rotundata, Genetic estimates, Genetic improvement, Key trait discovery, Trait profiling.

INTRODUCTION

Yam exhibits diverse attributes and performances across production environments. These attributes and performances are often exploited for the genetic improvement of the crop targeting tangible benefits to the society in the production and consumption systems. The diverse attributes and performances are extensively screened and tested by breeding programmes prior to the release of the best genotypes for commercial deployment. Genetic and non-genetic factors affect the genotype's performance in selection and evaluation experiments [1-4]. The genotype (G) and genotype by environment interaction (GEI) are the two sources of variation useful in genotype assessment. The GEI is the inconsistent genotypic responses in multi-environment trials leading to either change in the ranking of genotypes or changes in trait values of genotypes without changes in genotypic ranking [5]. High GEI variability diminishes the accuracy of yield estimates and correlation between genotype and phenotype [6]. Moreover, environmental variability can cause differential responses of genotypes in breeding trials that make the selection of superior genotypes difficult.

Several analytical techniques have been developed and utilized to assess the attributes and performances of genotypes across environments in plant breeding experiments [7]. These include univariate, bivariate and multivariate analysis methods. The different analytical techniques are used in the analysis of data from breeding trials depending on the number of variables considered, and the way the variables are measured, explained and how they contribute to the selection decision. Breeding programmes often consider and measure multiple variables and require analytical techniques that permit simultaneous analysis of large data sets for reduction of dimensionality and identification of important traits with sufficient discriminatory power for germplasm evaluation, characterization and management. Multivariate techniques such as principal component analysis (PCA) and canonical discriminant analysis (CDA) have been useful in distinguishing genotypes, grouping genotypes and identifying key traits accounting for

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variations in plants [8]. The key traits identified by the PCA and CDA techniques save cost, time and energy by removing traits that provide redundant information and focusing on important traits with genetic values that guide effective selection decision of the preferred genotype [9]. These techniques also facilitate graphical display of hidden factors, thereby interfacing between samples and variables [10]. The fixed-effect linear-bilinear models comprising the Sites Regression (SREG) [11] and the Additive Main effect and Multiplicative Interaction (AMMI) models [12] are useful for investigation of the genotypic responses in multi-environments. In these models, plant breeders graphically visualize the environmental and genotypic response patterns using biplots [5]. Linear mixed models or linear-bilinear mixed models are also widely utilized analytical tools for the analysis of data in multi-environment trials (METs) [13]. The fixed-effect linear models and bilinear models including factorial regression (FR) models and partial least squares (PLS) regression models, respectively, constitute the factor analytic (FA) form of the genetic variance-covariance for environments [5]. These models possess a number of merits such as accommodation of heterogeneity of block and error variance between environments and within-environment spatial correlation (error variance modelling); easy handling of incomplete data; more precise estimates of the breeding values of genotypes due to incorporation of coefficients of genetic relationship form pedigree or molecular marker information and consideration of genotypes as random effects in the factor analytic model for GEI [14].

Models that incorporate relationship matrices are powerful to dissect the genetic architecture of complex traits and impact fully aid successful implementation of breeding strategies and design [15, 16]. 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) [17, 18]. These matrices are useful for management of genetic diversity [19], genomics selection and parentage testing [20]. Models that utilize genomic data for determination of genetic relationships more accurately predict genetic effects compared to those that utilize expected relationships from pedigrees [18]. Breeding trial data analysis models incorporating relationship matrices have been effectively utilized in many crops to select subset of promising genotypes as parents in crosses generating new set of recombinants progenies or select superior genotypes for further testing in breeding stage to release as new variety. However, these have seldom been employed in analysis of yam breeding trials to facilitate selection of superior clones for commercial deployment or parents for crosses.

Traditional multivariate techniques such as CDA, PCA, AMMI and GGE biplots have been used for determination of relationship between traits and genotypes [1, 2, 21-24]. However, assessment of the genetic effects, and selection of key traits accounting for the largest amount of variation possible in breeding trials are very critical in the development and deployment of new cultivars. Incorporation of relationship matrix and appropriate multivariate technique(s) in yam MET dataset would serve as useful guide for breeders in the early identification of parental genotypes with desired complimentary traits for crossing as well as superior clones with varietal potential for release decision. Such an assessment is imperative especially with the current alarming erratic climate change in the target production environments. The objectives of this study were to: (1) estimate genetic parameters in white yam breeding trials using molecular marker information; and (2) identify key plant traits with sufficient discriminatory power for germplasm evaluation in yam breeding.

MATERIALS AND METHODS

Plant Materials, Trial Sites and Design

The yam clones comprised of three check varieties and 46 elite breeding lines from International Institute of Tropical Agriculture (IITA's) yam breeding programme (Table **1**). The trial sites represented three agro-ecological zones for yam in Nigeria: forest, forest-savannah transition, and the southern Guinea savannah. The detailed descriptions of agro-ecological characteristics of the trial sites are presented in Table **2**. 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 in a mixture of 70 g Macozeb, 75 ml Chlorpyrifos and 10 l tap water for 5 min and dried for 20 h under shade. 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 under non-staked condition with no external added fertilizer. The trial plots were hand weeded to maintain the plots free of weeds throughout the crop cycle.

Table 1: Description of Genotypes Utilized for the Study

Genotype	Status	Pedigree
TDr 11/00180	Improved	TDr 97/00840 × TDr 99/02626
TDr 10/00245	Improved	TDr 95/18544 × TDr 95/01932
TDr 11/01408	Improved	TDr 96/00604 (OP)
TDr 09/02079	Improved	TDr 07/01553 (OP)
TDr 10/00605	Improved	TDr 95/18544 × TDr 95/01932
TDr 09/00013	Improved	TDr 97/00793 × TDr 95/01932
TDr 09/00220	Improved	TDr 97/00793 × TDr 95/01932
TDr 10/00563	Improved	TDr 95/18544 × TDr 95/01932
TDr 09/00404	Improved	TDr 07/01553 × TDr 95/01932
TDr 09/00135	Improved	TDr 97/00793 × TDr 95/01932
TDr 11/01142	Improved	TDr 95/19158 (OP)
TDr 08/00983	Improved	TDr 97/00917 × TDr 99/02626
TDr 11/00055	Improved	TDr 04-219 × TDr 00/00196
TDr 10/00149	Improved	TDr 95/18544 × TDr 95/01932
TDr 10/00021	Improved	TDr 95/18544 × TDr 95/01932
TDr 11/00228	Improved	TDr 97/00205 × TDr 99/02626
TDr 11/01701	Improved	AGBANWOBE (OP)
TDr 10/00913	Improved	TDr 95/18544 × TDr 95/01932
TDr 09/00052	Improved	TDr 97/00793 × TDr 95/01932
TDr 09/00263	Improved	TDr 97/00793 × TDr 95/01932
TDr 10/00248	Improved	TDr 95/18544 × TDr 95/01932
TDr 09/00134	Improved	TDr 97/00793 × TDr 95/01932
TDr 09/00341	Improved	TDr 97/00793 × TDr 95/01932
TDr 10/00412	Improved	TDr 95/18544 × TDr 95/01932
TDr 11/00734	Improved	TDr 06-3 × TDr 1892
TDr 10/00144	Improved	TDr 95/18544 × TDr 95/01932
TDr 11/00015	Improved	TDr 04-219 × TDr 00/00196
TDr 10/00310	Improved	TDr 95/18544 × TDr 95/01932
TDr 10/00060	Improved	TDr 95/18544 × TDr 95/01932
TDr 11/00629	Improved	TDr 95/18544 × POUNA
TDr 11/00008	Improved	TDr 04-219 × TDr 00/00196
TDr 09/00295	Improved	TDr 97/00793 × TDr 95/01932
TDr 09/00122	Improved	TDr 97/00793 × TDr 95/01932
TDr 09/00001	Improved	TDr 97/00793 × TDr 95/01932
TDr 11/01272	Improved	TDr 96/00604 (OP)
TDr 11/00128	Improved	TDr 97/00840 × TDr 99/02626
TDr 10/00600	Improved	TDr 95/18544 × TDr 95/01932
TDr 10/00228	Improved	TDr 95/18544 × TDr 95/01932
TDr 09/00152	Improved	TDr 97/00793 × TDr 95/01932
TDr 09/00408	Improved	TDr 07/01553 × TDr 95/01932
TDr 09/00267	Improved	TDr 97/00793 × TDr 95/01932
TDr 10/01012	Improved	TDr 95/18544 × TDr 95/01932
TDr 10/00052	Improved	TDr 95/18544 × TDr 95/01932
TDr 10/00282	Improved	TDr 95/18544 × TDr 95/01932

TDr 11/00291	Improved	TDr 97/00205 × TDr 99/02626
TDr 09/00121	Improved	TDr 97/00793 × TDr 95/01932
TDr 89/02665	Released	Unknown
Danacha	Landrace	Unknown
Ojuiyawo	Landrace	Unknown

Table 2: Agro-ecological Characteristics of the Trial Sites

	Location			
Attribute	**Ibadan**	**Abuja**	**Ubiaja**	**Ikenne**
Coordinates				
Longitude	07°29.294"N	09°09.842"N	06°39.975"N	06°52.480"N
Latitude	003°53.129"E	007°20.708"E	006°20.638"E	003°46.120"E
Elevation (m)	227	459	330	71
Agro-ecological zone	Forest savannah transition	Southern Guinea savannah	Rainforest	Rainforest
Weather and climate attributes				
Rainfall (mm)	1410.5	1267.98	1741.17	1583.63
Temperature (min-max) (°C)	22.8–30.7	20.7–29.9	22.5–29.1	23.9–28.7
Relative humidity (min-max) (%)	54.3–91.8	74.0	86.0	88.1
Soil attributes				
pH(H_2O) (1:1)	6.30	3.65	5.49	4.72
OC (%)	0.51	0.19	0.52	0.79
N (%)	0.005	0.018	0.004	0.008
Bray P (ppm)	36.19	3.80	2.91	27.92
K (Cmol/kg)	0.605	0.141	0.111	0.485

Source: Geograpical Information System (GIS) and Analytical Services laboratories, IITA, Ibadan station, Nigeria.

Phenotypic Data

The phenotypic data included 25 traits assessed on 49 white yam clones that were evaluated at four sites in Nigeria (Ibadan, Abuja, Ubiaja and Ikenne) in 2017/2018 cropping season. The 25 traits comprised of agro-morphological and food quality traits measured using agreed yam ontology (http://www.cropontology.org/ontology/CO_343/Yam) and the standard operating protocol for yam variety performance evaluation trial [25] (Table 3). The leaf chlorophyll content (SCMR) was recorded using SPAD chlorophyll meter reader (SPAD-502, Konica Minolta, Osaka, Japan) as described by Markwell *et al*. [26]. The data were collected with an Android Galaxy Tab A 2016 using the field book app [27]. Protocols for traits that required more clarifications are explained as follow.

The disease severity score values for yam anthracnose disease (YAD) and yam mosaic virus (YMV) were converted to percentages and then used to estimate the area under disease progress curves (AUDPC) as described by Forbes *et al*. [28]:

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

where y_i = disease severity at the i^{th} observation, t_i = time (days) at the i^{th} observation, and n = total number of observations. The susceptibility scale values of YAD and YMV were estimated by first calculating the resistance scale values as described by Forbes *et al*. [28]:

$S_X = S_y \frac{D_X}{D_y}$ where S_y = the assigned susceptibility scale value, D_y = observed disease score (AUDPC or rAUDPC) for the standard genotype, S_X = estimated susceptibility scale value, D_X = observed disease score for the studied genotype and rAUDPC = relative AUDPC. The quotient of the assigned susceptibility value and the resistance measure of the check variety (AUDPC or rAUDPC) was used to obtain a constant. The resistance value of each genotype was then multiplied by the constant to obtain the susceptibility value of that genotype. The peel loss (%) was estimated using the formula:

Peel loss (%) = $\frac{WFP}{WUFTBR} \times 100$ where WFP is the weight of fresh peel and WUFTBR is the weight of unpeeled fresh tuber.

The dry matter content (%) was determined using the forced-air oven dry method [29] where the sampled tubers were washed, sliced, shredded and thoroughly mixed. A sub-sample of 100 g the shredded pieces was

Table 3: Detailed Description of Yam Traits Measured in the Study

SN	Trait Descriptor	Trait Acronym	Score Code – Descriptor State	Sample/Time Collected
Vegetative / establishment traits				
1	Days to first emergence	DAYFE	direct measurement (no. of days from planting to first emergence)	derived from recorded dates
2	Days to 50% sprout emergence	DAYSE	direct measurement (no. of days from planting to 50% emergence)	derived from recorded dates
3	Establishment rate	STRATE	direct measurement (proportion of emergence plants over total number planted)	plot basis @ 2 MAP
4	Leaf chlorophyll content (nmol/cm)*	SCMR	direct measurement (measured on 3 fully opened leaves)	on 5 plants @ 3MAP
5	Stem number per plant	STNP	direct measurement: done by counting	on 8 plants @ 4 MAP
6	Stem diameter per plant (cm)	STDP	direct measurement: done using vernier caliper	on 5 plants @ 5 MAP
7	Plant vigour	PLNV	1=low, 2=medium, 3=high	on 5 plants @ 5 MAP
Disease traits				
8	Yam mosaic virus severity score	YMV	1=no visible symptom of disease; 2=mild; 3=low; 4=intermediate; 5=high	on 8 plants @ 2, 3, 4, 5 and 6 MAP
9	Yam anthracnose severity score	YAD	1=no visible symptom of disease; 2=mild; 3=low; 4=intermediate; 5=high	on 8 plants @ 2, 3, 4, 5 and 6 MAP
10	Root knot nematode severity	RKN	1=no visible symptom of disease; 2=mild; 3=low; 4=intermediate; 5=high	at harvest (8 MAP)
11	*Scutellonema bradys* nematode severity	SBN	1=no visible symptom of disease; 2=mild; 3=low; 4=intermediate; 5=high	at harvest (8 MAP)
Tuber and quality traits				
12	Tuber number per plant	TTNPL	direct measurement: done by counting	at harvest (8 MAP)
13	Total fresh tuber yield ($t.ha^{-1}$)	TBRYLD	direct measurement	at harvest (8 MAP)
14	Tuber dry matter content (%)	DMC	direct measurement	
15	Peel loss (%)	PLOSS	direct measurement	
16	Starch content (%)	SYLD	direct measurement	
17	Pasting temperature	PTEMP	direct measurement	
18	Peak viscosity	PV	direct measurement	
19	Time to peak viscosity	PTIME	direct measurement	
20	Holding strength/setback viscosity	HS	direct measurement	
21	Breaking down viscosity value	BV	direct measurement	
22	Final paste viscosity	FPV	direct measurement	
23	Flour yield (%)	FYLD	direct measurement (derived estimate)	
24	Ash content (%)	ASHC	direct measurement (derived estimate)	
25	Protein content (%)	PROTEINC	direct measurement (derived estimate)	

*The leaf chlorophyll content (SCMR) was recorded using Soil Plant Analytical Development (SPAD) chlorophyll meter reader (SPAD-502, Konica Minolta, Osaka, Japan) as described by Markwell *et al*. [26].

oven dried at 105 °C for 24 h and the tuber dry matter was then determined as the percentage of dry wet over wet weight. The extraction and drying of starch were done using a modified protocol of Asaoka *et al*. [30]. Tuber samples of each genotype were randomly selected, weighed, and washed. The sampled tubers were peeled, shredded and mixed in a container. About 100 g of each grated and mixed sample was put in a bottle, followed by addition of 200 ml of distilled water and ground for 5 min using the LabMill. After blending, 3 l of water was added prior to sieving using 125 µm mesh or 90 mm test sieve (Yokyo SANPO).

The mixture was left for 2 h to permit settling of starch particles and decantation of supernatant. The starch particles were put in dishes of known masses and dried to constant mass in an oven at 60 °C. The starch yield (%) was determined using the method of Krochmal & Kilbride [31]:

$$\text{Starch yield } (\%) = \frac{WDS}{WFTBR} \times 100 = \frac{W_3 - W_1}{W_2 - W_1} \times 100$$

where WDS is the weight of dried starch content, WFTBR is the weight of fresh tuber, W_1 = mass of evaporating dish; W_2 = mass of evaporating dish + mass of starch before drying; and W_3 = mass of evaporating dish + mass of starch after drying.

The pasting profile of starch was determined using a Rapid Visco-Analyser (RVA) connected to a computer with thermocline for windows version 1.1 software [32, 33]. Data collected on starch pasting attributes included: pasting temperature (temperature at which irreversible swelling of the starch granules occurs); peak viscosity (highest viscosity during the 95 °C heating period); holding strength/hot paste stability viscosity (lowest viscosity at the end of the 95 °C heating period); breakdown value (change in viscosity from peak to holding strength); final or cold paste viscosity (highest viscosity at end of the 50 °C cooling period) and peak time (time taken to reach peak viscosity). The flour yield or content (%) was determined using similar method as the starch [30]:

$$\text{Flour yield } (\%) = \frac{WDS}{WFTBR} \times 100$$ where WDF is the weight of dried flour content and WFTBR is the weight of fresh tuber.

The ash content was determined using the protocol described by AOAC [34]. About 2 g dried sample of each genotype was weighed into a clean porcelain crucible. The crucible was put in a muffle furnace set at 600 °C and left for 6 h. The crucibles containing charred samples were transferred to a desecrator, cooled and reweighed.

The percent ash was estimated as: % ash = $\frac{W_3 - W_1}{W_2 - W_1} \times 100$ where W_1 = mass of empty crucible; W_2 = mass of crucible + yam sample; and W_3 = mass of crucible + ash.

Protein content was determined using the micro-Kjeldahl method (N × 6.25) [35].

Molecular Data

Young fresh leaves were collected from field grown three plants per clone using dried ice and lyophilized before DNA extraction. Genomic DNA was extracted using modified CTAB protocol with slight modification [36]. DNA quality and concentration were accessed using both agarose gel and nanodrop following Aljanabi & Martinez [37]. Concentrated DNA of 50 µL 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 v.5.2.43 [38, 39]. The VCF file was filtered for missing value and polymorphic SNPs with quality parameter and a call rate > 80%, depth >95%, and minor allele frequency > 5%. After filtering, 6337 polymorphic SNP markers were retained and used to construct genomic relationship matrix in the R [40] package rrBLUP [41]. The missing data for markers were imputed using beagle 4 [42]. The SNP distribution and density along the different chromosomes was accessed using CMplot R package [43]. The VCF file with the final SNPs markers number was converted to the additive format in 0, 1, 2 where zero stands for genotype with no minor allele, 1 for heterozygote and 2 for homozygote minor allele count at each locus using recodeA function implemented in plink [44]. The deviation of 1 from gene content or MAF matrix were obtained to generate score of -1, 0, 1 to be used in rrBLUP to construct the genomic relationship G-matrix.

Data Analyses

Different analysis pipelines were employed to dissect the genetic and non-genetic factors influencing the performance of yam clones in multi-location trial dataset. The data collected were first subjected to a linear mixed model by residual maximum likelihood (REML) procedure [45] to estimate the variance parameters and the empirical Best Linear Unbiased Predictions (EBLUPs) for random effects using ASReml-R 4 [46].

The linear mixed model used was

$y = X_{\beta} + Z_u u + Z_g u_a + Z_g u_{\tilde{a}} + \varepsilon$ where y is the data vector of the response variable across p locations with Nj plots per location j. Each location was treated as separate trial so that $p=4$; β is the vector of fixed effects associated with the corresponding design matrix (X), including the location main and location specific design-based replication effects. The term u is a vector of random effects associated with location specific field blocking structures (block within replication) used to capture extraneous variation with the corresponding design matrix Z_u; u_a and $u_{\tilde{a}}$ are the vectors of random additive and non-additive (residual) genetic within location effects, respectively, with corresponding design matrix Z_g. The genotype (clone) as associated with G-matrix and individual identity was fitted to obtain unbiased estimates of genetic variance. Accordingly, the genetic variance was partitioned to the additive effect which was associated with a covariance structure proportional to genetic relationships derived from the molecular markers and the non-additive genetic effect which explained by individual identity rather than the genomic relationship matrix following the approach of Borgognone *et al*. [47] and Ovenden *et al*. [48]. ε is the vector of errors or residuals modelled random within each trial.

From the variance component analysis, different genetic parameters such as additive genetic variance, non-additive genetic variance, non-genetic variance associated with among plots and within plot effect, proportion of total genetic variances that are additive, trait heritability ((both narrow sense (h^2) and broad sense (H^2)), genotypic coefficients of variation (GCV), phenotypic coefficient of variation (PCV), expected genetic advance (GA), and genetic advance based on mean (GAM) from attempting superior clone selection were determined. The GCV and PCV were determined following the formula described in Burton & Devane [49]. The GCV and PCV values were categorized using the technique proposed by Deshmukh *et al*. [50] as follows: values <10% = low, values that are 10 – 20% = medium and values >20% = high.

Narrow (h^2) and broad (H^2) sense heritability values were determined using a formula by Robinson *et al*. [51]. The h^2 and H^2 values were considered as low for values that range from 0 – 30%, moderate for values that range from 30 – 60% and high for those >60% as per Robinson *et al*. [51]. 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 equation by Shukla *et al*. [52]. The GAM values were classified as low for values <10%, moderate for values ranging from 10-20% and high for values >20% as described by Shukla *et al*. [52].

The BLUP prediction of genotypic values for the clones extracted for each trait in linear mixed model with genomic relationship matrix were subjected to the multivariate analysis that combined the principal component (PCA) and canonical discriminant analysis (CDA) using the procedure PRINCOMP and CANDISC in SAS version 9.5 [53]. The PCA analysis was used to remove highly correlated traits that provide redundant information in the MET dataset while CDA was applied to the retained traits with PCA analysis for assessing the EBLUP differences among yam clones and identify key traits that best discriminate the yam clones effectively in the dataset. The PCA was performed on correlation matrix option as units of measurement of the individual traits in the dataset differ [54]. The principal components that exhibited eigenvalue > 1.0 according to the Kaiser criterion [55] were retained as sufficient to explain the largest amount of variation possible in dataset. The signgificance of trait contribution to the variation accounted by the retained principal component was based on the absolute eigenvector arbitrary cutoff value of 0.35 [56]. Canonical discriminant analysis was applied to small number of orthogonal traits extracted by PCA that accounted for the largest amount of variation possible among the 25 traits describing the 49 yam clones in METs.

RESULTS

Quantitative Genetic Parameter Estimates for Measured Traits

The genotypes exhibited wide ranges of variability within most of the measured traits (Table **4**). Traits with wide range of variability included: days to first emergence (14.9–24.6 days), days to 50% emergence (26.7–38.1 days), establishment rate (78.8–98.8%), leaf chlorophyll content (40.8–50.5 SPAD value), total tuber yield (6.1–15.6 t ha^{-1}), starch pasting property traits [breakdown value (70.50–717.75 cP), final peak viscosity (2055.50–3415.50 cP), holding strength (113.22–533.75 cP), peak viscosity (1545.00–2600.75 cP)], ash content (0.71–4.81%), peel loss (8.69–33.63%), protein content (2.88–7.01%), and starch yield (15.82–26.91%).

The genetic and non-genetic effects were substantial in contributing to the variation in trait performances in the current set of materials but to varied degrees (Table **4**). The non-genetic (environmental) effects contributed to higher variation in the dataset than the genetic effect for the majority of the traits except yam mosaic virus severity score, tuber number per plant, ash content, flour yield, peel loss, and protein content. The percentage of total genetic variance that are additive and non-additive (dominant, epistatic) varied among the measured traits. The additive genetic variance accounted for the highest proportion of total genetic variance in the dataset for traits such as stem diameter, plant vigour, yam anthracnose disease susceptibility scale, peel loss and the starch peak and setback viscosities. In contrast, majority of the measured traits such as days to first sprout emergence, days to 50% sprout emergence, stem number per plant, plant establishment rate, leaf chlorophyll content, tuber dry matter, yam mosaic virus susceptibility scale, tuber number per plant, fresh tuber yield, starch RVA attributes such as breakdown, pasting tempeture, time to peak viscosity and peak viscosities, and quality attributes such as ash content, flour and starch yield had the highest proportion of non-additive genetic variance. The additive genetic variance was nill or nigligible for leaf chlorophyll content, dry matter, root-knot nematode susceptibiltiy score, flour and starch yield.

The narrow sense heritability was generally low (<0.30) for all traits except yam anthracnose susceptibility scale (0.31), ash content (0.30) and peel loss (0.89). The broad sense heritability estimates

Table 4: Estimated Genetic and Non-genetic Parameters of Agronomic and Quality Traits of white Yam Clones from Multi-Location Trials

Trait	Mean±SE	Range	σ^2_a	σ^2_{rg}	σ^2_{ng}
Days to first sprout emergence	19.84±2.80	14.88-24.63	1.86	4.54	21.4
Days to 50% sprout emergence	33.01±3.43	26.75-38.13	0.32	4.45	28.9
Stem number per plant	6.07±0.41	4.1-7.08	0.28	0.13	0.55
Stem diameter per plant (cm)	1.98±0.37	1.17-3.25	0.06	0.14	0.32
Establishment rate	91.51±5.45	78.75-98.75	21.11	33.93	96.3
Leaf chlorophyll content (nmol/cm)	46.14±2.79	40.8-50.51	0	7.59	16.101
Plant vigour	2.39±0.19	2.06-2.71	0.02	0.014	0.31
Tuber dry matter content	31.96±1.47	27.61-35.96	0.05	4.22	7.61
Root knot nematode severity	1.46±0.38	1.1-1.95	0.0001	0.03	0.15
Scutellonema bradys nematode severity	1.45±0.21	1.1-2.08	0.025	0.025	0.086
Yam mosaic virus severity score	2.86±0.19	2.16-3.64	0.03	0.09	0.09
Yam anthracnose severity score	2.50±0.23	2.19-3.34	0.05	0.008	0.11
Tuber number per plant	1.58±0.20	1.13-2.46	0.07	0.11	0.101
Total fresh tuber yield (t ha^{-1})	10.33±1.96	6.14-15.61	1.73	3.53	8.52
Breaking down viscosity value	380.35±77.84	70.5-717.75	1240.31	9529.6	67941.3
Final paste viscosity	2527.10±150.65	2055.5-3415.5	43747.92	25652.1	80754.9
Holding strength/setback viscosity	895.69±113.22	533.75-1405.5	20554.88	17651.3	44762.9
Pasting temperature	81.40±0.56	79.77-83.37	0.058	0.33	1.13
Pasting time	4.97±0.14	4.58-6.65	0.015	0.065	0.081
Peak viscosity	2011.81±130.18	1545-2600.75	9312.091	21786.6	53391.8
Ash content	2.88±0.24	0.71-4.81	0.182	0.339	0.089
Flour yield	27.23±1.63	20.79-31.11	0	4.76	4.05
Peel loss	18.74±1.37	8.69-33.63	24.32	1.76	1.11
Protein content	4.70±0.24	2.88-7.01	0.24	0.51	0.082
Starch content	22.11±2.62	15.82-26.91	0.058	4.39	5.275

SE=Standard error, σ^2_a=additive genetic variance, σ^2_{rg}=residual genetic variance, σ^2_{ng}= non-genetic variance.

Table 4: Continued.

Trait	% σ^2_a	σ^2_g/σ^2_{ng}	h^2	H^2	GCV	PCV	GA	GAM
Days to first sprout emergence	29	0.30	0.07	0.23	12.8	26.6	2.5	12.6
Days to 50% sprout emergence	7	0.17	0.01	0.14	6.6	17.6	1.7	5.1
Stem number per plant	68	0.75	0.29	0.43	10.5	16.1	0.9	14.3
Stem diameter per plant (cm)	30	0.63	0.11	0.38	22.6	36.4	0.6	28.5
Establishment rate	38	0.57	0.14	0.36	8.1	13.4	9.1	10.0
Leaf chlorophyll content (nmol/cm)	0	0.47	0	0.32	6.0	10.5	3.2	7.0
Plant vigour	59	0.11	0.05	0.10	7.7	24.5	0.1	5.1
Tuber dry matter content	1	0.56	0.004	0.36	6.5	10.8	2.6	8.1
Root knot nematode severity	0	0.20	0.001	0.17	11.9	29.1	0.1	10.2
Scutellonema bradys nematode severity	50	0.58	0.18	0.37	15.4	25.4	0.3	19.4
Yam mosaic virus severity score	25	1.33	0.15	0.58	12.1	16.0	0.5	17.5
Yam anthracnose severity score	86	0.53	0.31	0.35	9.6	16.4	0.3	11.8
Tuber number per plant	39	1.78	0.25	0.65	26.9	33.6	0.7	44.9
Total fresh tuber yield (t ha^{-1})	33	0.62	0.13	0.38	22.2	35.9	2.9	28.1
Breaking down viscosity value	12	0.16	0.05	0.39	27.28	73.76	225.40	67.30
Final paste viscosity	63	0.86	0.29	0.46	10.42	15.33	367.19	24.88
Holding strength/setback viscosity	54	0.85	0.25	0.46	21.82	32.16	272.95	47.41
Pasting temperature	15	0.34	0.04	0.26	0.77	1.51	0.66	1.58
Pasting time	19	0.99	0.09	0.50	5.69	8.07	0.41	13.87
Peak viscosity	30	0.58	0.11	0.37	8.77	14.45	221.55	22.63
Ash content	35	5.85	0.30	0.85	25.06	27.12	1.37	22.63
Flour yield	0	1.18	0	0.54	8.01	10.90	3.30	22.63
Peel loss	93	23.50	0.89	0.96	27.25	27.82	10.31	22.63
Protein content	32	9.15	0.29	0.90	18.43	19.41	1.69	22.63
Starch content	1	0.84	0.006	0.46	9.54	14.10	2.95	22.63

%σ^2_a=% of total genetic variance that is additive, σ^2_g/σ^2_{ng}= ratio of total genetic variance to non-generation variance, h^2=narrow sense heritability H^2=broad sense heritability, GCV=genotypic coefficient of variation, PCV=phenotypic coefficient of variation, GA=genetic advance, GAM=genetic advance based on mean.

ranged between 0.10 (plant vigour) and 0.65 (tuber number per plant) for agro-morphological traits, between 0.17 (root-knot nematode susceptibility score) and 0.58 (yam mosaic virus susceptibility scale) for biotic stress resistance traits, between 0.26 (pasting temperature) and 0.5 (time to peak viscosity) for starch pasting property attributes, and between 0.46 (starch yield) and 0.96 (peel loss) for food quality traits. Traits with high broad-sense heritability estimates (> 0.6) were tuber number per plant (0.65), ash content (0.85), protein content (0.90) and peel loss (0.96). Peel loss combined high narrow and broad sense hertibality estimates whilst days to first sprout emergence, days to 50% sprout emergence, root-knot nematodes susceptibilty score, plant vigour, pasting temperature had both low narrow and broad sense heritability values (< 0.3). The narrow sense heritability was generally low (<0.30) for all traits except yam anthracnose susceptibility scale (0.31), ash content (0.30) and peel loss (0.89). The broad sense heritability estimates ranged between 0.10 (plant vigour) and 0.65 (tuber number per plant) for agro-morphological traits, between 0.17 (root-knot nematode susceptibility score) and 0.58 (yam mosaic virus susceptibility scale) for biotic stress resistance traits, between 0.26 (pasting temperature) and 0.5 (time to peak viscosity) for starch pasting property attributes, and between 0.46 (starch yield) and 0.96 (peel loss) for food quality traits. Traits with high broad-sense heritability estimates (> 0.6) were tuber number per plant (0.65), ash content (0.85), protein content (0.90) and peel loss (0.96).

Peel loss combined high narrow and broad sense hertibality estimates whilst days to first sprout emergence, days to 50% sprout emergence, root-knot nematodes susceptibilty score, plant vigour, pasting

temperature had both low narrow and broad sense heritability values (< 0.3). The remaining traits had low GCV values ranging between 6.5 and 9.6%. Traits that exhibited the high PCV values were starch breakdown viscosity (73.76%), stem number per plant (36.4%), fresh tuber yield (35.6%), tuber number per plant (33.6%), starch setback viscosity (32.16%), tuber dry matter content (29.1%), ash content (27.12%), peel loss (27.25%), days to first sprout emergence (26.6%), *Scutellonema bradys* susceptibility score (25.4%), and plant vigour (24.5%) whereas those with the lowest PCV were starch pasting temperature (1.51%) and time to peack viscosity (8.7%).

Genetic advance as percent of the mean (GAM) ranged from 0.8–59.3% (Table **6, 4**). High GAM values

Table 5: Eigen Vectors, Eigen Values, Percent Variation and Accumulated Variation Accounted by the First Nine Principal Components

Trait	Principal components								
	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**	**PC9**
ASHC	0.00	0.03	-0.25	**-0.36**	-0.02	0.30	-0.08	0.10	-0.12
BV	0.29	0.29	0.05	0.00	-0.25	0.08	0.18	0.06	-0.15
DAYFE	-0.12	0.13	**-0.36**	0.14	0.21	0.00	-0.02	0.21	**0.39**
DAYSE	-0.02	0.19	**-0.41**	0.09	0.17	0.19	0.10	0.02	0.17
DMC	0.29	0.12	0.01	0.18	0.05	0.19	**-0.44**	-0.01	-0.01
FPV	-0.06	**-0.37**	0.15	**0.35**	0.07	0.22	0.06	0.26	-0.04
FYLD	0.21	0.15	0.03	0.32	0.33	-0.18	-0.17	-0.15	-0.23
HS	-0.26	-0.30	0.16	0.16	0.05	0.16	-0.13	0.26	-0.19
SCMR	0.04	0.28	0.04	-0.04	-0.01	0.15	-0.28	0.07	**0.48**
PLNV	-0.16	0.27	0.31	0.12	-0.02	0.28	-0.08	-0.23	-0.16
PLOSS	-0.01	-0.11	0.17	-0.29	-0.30	0.24	-0.31	0.27	0.06
PROTEINC	0.03	0.19	0.07	0.25	0.00	-0.25	0.26	**0.36**	0.05
PTEMP	**-0.35**	0.06	-0.03	-0.01	0.21	0.05	0.09	-0.04	-0.18
PTIME	-0.18	**-0.38**	-0.05	0.13	0.10	0.01	-0.05	-0.13	**0.36**
PV	0.32	-0.05	0.07	0.31	-0.09	0.19	0.30	0.14	0.03
RKN	0.18	0.02	0.09	-0.04	0.03	**0.41**	0.33	0.03	0.10
SBN	0.15	-0.21	-0.10	0.25	-0.10	**0.36**	0.03	-0.33	0.13
YAD	0.18	-0.15	-0.09	0.06	-0.33	-0.31	-0.09	0.34	0.04
YMV	0.13	-0.21	-0.18	-0.15	-0.21	-0.06	0.25	**-0.36**	0.00
STDP	-0.23	0.26	0.07	0.14	-0.33	0.06	0.10	0.11	0.12
STNP	0.21	-0.08	0.27	-0.31	0.33	-0.05	0.11	0.09	0.19
STRATE	0.00	-0.04	0.28	0.12	-0.26	-0.25	-0.06	-0.33	**0.38**
SYLD	0.31	-0.05	-0.01	0.09	0.09	-0.06	**-0.35**	-0.01	-0.06
TBRNP	0.27	-0.12	0.22	-0.25	0.34	0.00	0.13	0.10	0.14
TBRYLD	-0.19	0.19	**0.43**	-0.03	0.13	0.01	0.09	-0.04	0.16
Eigen value	4.09	3.14	2.75	2.13	1.75	1.52	1.31	1.20	1.08
Variation (%)	16.36	12.58	11.00	8.50	6.98	6.09	5.22	4.79	4.33
Accumulated variation (%)	16.36	28.94	39.94	48.44	55.42	61.51	66.73	71.52	75.85

PC=Principal component; values in bolds represent traits that contributed most to variability in the various PCs; ASHC=ash content; BV=breaking value; DAYFE=days to first sprout emergence; DAYSE=days to 50% sprout emergence; DMC=tuber dry matter content; FPV=final paste viscosity; FYLD=flour yield; HS=holding strength; SCMR=leaf chlorophyll content; PLNV=plant vigour; PLOSS=protein content; PROTEINC=protein content; PTEMP=pasting temperature; PTIME=pasting time; PV=peak viscosity; RKN=root knot nematode; SBN=*Scutellonema bradys* nematode; YAD=yam anthracnose severity; YMV=yam mosaic virus; STDP=stem diameter per plant; STNP=stem number per plant; STRATE=establishment rate; SYLD=starch content; TBRNP=tuber number per plant; TBRYLD=total fresh tuber yield.

were exhibited for stem number per plant (30.3%), *Scutellonema bradys* nematode (20.7%), tuber number per plant (44.3%), fresh tuber yield (28.1%), starch breakdown viscosity (59.3%), holding strength (30.5%), ash content (47.6%), peel loss (55.0%) and protein content (36.0%); whilst days to 50% sprout emergence (5.1%), establishment rate (9.9%), leaf chlorophyll content (6.9%), plant vigour (4.2%), tuber dry matter content (8.1%), root knot nematode (6.8%), pasting temperature (0.8%) and time to peak pasting temperature (8.2%) exhibited low GAM.

Trait selection for breeding

Principal component analysis efficiently reduced the possible redundancy of information with the traits that have some degree of correlation in the dataset. Nine explicative components, each exhibiting eigenvalue > 1.0 explained about 76% of the total variation of the 25 traits used to describe the 49 clones in METs (Table **5**).

Of the 25 traits recorded to describe the yam clones, 15 (emboldened black) were considered important traits that accounted for the largest amount of variation possible in dataset (Table **5**). The 15 traits with the absulute eigenvector value > 0.35 that significantly captured most of the variation in the MET dataset were days to first emergence (DAYFE), days to 50% sprout emergence (DAYSE), stand establishement rate (STRATE), leaf chlorophyll content (SCMR), root knot nematode susceptibility score (RKN), *Scutellonema brady* nematode susceptibility score (SBN), yam mosaic virus susceptibility scale (YMV), fresh tuber yield (TBRYLD), tuber dry matter content (DMC), starch pasting property attributes final peak viscosity (FPV), time to peak viscosity (PTIME) and pasting temperature (PTEMP), starch yield (SYLD), ash content (ASHC) and protein contenet (PROTEINC). Of the 15 important traits extracted with the PCA, ash content, protein content and starch yield were recorded at single location (at Ibadan) while the starch pasting property traits FPV, PTEMP, and PTIME were recorded at two locations (at Abuja and Ibadan). The remaining nine traits were recorded to describe the yam clones at all the four locations.

Canonical discriminant analysis (CDA) of the nine traits assessed at all the test locations revealed that three canonical discrimiant variables with eigenvalues > 1.0 explained 70% of the total variation among the yam clones (Table **6**). When cononical coefficients were collectively examined, traits with absulute eigenvalues > 0.5 contributed most to the variability noted in genotypes. Accordingly, five traits namely tuber dry matter content, yam mosaic virus susceptibility scale, fresh tuber yield, root knot nematode susceptibility score and *Scutellonema brady* nematode susceptibility score were most effective in distinguishing the genotypes (Table **6**). Of the five most important distiguishing traits, fresh tuber yield, tuber dry matter and yam mosaic virus susceptibility scale exhibited the highest correlation coefficients with discriminant functions (Table **7**).

Table 6: Canonical Discriminant Analysis of Selected Growth, Yield and Disease Traits of Yam

Variable	CAN1	CAN2	CAN3
Days to first sprout emergence	-0.161	-0.310	-0.299
Days to 50% sprout emergence	0.256	0.354	0.298
Tuber dry matter content	0.514	-0.592	**1.018**
Leaf chlorophyll content (nmol/cm)	0.263	0.149	0.528
Root knot nematode severity	-0.516	0.523	**1.048**
Scutellonema bradys nematode severity	0.815	**-1.290**	-0.951
Yam mosaic virus severity score	**0.976**	0.907	0.191
Establishment rate	-0.010	0.055	0.019
Total fresh tuber yield (t ha^{-1})	**-0.707**	-0.174	0.219
Eigen value	1.91	1.23	1.01
Variation (%)	32.09	20.70	17.08
Accumulated variation (%)	32.09	52.79	69.87
Canonical correlation	0.81	0.74	0.71

CAN=canonical function.

Table 7: Correlations between Data Variates and Discriminant Functions

SN		Discriminant Function		
	Variable	1	2	3
1	DAYFE	-0.02	-0.05	-0.04
2	DAYSE	0.06	0.02	0.04
3	DMC	0.24	-0.38	**0.56**
4	SCMR	0.00	-0.06	0.30
5	RKN	0.00	-0.01	0.10
6	SBN	0.27	-0.32	-0.20
7	YMV	**0.50**	0.49	-0.10
8	STRATE	-0.03	-0.01	0.02
9	TBRYLD	**-0.35**	-0.04	0.07

DAYFE=Days to first emergence, DAYSE=Days to 50% emergence, DM=dry matter content, SCMR=leaf chlorophyll content, RKN=root knot nematode, SBN=*Scutellonema bradys* (yam nematode), YMV=susceptibility scale value for yam mosaic virus, STRATE=establishment rate, TTBRYLD=total fresh tuber yield, SN=serial number.

DISCUSSION

This study dissected the nature and magnitude of genetic and non-genetic factors explaining the variation in dataset from multilocation trials using phenotypic and molecular marker information. Findings showed the presence of useful variation in the current set of materials for growth, tuber yield and food quality traits that could be exploited through direct selection or population improvement scheme. The size of phenotypic variance that is due 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 selective or recombination breeding. The total genetic variance was low for large array of measured traits including fresh tuber yield in current dataset indicating that large proportions of the total variation was non-heritable or environmental. These findings are consistent with Egesi & Asiedu [24], who also found higher total genetic variance compared to the non-genetic variance for fresh tuber yield in yam. The high non-genetic effects on trait variations for the yam clones in the current dataset highlights the potential to improve these traits through use of a breeding method that utilizes high selection accuracy through manipulation of the growth environment or following population improvement that adds new variants into the existing or contributes to the genetic variance change in current genetic background. Traits such as yam mosaic virus susceptibility, tuber number per plant, ash content, flour yield, peel loss and protein content had large proportions of the phenotypic variation attributed to genetic factors and direct selection in short term would typically exploit the pre-existing genetic variation in the current set of materials. The slightly higher PCV values compared to the GCV generally imply that some traits were less sensitive to environmental effects. This reflects the tolerance of some clones in the current set of materials to the environmental changes around its specific genotypic optimum for the traits hence selection efficiencies were relatively stable in different locations for these traits. Traits with high PCV and GCV signify high possibility of selecting clones possessing superior values for the trait in the next clonal generation. Moreover, traits that had high broad-sense heritability ($H^2 \geq 0.6$) captured higher residual genetic variance (the dominance and epistasis) effects than contribution by additive genetic effect to the total genetic effect except one trait (*i.e*. peel loss), which combined higher additive and residual genetic effects to the total genetic effect. The broad-sense heritability is more important in a clonally reproducing crop's selection programme than the sexual and outcrossing crops as clonal propagation captures all genetic effects: additive, dominance and epistasis and can pass the genotype intact unto the next generation. Traits that exhibited high heritability and a high genetic advance of mean indicate their effective improvement through selective breeding. The traits with high heritability and high genetic advance also imply that they are under the control of additive genes, whilst those with high heritability and low genetic advance are under the control of non-additive genes, which hinder their genetic improvement through direct selection in the outcrossing crop but not in clonal propagating crops like yam. These findings agree with the proposition that traits with high H^2 and h^2 estimates implied their potential usefulness for genetic

improvement [57]. Johnson *et al*. [58] also noted the relevance of combining heritability with a genetic advance for efficient predictability of response to selection.

The BLUP prediction of genotypic and breeding values of traits by incorporating genomic relationship matrix G in current dataset demonstrated as a useful guide for yam breeders for selection and identification of potential parents with desired complimentary traits for hybridization and superior clones with variety potential for commercial deployment than using the analytic model implementing the phenotypic data alone. These findings agree with [59] who noted that earlier parental identification for crossing as a major merit of genomic selection. Genomic selection based on genetic values from genomic relationship matrix has been suggested for incorporation into breeding programmes of various crops [38, 47, 60–64], including root and tubers [65]. In yam, breeding practices are challenged by long generation cycle from seed to seed requiring many cycles of phenotypic selection to identify superior genotypes for crosses and variety testing. Better knowledge on the genetic merits of the breeding materials enables crop breeders to circumvent many cycles of phenotype-based selection by discarding genotypes with low genetic merits at an early stage of the breeding programme, whilst retaining those with high genetic merits for further crossing and subsequent selection in breeding stage. The reduction of the cycle of breeding and field evaluations through BLUP prediction with relationship matrix saves resources and increases the pace of cultivar release.

The multivariate techniques utilized in this study identified relevant traits in discriminating the yam clones in METs and worth for further dissection of performance stability across test locations. The principal component analysis identified linear combination of 15 traits from the 25 recorded traits that minimize within group variance and maximize between group variance for discriminating the yam clones effectively. Of the 15 traits identified relevant, nine were recorded at four locations and subjected to the canonical discriminant analysis. The canonical discriminant analysis further identified three traits namely tuber dry matter content, fresh tuber yield and yam mosaic virus disease susceptibility as highly distinguishing traits for the observed variation among individual clones in the dataset. These findings are in agreement with Eticha *et al*. [8] who also identified key traits that contributed to variability in agronomic and quality traits of hull-less spring barley using principal component analysis and canonical discriminant analysis.

CONCLUSIONS

The genetic parameter estimates established that the non-genetic effects contribute more to the total phenotypic variability in most of the studied traits in white yams than the genetic effects. Reduction of trait data dimensionality using PCA and subsequent CDA identified tuber dry matter content, yam mosaic virus severity score and fresh tuber yield as most important traits in distinguishing white yam genotypes variability in MET.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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