



Article Genotype-by-Environment Interaction of Yam (Dioscorea species) for Yam Mosaic Virus Resistance, Dry Matter Content and Yield in Uganda

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Abstract: Often, yam cultivars grown in different agro-ecologies show differential responses across production environments, a term known as genotype-by-environment interaction. Such genotype-byenvironment interaction makes selection of the best genotypes under varied production environments more complex. This study evaluated twenty yam genotypes in six test environments to assess genotype, environment, and their interaction effects on tuber yield, response to yam mosaic virus, and dry matter content. The experiments were conducted over two seasons across three locations in Uganda, using a randomized complete block design with three replications. There were significant effects ($p \le 0.001$) for genotype (G), environment (E), and genotype-by-environment interaction for all key traits assessed. Serere (2021) and Namulonge (2021) were identified as the most discriminating and representative environments for testing responses to yam mosaic virus, respectively. Serere (2021) was recognized as the most discriminating environment, whereas Arua (2021) emerged closest to an ideal environment for assessing yam tuber yield. The tested genotypes also exhibited resistance to yam mosaic virus disease, had high tuber yields and dry matter content. Genotypes UGY16020, UGY16034, UGY16042, and UGY16080 demonstrated highest resistance to yam mosaic virus disease, along with high yield and dry matter content, and are thus potential parents for yam genetic improvement. Further evaluation of the four genotypes should be carried out within farmers' production systems for selection, improvement and release as new yam varieties for Uganda.

Keywords: *Dioscorea*; yield stability; environments; genotype; yam mosaic virus; dry matter; disease resistance; Uganda

1. Introduction

Yam (*Dioscorea* spp.) is a major strategic crop for sustainable food production in Africa, given its superior productivity compared to other crops [1]. It is an important tuber crop with major food, commercial and socio-cultural values. *Dioscorea alata* is the most widely cultivated species globally, but ranks second to *Dioscorea rotundata* with respect to yam quantity produced in Africa [2]. The significance of yam in terms of production volume



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Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). and value cannot be over-emphasized. Africa accounts for over 95% of the world's annual production of about 49 million tons [3]. This is mostly produced within the yam belt region in West Africa, which includes Benin, Ghana, Ivory Coast, Nigeria and Togo, with Nigeria as the world's leading yam producer, accounting for more than 65% of worldwide production (72.6 million tonnes) [3]. Within the yam belt, over 60 million people are directly involved in yam production [4]. Yam is, therefore, an economically important part of the Gross Domestic Product (GDP) of these top producers and exporters in West Africa. For instance, Ghana's yam exports between 2017 and 2018 increased to USD 5.4 million [5] from USD 3.4 million.

Yams are widely used as an important food staple and fallback crop in Africa, Asia, the Caribbean, the Pacific Islands and South America [6]. Significantly, yams are essentially carbohydrate foods that are laden with valuable nutrients including relatively high protein, fats, ascorbic acid (Vitamin C), and dietary fiber levels [7]. Yams are also low in saturated fat and sodium [8]. The yam tuber is a rich source of minerals including copper, calcium, potassium, iron, manganese and phosphorus. A 100 g serving of yam tuber provides about 816 mg of Potassium [9]. Its high potassium and low sodium balance help to control blood pressure and offer protection against osteoporosis and heart disease. Yam products have a lower glycemic index than potato products, thus providing a more sustained form of energy and better protection against obesity and diabetes [9]. The proximate composition of edible yam tubers includes water (65 to 75%), protein (1 to 2.5%), fat (0.05 to 0.20%), and carbohydrates which are mainly starch (15 to 25%), as well as fiber (0.5 to 1.5%), and ash (0.7 to 2.0%) [10]. Yams also contain 8 to 10 mg/100 g of ascorbic acid, most of which is retained during cooking [7]. Yams are a rich source of vitamin B6, which is useful in reducing the risk of heart disease.

Yam cultivation is best suited to humid and sub-humid lowlands. The most suitable agro-ecological zones for yam production (also called yam agroecology) are deciduous forest and savannah areas [4], and there is evidence of strong genotype and environment interaction effect [11]. Thus, multi-location trials are important in yam breeding programs to enable the identification of genotypes with desired performance for broad or particular adaptation [12]. Stable genotypes are those that show minimal genotype-by-environment interaction across environments [13,14].

There exists limited scientific information and data on yams in Eastern Africa [7]. In Uganda, yams are grown on small-scale farms, often intercropped in banana fields with crops such as coffee, cassava and cocoyam, or as individual plants grown against trees for support. Yams are also mono-cropped on relatively large plots in eastern, northern and north-western Uganda where it has widespread importance [15]. The crop plays a vital role in smallholder farmers' livelihoods, particularly in densely populated areas of central, northern, north-western, and eastern Uganda. Yams have become an important cash crop in many parts of Uganda, allowing farmers to earn income from local and cross-border markets. In Uganda, yams are grown within the broad altitude range of 1140 to 2200 masl and wide range of soils, although mainly in clay, clay loam, sandy and sandy loam types [16]. In most parts of Uganda, yams are planted in March or April and harvested during November and December.

A better understanding of target environments is essential for a yam breeding effort that is committed to developing and identifying improved genotypes which are superior in terms of production, tuber quality and utilization potential [17]. Hyman et al. [18] emphasized that target environments composed of a set of farms and seasons are often highly variable and may be the cause of differential phenotypic expressions of plants within a crop under cultivation. Moreover, a major factor limiting efficiency of plant breeding programs is the connection of plant phenotypic expression. This generally depends on the environment and genotype-by-environment interaction (GEI) [19], which influences the nature, magnitude and predictability of selection. Although GEI poses a big challenge to breeding program efficiency, it cannot be ignored but could instead be exploited [17]. Characterizing and defining target sets of environments (TSE) for breeding and cultivar recommendation are among the strategies to exploit space and time dimensions of GEI. Environmental profiling helps strategically to locate experimental or selection sites, with greater power in predicting performance of breeding trials.

In this study, environments for yam cultivation were defined based on their cultivation methods, farmers' preferences and the cultivar produced. This helps to understand the distribution and zoning of yam cultivars in Uganda. Several studies have reported a strong genotype and environment interaction (GEI) in yam [20]. A stability study by Otoo et al. [2] of seven white yam genotypes in 13 environments in Ghana [21] showed that genotypes accounted for 8.9%, environment 30.8%, and genotype-by-environment (G \times E) 43.7% of the total variation. It was concluded that yam improvement, therefore, should be focused on multiple disease and pest resistance, and performance guaranteeing crop performance stability. Regarding disease incidence, severity, and environmental effects, Pinnschmidt and Hovmøller [22] explain that one major problem frequently encountered in deploying resistant host plants for disease control is the plasticity of phenotypic expression of resistance across different environments, due to interactions between host genotypes and environment. Earlier reports attributed variation in yam yield performance to inherent genotypic characteristics and preferences for different environmental conditions [2,14]. Therefore, careful evaluation is critical for identifying suitable genotypes to give the highest possible yield in different environments [20]. High yield and stability of genotypes across different environments are very important attributes desired by plant breeders. As a result, breeding materials require testing in diverse environments to assess consistency in genotypic performance, to identify superior varieties for wider or specific adaptation [23]. Genotypes are considered stable when their genotype-by-environment interaction effect remains insignificant from one environment to another and across years [24].

The principal aim of our study was to evaluate the effect of genotype-by-environment interaction on yam mosaic virus disease, tuber yield and dry matter content of yam genotypes in six test environments within Uganda. In addition, we examined the magnitude of genotype-by-environment interaction and report yam performances for traits studied in different Ugandan agro-ecologies.

2. Materials and Methods

2.1. Genetic Materials

A total of 20 yam genotypes, comprising 14 landraces assembled at the National Crops Resources Research Institute (NaCRRI), Uganda and six new introductions from West Africa, were evaluated in this study (Table 1).

S/N	Field Code	Status	Origin
1	UGY16001	Landrace	Uganda
2	UGY16012	Landrace	Uganda
3	UGY16020	Landrace	Uganda
4	UGY16080	Landrace	Uganda
5	UGY16085	Landrace	Uganda
6	UGY16003	Landrace	Uganda
7	UGY16013	Landrace	Uganda
8	UGY16022	Landrace	Uganda
9	UGY16034	Landrace	Uganda
10	UGY16039	Landrace	Uganda
11	UGY16042	Landrace	Uganda
12	UGY16064	Introduced	Nigeria
13	UGY16065	Introduced	Nigeria
14	UGY16066	Introduced	Nigeria
15	UGY16067	Introduced	Nigeria

Table 1. List of yam (Dioscorea spp.) genotypes used in the study.

S/N	Field Code	Status	Origin
16	UGY16069	Landrace	Uganda
17	UGY16070	Landrace	Uganda
18	UGY16071	Landrace	Uganda
19	UGY16073	Introduced	Nigeria
20	UGY16075	Introduced	Nigeria

Table 1. Cont.

2.2. Experimental Sites and Cropping Seasons

The trials were conducted at three sites; Arua, Serere, and Namulonge in northwestern, eastern, and central Uganda, respectively (Figure 1). The trials were established in two cropping seasons in March 2020 and December 2021, with each cropping season lasting nine months (March 2020 to December 2020, and March 2021 to December 2021). Each cropping season and location combination was considered an environment, giving a total of six environments (Table 2). Weather instruments available at these research stations were used for recording temperature and rainfall data during the experiments.



Figure 1. Pictures of yam trials at three experimental sites. (A) = Serere; (B-D) = Namulonge; (E) = Arua.

Table 2. Geographical characteristics of environments for the genotype-by-environment interaction study.

E a	Code	Location	Latitude	Longitude	Altitude (m)	Cropping Season
E ₁	Namu_2020 ^b	Namulonge	1°31′47.6″ N	33°27′24.7″ E	1140	2020
E_2	Namu_2021	Namulonge	0°31′39.3′′ N	32°37′20.7″ E	1156	2021
E ₃	Serere_2020 c	Serere	1°31′47.6′′ N	33°27′24.7″ E	1125	2020
E_4	Serere_2021	Serere	1°31′58.5′′ N	33°27′17.8″ E	1121	2021
E ₅	Arua_2020 ^d	Arua	3°4′44.4″ N	30°56′43.8″ E	1198	2020
E ₆	Arua_2021	Arua	3°4′39.9″ N	30°56′50.0″ E	1197	2021

^a Environments in which GEI trials were conducted;
 ^b National Crops Resources Research Institute, Namulonge;
 ^c National Semi-Arid Resource Research Institute, Serere;
 ^d Abi Zonal Agricultural Research and Development Institute, Arua.

2.3. Experimental Design and Trial Management

All trials were laid out in a randomized complete block design (RCBD) with three replications. In each replication, a plot comprised of eight plants (two rows with four mounds per row) established at a spacing of $1.2 \text{ m} \times 1.2 \text{ m}$. Before planting, mounds were sprayed with pre–emergence herbicide to control weeds, and setts were pre-sprouted to ensure uniform sprouting times. All plants were tagged for ease of identification during data collection. No fertilizer was applied, and weed control was done manually when necessary. Mounds were re–shaped by covering them with topsoil to avoid exposure of tubers to air. Vines were tailed with ropes and twines at eight weeks after planting.

2.4. Data Collection

2.4.1. Baseline Soil Characterization

Soil samples were collected from all environments, and analyses were conducted at the soil science department of the College of Agriculture and Environmental Sciences, Makerere University. The analyses tested soil texture by the hydrometer method [25], soil pH (2.5:1 H₂O) by using a pH meter [26], and cation-exchange capacity (CEC) was determined by the simple barium chloride method [27]. The exchangeable K⁺, Mg²⁺, and Na⁺ were determined using atomic absorption spectrophotometer, exchangeable acidity by titration method [28], and exchangeable Al³⁺ in soil was determined by titrimetry method [29]. Total N was determined by the Kjeldahl technique [28], available P was extracted and determined using Bray 1 [30], and ammonium and nitrate ion concentrations were determined using the steam distillation method [31].

2.4.2. Traits Measurement

Data were collected for yam mosaic virus severity, yam tuber yield expressed as kg/plot, and percent dry matter content (%). All measurements were taken based on the standard operating protocol for the yam varietal performance evaluation trial [32] and the trait ontology dictionary described in YamBase (https://yambase.org/ (accessed on: 18 December 2018) (Table 3).

Descriptor	Description	Period of Collection
Yam virus disease severity	 1 = No visible symptoms, 2 = Mosaic on most leaves, 3 = Mild symptoms, 4 = Severe mosaic, 5 = Severe leaf distortion and stunting 	Monthly
Tuber yield	Weight per plot	
	Calculated using the oven method and presented in percentage:	- Between 1–14 days after
Dry matter content	$= \frac{\text{weight of dry sample (g)}}{\text{weight of wet sample (g)}} \times 100$	harvesting

 Table 3. Trait descriptors used for the evaluation of yam genotypes.

Source: [32]; https://yambase.org/ (accessed on: 18 December 2018)

2.5. Data Analyses

Analysis of variance for the studied traits was combined across environments using a linear model implemented in the R package [33]. Violations of assumptions of analysis variance were tested before making mean comparison and other downstream analyses. Means were separated using Fisher's protected least significant difference. The linear model used in the analysis was:

$$Y_{ij} = \mu + \beta_i + G_i + E_j + GE_{ij} + \varepsilon_{ij}$$

where Y_{ij} = trait value of genotype, μ = grand mean, β_i = i-th block effect, G_i = i-th treatment effect, E_j = j-th environmental effect, GE_{ij} = ij-th genotype-by-environment effect, and ε_{ij} = treatment × block interaction, treated as error term.

The means data obtained from the analysis variance were later utilized in AMMI analysis [34] for the determination of the stability of the different yam genotypes, using the *"Metan"* package in R software [35] with the model:

$$Y_{ijk} = \ \mu + G_i + E_j + \sum_{K=1}^M \lambda_k \times \alpha_{ik} \times \gamma_{jk} + \rho_{ij}$$

where Y_{ijk} = the yield of the i-th genotype in the j-th environment, G_i = the effect of the i-th genotype (genotype mean minus the grand mean), E_j = the effect of the j-th environment (environment mean minus the grand mean), λ_k = the square root of the eigenvalue of the k-th Interaction Principal Component (IPCA) axis, α_{ik} and γ_{jk} = the principal component scores for IPCA axis k of the i-th genotypes and the j-th environment, respectively, and ρ_{ij} = the deviation of genotype i-th on environment j-th from the model.

To determine the mega-environments and visualize the "*which*—*won*—*where*" pattern, genotype plus genotype-vs-environment interaction (GGE) analysis was performed using "*Metan*" package in R software [35]. The GGE biplot was based on singular value decomposition (SVD) of the principal components, as described by [36], and the GGE model below implemented:

$$Y_{ij} = \mu_i + \beta_j + \sum \lambda_k \times \alpha_{ik} \times \gamma_{jk} + \varepsilon_{ij}$$

where y_{ij} is the performance of genotype i-th in environment j-th, μ is the grand mean, β_j is the main effect of j-th environment, k is the number of principal components (PC), λ_k is the singular value of the kth PC, α_{ik} and γ_{jk} are the scores for PC of i-th genotypes and j-th environment, respectively, and ε_{ij} is the residual associated with genotype i-th and environment j-th.

For mega-environment delineation of the experimental site, the "*which*—*won*—*where*" scatter plot was constructed with a polygon drawn by symmetrical scaling connecting genotypes distant from the biplot, such that the polygon contained all genotypes. Then the polygon was dissected by perpendicular lines drawn to the sides and running from the biplot origin [36]. The environmental vectors were projected from the axis. The ranking plot based on mean versus stability was generated by symmetrical scaling using the concept of average environment coordinate (AEC) to draw the average line and the arrow line pointing to the direction of increasing yield mean performance [37,38]. The comparison plot of genotype ranking relative to ideal genotype was generated by symmetrical scaling, using the same concept of AEC to draw an analogy between the genotypes and an ideal genotype.

3. Results

3.1. Baseline Soil Characteristics and Weather Conditions at Experimental Locations

Before planting, soil nutrient composition in each experimental field was determined (Table 4). Although phosphorus, copper, iron, and zinc levels were low, total nutrient profiles for experimental fields were within the range considered effective to sustain yam production. Weather data gathered throughout the trial period revealed fluctuations in temperature and rainfall at experimental sites. Nonetheless, meteorological conditions remained within the range required to maintain yam growth and yield (Table 4).

3.2. Performance of Yam Genotypes for Studied Traits across Six Test Environments

The analysis of variance (ANOVA) for yam mosaic virus, total yield of yams, and dry matter content revealed significant different ($p \le 0.001$) effects of genotypes, environments, and genotypes × environment interactions (Table 5). For yam mosaic virus, the contributions of genotype, environment, and genotype × environment interactions were 49.7%, 41.4%, and 8.8%, respectively, whilst percentage variations due to genotype, environment, and genotype × environment interactions for total tuber yield were 46.0%, 50.4%, and 3.6%,

respectively. For dry matter content, environment contributed the largest proportion of variation (72.4%), followed by genotypic effects (17.1%), while the lowest contributor to observed phenotypic variation (10.5%) was genotype-by-environment interaction (Table 5).

Table 4. Soil and weather characteristics at locations used as six test environments in the yam genotype-by-environment interaction trials.

Parameter	Critical ^a	E ₁ ^b	E ₂	E ₃	E ₄	E ₅	E ₆
Silt (%)		15.00	15.00	34.00	32.00	14.00	13.00
Clay (%)		40.00	43.00	15.00	16.00	34.00	35.00
Sand (%)		45.00	42.00	51.00	52.00	52.00	52.00
Ph (Paste extract)	4-8	5.13	5.19	5.27	4.96	6.69	6.25
Organic matter (%)	3.00	3.19	2.28	1.00	1.30	3.00	3.01
Nitrogen (mg/kg)	20.00	37.33	32.67	23.33	24.22	28.00	28.44
Potassium (mg/kg)	58.00	66.25	70.00	66.25	68.54	71.25	70.56
Phosphorus (mg/kg)	10.00	2.83	1.78	1.80	1.71	3.86	3.18
Copper (mg/kg)	5.00	9.11	9.04	20.95	19.69	8.16	8.07
Iron (mg/kg)	50.00	18.30	16.15	18.26	18.96	14.47	15.58
Manganese (mg/kg)	20.00	0.44	0.37	0.16	0.16	0.26	0.34
Zinc (mg/kg)	1.00	0.95	0.32	0.10	0.20	0.45	0.51
Av. Rainfall (mm/day)		6.31	4.99	6.20	4.53	7.88	5.20
Av. Min T ^c (°C/day)		18.80	18.01	18.82	19.12	19.67	20.02
Av. Max T ^d (°C/day)		27.11	25.54	27.27	28.13	28.14	29.12

^a Critical values of levels for nutrients required for yam growth, ^b six test environments (E1–E6) as defined in Table 2, ^c annual minimum temperature, ^d annual maximum temperature.

Table 5. Analysis of variance for performance of 20 yam genotypes evaluated in six test environments within Uganda with respect to yam mosaic virus, tuber yield and dry matter content.

Source of Variance	DF ^a	YMV ^b	TWY ^c	DMC ^d
Replication	2	0.09	8.52	5.41
Genotypes	19	1.74 ***	1037.22 ***	71.33 ***
Environment	5	1.45 ***	1135.69 ***	302.42 ***
Genotype \times Environment	95	0.31 ***	80.71 ***	43.92 ***
Residuals	238	0.11	54.23	11.24

^a Degrees of freedom; ^b yam mosaic virus; ^c total yield of yams; ^d dry matter content (%); level of significance *** (1%).

Despite the study showing significant differences in disease severity between tested genotypes across the six test environments, the severities recorded were generally mild to moderate. The mean disease severity score ranged from 1.3 to 2.2, with an average of 1.8 across environments (Table 6). Genotypes with the most outstanding performance for yam mosaic virus disease tolerance were UGY16001, UGY16085, UGY16012, UGY16042, UGY16080, and UGY16034, each with mean severity scores less than 2.0. The worst performing genotypes had severity scores above 2.0, including genotypes UGY16064, UGY16065, UGY16067, UGY16070, UGY16073, and UGY16075. Based on the studied environments, the lowest mean yam mosaic virus severity scores were recorded at Namulonge 2020 (1.7) and Namulonge 2021 (1.6). On average, genotypes scored slightly higher at Serere in both seasons: 1.8 in 2020 and 2.0 in 2021 (Table 6).

Genotypes	E ₁ ^a	E ₂ ^b	E ₃ ^c	E ₄ d	E ₅ ^e	E ₆ f	Mean
UGY16001	1.8	1.9	1.2	1.2	1.8	1.9	1.6
UGY16003	2.0	1.7	1.7	2.0	2.4	2.0	2.0
UGY16012	1.4	1.4	1.1	1.7	1.2	1.8	1.5
UGY16013	1.8	1.6	1.7	1.7	2.5	2.0	1.9
UGY16020	1.3	1.4	1.1	1.3	1.3	1.9	1.4
UGY16022	1.8	1.5	1.6	2.1	2.3	2.0	1.9
UGY16034	1.4	1.4	1.3	1.0	1.4	1.3	1.3
UGY16039	1.9	1.7	2.0	1.5	2.4	2.0	1.9
UGY16042	1.5	1.4	1.1	1.0	1.8	1.6	1.4
UGY16064	1.9	1.4	2.7	2.6	2.1	2.0	2.1
UGY16065	1.6	1.5	2.7	2.5	2.5	2.0	2.1
UGY16066	1.5	1.4	2.2	2.7	2.1	2.0	2.0
UGY16067	2.0	2.0	2.7	2.5	1.9	2.0	2.2
UGY16069	1.9	1.4	2.0	2.4	2.2	2.0	2.0
UGY16070	1.9	1.4	2.1	2.6	2.5	2.0	2.1
UGY16071	1.9	1.7	1.8	2.0	1.6	2.0	1.8
UGY16073	1.9	1.5	2.5	2.9	2.1	2.0	2.2
UGY16075	2.4	1.6	2.2	2.9	2.3	1.8	2.2
UGY16080	1.5	1.4	1.3	1.1	1.3	1.7	1.4
UGY16085	1.5	1.6	1.2	1.5	1.7	1.7	1.5
Mean	1.7	1.6	1.8	2.0	2.0	1.9	1.8
LSD g	0.6	0.4	0.5	0.5	0.7	0.4	0.2
CV ^h	19.2	19.3	16.5	15	21.2	13.3	17.9

Table 6. Mean yam mosaic virus severities for 20 yam genotypes assessed in six test environments within Uganda.

^a Namulonge 2020, ^b Namulonge 2021, ^c Serere 2020, ^d Serere 2021, ^e Arua_2020, ^f Arua 2021, ^g least significant difference, ^h coefficient of variation.

The mean tuber yield of yams ranged from 8.1 kg/plot to 31.9 kg/plot, with an average of 18.4 kg/plot across the test environments (Table 7; Figure 2). Genotypes UGY16034, UGY16085, UGY16012, and UGY16020 had the highest tuber weights, with mean values of 31.9 kg/plot, 29.6 kg/plot, 29.0 kg/plot, and 28.6 kg/plot, respectively. The lowest genotype performance across the test environments was UGY16070 (8.1 kg/plot), followed by UGY16022 (9.2 kg/plot) and UGY16003 (11.8 kg/plot). Serere 2020 had the highest total mean weight at 22.6 kg/plot, followed by Namulonge 2021 and Arua 2021, with 22.0 kg/plot and 20.6 kg/plot yields, respectively. The worst performing environment was Arua 2021, with a mean total weight of yam of 11.5 kg/plot (Table 7).

Table 7. Mean tuber yield (kg/plot) of 20 yam genotypes evaluated in six test environments in Uganda.

Genotypes	E ₁ ^a	E ₂ ^b	E ₃ ^c	E ₄ ^d	E ₅ ^e	E ₆ f	Mean
UGY16001	18.5	30.6	32.7	33.8	26.7	16.6	26.5
UGY16003	14.1	12.9	18.7	10.8	10.8	3.5	11.8
UGY16012	17.7	39.1	37.1	32.6	34.5	13.2	29.0
UGY16013	11.4	11.6	17.5	12.3	15.4	3.6	12.0
UGY16020	20.4	35.1	39.4	36.5	23.2	17.1	28.6
UGY16022	9.7	11.9	14.6	10.2	4.8	3.9	9.2
UGY16034	35.5	31.3	25.5	32.4	40.7	25.8	31.9
UGY16039	8.7	29.1	16.0	8.6	9.1	8.3	13.3
UGY16042	12.9	25.2	33.6	40.2	27.8	19.8	26.6
UGY16064	14.7	9.8	13.9	7.1	19.1	3.1	11.3
UGY16065	15.3	16.7	17.5	12.0	26.5	8.0	16.0
UGY16066	19.4	21.1	23.7	10.8	20.2	12.7	18.0
UGY16067	10.0	11.4	18.7	15.3	18.4	9.0	13.8

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UGY16069	19.5	17.3	15.9	8.2	13.7	10.2	14.1
UGY16070	7.5	10.3	13.7	7.6	5.4	4.2	8.1
UGY16071	14.7	15.1	19.1	10.7	17.7	6.2	13.9
UGY16073	13.3	20.9	17.0	9.5	25.9	9.3	16.0
UGY16075	9.8	24.6	21.9	13.7	23.9	8.2	17.0
UGY16080	11.2	28.6	23.7	30.9	18.3	19.9	22.1
UGY16085	17.4	37.4	32.3	33.8	29.4	27.0	29.6
Mean	15.1	22.0	22.6	18.8	20.6	11.5	18.4
LSD g	10.4	13.4	11.7	11.9	15.2	8.1	4.8
CV ^h	41.6	36.9	31.3	38.3	44.8	42.8	39.9

Table 7. Cont.

^a Namulonge 2020, ^b Namulonge 2021, ^c Serere 2020, ^d Serere 2021, ^e Arua 2020, ^f Arua 2021, ^g least significant difference, ^h coefficient of variation.



Figure 2. Pictures of harvested tubers from experimental sites.

Mean yam dry matter content ranged from 25.1% to 33.5%, with an average of 28.4% across test environments. The genotype with least dry matter content across the environments was UGY16069 (25.1%), while UGY16064 (33.5%) registered the highest DMC (Table 8). Arua 2021 had the highest mean dry matter content of 31.6% followed by Namulonge 2020 with a mean dry matter content of 30%. The lowest performing environments were Serere 2020 and Serere 2021 with mean dry matter content of 25.1% and 27.2%, respectively (Table 8).

Genotypes	E ₁ ^a	E ₂ ^b	E ₃ c	E ₄ ^d	E ₅ e	E ₆ f	Mean
UGY16001	31.5	27.8	26.3	24.1	27.5	33.6	28.5
UGY16003	31.0	25.9	23.7	27.3	33.2	24.8	27.6
UGY16012	28.2	28.5	23.0	29.1	24.7	21.2	25.8
UGY16013	30.3	21.4	27.3	31.6	29.3	30.5	28.4
UGY16020	27.9	28.9	23.0	32.7	25.3	35.5	28.9
UGY16022	30.9	28.6	28.0	27.7	32.3	33.1	30.1
UGY16034	29.1	25.2	22.3	26.2	22.2	30.8	26.0
UGY16039	33.4	32.1	28.7	26.5	33.0	33.3	31.2
UGY16042	29.7	27.7	23.0	24.5	29.2	33.6	27.9
UGY16064	41.1	39.5	29.0	31.2	31.2	29.2	33.5
UGY16065	29.4	30.8	21.0	28.3	30.7	33.5	29.0
UGY16066	33.6	24.0	20.3	34.8	31.8	33.2	29.6
UGY16067	31.3	27.8	29.7	24.1	31.3	29.6	29.0
UGY16069	22.7	25.0	24.0	17.2	24.2	40.1	25.5
UGY16070	28.6	28.5	25.3	27.7	32.0	33.5	29.3
UGY16071	20.6	21.3	30.0	28.5	24.8	25.0	25.1
UGY16073	35.9	27.9	18.7	21.7	28.3	30.6	27.2
UGY16075	29.9	30.1	33.4	24.2	27.5	28.9	29.0
UGY16080	26.2	28.1	20.0	30.2	24.8	38.3	27.9
UGY16085	28.4	28.5	26.3	26.5	26.0	34.2	28.3
Mean	30.0	27.9	25.1	27.2	28.5	31.6	28.4
LSD g	5.7	8.4	6.5	0.9	6.0	0.7	2.2
CV ^h	11.5	18.3	15.7	2.1	12.8	1.4	11.8

Table 8. Mean dry matter content of 20 yam genotypes evaluated in six environments within Uganda.

^a Namulonge 2020, ^b Namulonge 2021, ^c Serere 2020, ^d Serere 2021, ^e Arua 2020, ^f Arua 2021, ^g least significant difference; ^h coefficient of variation.

3.3. Additive Main Effect and Multiplicative Interaction (AMMI) Results

AMMI analysis showed a significant effect (p < 0.01) of genotypes, environments and interaction between genotype and environment for all traits. The first interaction principal component axis (IPCA 1) was significant ($p \le 0.001$) for all studied traits. Meanwhile, only dry matter content and yam mosaic virus were highly significant ($p \le 0.001$) for the second interaction principal component axis (IPCA 2) (Table 9). The first two IPCAs (IPCA 1 and IPCA 2) accounted for more than 60% of the variability in GEI for all traits investigated (Table 9).

Table 9. AMMI analysis of 20 yam genotypes evaluated in six test environments within Uganda.

SOV ^a	Df ^b	DMC ^c	TWY ^d	YMV ^e
Genotypes	19	71.3 ***	1037.2 ***	1.7 ***
Environments	5	302.4 ***	1135.7 ***	1.4 ***
Replication	12	9.75	75.3	0.2
Genotype \times Environment	95	43.9 ***	80.7 **	0.3 ***
IPCA 1	23	64.0 ***	167.4 ***	0.8 ***
IPCA 2	21	49.2 ***	71.2	0.2 **
IPCA 3	19	51.6	65.7	0.2
Error	228	11.3	52.7	0.1
Total	359	27.1	128.1	0.3

^a Source of variance, ^b degrees of freedom, ^c dry matter content, ^d total weight of yam, ^e yam mosaic virus; level of significance *** (1%), ** (5%).

The AMMI biplots (Figure 3) depicted correlations between IPCA 1 and genotype means for the various traits studied. Genotype UGY16022 had the lowest absolute IPCA 1 (0.033) value for dry matter content, and was thus the most stable genotype throughout the six-test environments, followed by UGY16066 (0.09) and UGY16073 (0.18) (Table 10; Figure 3A). Based on the absolute score for IPAC 1 (2.717), UGY16069 showed the least stable dry matter response in the six environments. With the exception of genotypes

UGY16022, UGY16066, and UGY16073, most of the genotypes in the dry matter content evaluation had absolute IPAC scores that were far from zero, indicating that the genotypes' performance was usually unstable for the trait (Table 10; Figure 3A).



Figure 3. AMMI1 biplot for mean dry matter content (**A**), the total weight of tubers (**B**), yam mosaic virus (**C**), and their respective PC 1 scores for 20 yam genotypes evaluated in six environments.

Table 10. Genotype means for traits, stability index (IPCA 1), and ranking across six test environments in Uganda.

Constras		DMC ^a			TWY ^b			YMV ^c	
Genotype	Mean	IPCA1	Rank	Mean	IPCA1	Rank	Mean	IPCA1	Rank
UGY16001	28.48	-0.38	5	26.48	-1.43	8	1.64	0.61	20
UGY16003	27.62	1.45	12	11.79	0.56	5	1.97	0.09	1
UGY16012	25.77	1.74	14	29.04	-1.48	17	1.46	0.17	10
UGY16013	28.40	0.38	11	11.97	0.46	1	1.87	0.22	6
UGY16020	28.87	-0.85	10	28.61	-2.12	16	1.39	0.32	12
UGY16022	30.10	0.03	1	9.19	-0.01	6	1.90	0.01	2
UGY16034	25.96	-0.31	7	31.85	1.68	18	1.31	0.31	7
UGY16039	31.18	0.25	6	13.31	-0.35	19	1.92	0.27	11
UGY16042	27.93	-0.55	3	26.57	-2.42	20	1.39	0.45	13
UGY16064	33.53	1.83	18	11.28	1.75	12	2.10	-0.49	16
UGY16065	28.95	-0.38	8	15.98	1.39	10	2.13	-0.47	18
UGY16066	29.61	0.09	17	17.97	1.26	9	1.98	-0.48	15
UGY16067	28.99	0.62	9	13.81	0.19	4	2.20	-0.26	14
UGY16069	25.52	-2.72	20	14.14	1.58	14	1.99	-0.22	3
UGY16070	29.27	-0.29	2	8.10	0.15	3	2.07	-0.33	8
UGY16071	25.05	0.59	19	13.89	0.94	2	1.83	0.09	4
UGY16073	27.18	0.18	15	15.98	1.28	11	2.16	-0.55	19
UGY16075	28.99	0.72	13	17.00	0.03	7	2.21	-0.39	17
UGY16080	27.93	-1.72	16	22.12	-1.96	15	1.37	0.35	9
UGY16085	28.33	-0.65	4	29.58	-1.53	13	1.52	0.29	5

^a dry matter content, ^b total yield of yams, ^c yam mosaic virus.

The most favorable environment identified for dry matter content was Namulonge 2021 with the lowest absolute IPAC 1 score of 0.41 and a mean of 27.880 (Table 11). In terms of total tuber yield, genotypes UGY16022, UGY16075, and UGY16070 were the most stable in the test environment with low IPAC 1 absolute scores (Table 10; Figure 3B). The least stable genotypes were UGY16020 (2.10) and UGY16042 (2.42).

Environment	DMC ^a		TWY ^b		YMV ^c	
	Mean	IPCA 1	Mean	IPCA 1	Mean	IPCA 1
Arua 2020 ^d	28.47	0.74	20.57	2.01	1.97	0.07
Arua 2021	31.63	-4.23	11.48	0.38	1.88	0.46
Namulonge 2020 ^e	29.98	1.53	15.08	3.88	1.75	0.35
Namulonge 2021	27.88	0.41	22.00	-1.31	1.56	0.82
Serere 2020 ^f	25.15	0.78	22.63	-1.34	1.81	-0.67
Serere 2021	27.20	0.77	18.84	-3.62	1.96	-1.03

Table 11. Environments' mean traits and stability index (IPAC 1) scores evaluated across six test environments in Uganda.

^a Dry matter content (%), ^b total weight of yams; ^c yam mosaic virus, ^d Abi Zonal Agricultural Research and Development Institute, Arua, ^e National Crops Resources Research Institute (NaCRRI), Namulonge, ^f National Semi-Arid Resource Research Institute, Serere.

Analysis of yam mosaic virus disease incidence in the test environments revealed relatively high absolute IPAC 1 scores, compared to values obtained for dry matter content and total yield of yam. The top three most stable genotypes in response to yam mosaic virus were UGY16022, UGY16071, and UGY16003 (Table 10; Figure 3C). Yam mosaic virus returned the highest IPAC 1 score of 1.030 for Serere 2021 and the lowest IPAC 1 score of 0.073 for Arua 2020 (Table 11).

3.4. Stability and "Which-Won-Where" Pattern of Genotypes for Traits Studied

For GGE analysis, the first two PCs explained 87.38% of the total interaction variations (PC 1-77.34%) and PC2_10.04%) for yam mosaic virus severity (Figure 4). The "which—won—where" GGE ranking biplot and stability provides a visual representation of the genotype results and genotype × environment interactions for yam mosaic virus (Figure 4A,B). The six environments were divided into three mega-environments: (i) Serere 2020 and Serere 2021 with genotype UGY16073 as the best performer; (ii) Arua 2020 with genotype UGY16039 as the best performer; and (iii) Arua 2021, Namulonge 2020, and Namulonge 2021 with genotype UGY16003 as the best performer (Figure 5A). This can be observed by the long length of Serere 2021 vectors from the origin. Namulonge 2021 was the most discriminating of the test environments, demonstrated on the average environment axis where it occupies a small angle (Figure 5B).



Figure 4. GGE ranking biplot showing (**A**) mean performance and (**B**) stability of 20 yam genotypes for yam mosaic virus, evaluated in six environments.





The six test environments were grouped into three mega-environments according to their total yield of yams. The first mega-environment included Serere 2021 and Serere 2020 with the best genotype as UGY16020 (Figure 6A,B). The second mega-environment included only one environment, Namulonge 2021 with genotype UGY16085 as the best performer. The third mega-environment consisted of three major environments, Arua 2020, Namulonge 2020, and Arua2021 with genotype UGY16034 as the best performer (Figure 6A). The best performing genotype in terms of yield (UGY16034) was also the most unstable (Figure 6B). Other genotypes such as UGY16003, UGY16067, and UGY16075 were observed to be stable across the environment, but with low yield and performance compared to other studied genotypes. The GGE polygon plot provides a visual assessment of the GEI. The GGE biplots explained 88.16% of the total variations, with 77.95% and 10.21% for PC1 and PC2 (Figure 7A). The GGE biplot shows that Serere 2021 was the most discriminating environment, whilst Arua 2021 was the lowest performing of the six text environments (Figure 7B). This was revealed by the long and short environment vectors of Serere 2021 and Arua 2021 respectively. Arua 2021 was the most representative of the mega environment of all the six test environments, observable by the small angle from the average environment axis (Figure 7B).

For dry matter content, the GGE ranking and stability biplot (Figure 8) gives a good visual assessment with both PC1 and PC2 explaining about 58.33% of the total variation observed. The biplot indicated that the six test environments were grouped into three mega-environments in terms of dry matter content. The first mega-environment included only Arua 2021 with the best genotype being UGY16069 (Figure 8A). The second mega-environment comprised Namulonge 2020, Namulonge 2021, Arua 2020, and Serere 2021 with the best performing genotype being UGY16064 (Figure 8A). The third mega-environment consisted of Serere 2020, with genotype UGY16003 as the best performer. The GGE biplot (Figure 9A,B) showed that Arua 2021 was the most discriminating environment, while Serere 2021 was the least discriminating of the six test environments. This was revealed by the long and short environment vectors of Arua 2021 and Serere 2021, respectively. Of all the six environments, Arua 2020 was the most representative of the mega-environment, according to the small angle from the average environment axis (Figure 9B).



Figure 6. GGE ranking biplot showing the mean (**A**) overall performance and (**B**) stability for total yield of yams (kg/plot) of 20 yam genotypes evaluated in six environments.



Figure 7. GGE biplots based on symmetrical scaling for (**A**) the "which-won-where" pattern and (**B**) the discriminating power and representativeness of test environments, involving 20 yam genotypes for total yield of yams (kg/plot) evaluated in six environments.



Figure 8. GGE ranking biplots showing (**A**) the mean performance and (**B**) stability for dry matter content of 20 yam genotypes evaluated in six environments.



Figure 9. GGE scatterplots based on symmetrical scaling for (**A**) the "which-won-where" pattern (**A**) and the discriminating power and (**B**) representativeness of test environments for dry matter content involving 20 yam genotypes evaluated in six environments.

3.5. Pearson Correlations among Traits Studied

A highly significant negative correlation (r = -0.85, d.f. = 19) was observed between yam mosaic virus and total yield of yams, whilst a non-significant positive correlation (r = 0.35, d.f = 19) was observed between dry matter content and yam mosaic virus.

4. Discussion

The overall goal of this study was to evaluate the performance of Ugandan yam genotypes across six test environments for yield, viral disease resistance, and dry matter content. The significant variation expressed in mosaic virus resistance, total yield of yam, and dry matter content of genotypes presents an important opportunity for yam breeding in Uganda. This variability could serve as the foundation for making progress in the genetic improvement of yams via selection for these traits. In this study, genotype × environment effects were highly significant for all traits studied, indicating significant variation in genotype mean performance across environments, which had a significant impact on the studied genotypes. The high genotype-by-environment interaction effect on the several traits suggests that selection for these traits can be effectively achieved by evaluating genotypes in different target environments. Tuber yield and dry matter content in yam, like other quantitative traits, are strongly impacted by genotype–environment interaction [14,21]. This characteristic makes it difficult for the selection of such genotypes for universal adaption. According to Nduwumuremyi et al. [39], the existence of a strong genotype–environment interaction for quantitative variables like tuber yield, dry matter content, and yam mosaic virus might hinder efforts to choose superior genotypes for diverse environments. This is because such performance cannot be duplicated in environments with varying environmental conditions [40].

Different yam genotypes have intrinsic varietal traits and preferences for various environmental conditions [21], particularly introduced genotypes in new environments [41]. As a result, genotypes must be assessed across several locations to discover specific places where they best fit, and where they may achieve their maximum yield potential [14]. This means that a standard yam variety selection approach for traits such as high dry matter content, high tuber yield, and yam mosaic virus resistance requires additional environments for screening resistance [2]. Breeders can use stability analysis to measure the level of genotype by environment interaction and classify genotypes as widely or narrowly adapted, based on stability indices [42]. As a result, breeding programs in Uganda that are aimed at developing yams for the above qualities should subject genotypes to multilocational assessment, with an emphasis on traits that are heavily impacted by environmental variables. Although this technique is more expensive, it provides greater precision in determining the top-performing genotypes in terms of dry matter content, tuber yield, and yam mosaic virus resistance.

The genotype main effect and genotype \times environment (GGE) biplot depicts the genotypes' overall effect as well as genotype \times environment interaction [43]. The "which-wonwhere" pattern of the GGE biplot's polygon view-based interaction is effective for identifying elite genotypes in single or multiple settings [36,38]. The use of GGE biplots in this work identified genotypes that coupled high mean performance with high stability, as well as highlighting preferences and adaption to particular situations. In terms of dry matter content, genotype UGY16069 was best suited to the Arua 2021 environment, whereas genotype UGY16003 performed best in Serere 2020. Genotype UGY16054, on the other hand, was well adapted to four environments: Namulonge 2020, Namulonge 2021, Arua 2020, and Serere 2021. Nonetheless, the ranking GGE biplot revealed that genotype UGY16071 performed best overall, despite being rather unstable across the test conditions. However, genotype performance for total weight of yam indicated that UGY16034 was the best performer although unstable, whereas genotype UGY16020 was primarily suited to two environments, Serere 2021 and Serere 2020. Other genotypes were adapted to a single environment, such as UGY16085 in Namulonge 2021, whereas genotype UGY16034 performed particularly well in three environments (Arua 2020, Namulonge 2020, and Arua 2021). A similar outcome was observed for yam mosaic virus, where the most common vertex genotypes were UGY16073, UGY16039, and UGY16003, identified as adapters for different environments. Earlier research on genotype \times environment analyses also found this phenomenon of distinct adaptability or environmental preferences by various yam genotypes. In Ghana, in research comprising 12 Dioscorea rotundata genotypes in 16 settings, Otoo et al. [2] used the GGE biplot to identify uniquely suited cultivars, validating the environmental uniqueness of distinct yam genotypes as per this current study.

According to Dhillon et al. [44], a genotype is deemed stable if its yielding ability varies little when planted in different conditions. Yan and Tinker [36] and Gurmu et al. [45]

suggested that stable genotypes are those whose variances remain largely consistent from one environment to the next. A persistently underperforming genotype, on the other hand, may also be stable. Nonetheless, in addition to greater performance for an attribute of interest, stability should always be addressed. According to a report by Purchase et al. [46], a yield stability index that combined rankings for high yield and stability (based on the AMMI stability value) can reveal genotypes that are stable across environments [47]. According to the findings of this study, genotype UGY16022 was stable but not the best performer in terms of yam mosaic virus severity score across all contexts. Furthermore, for total yield, genotype UGY16070 was the worst performer, although it was relatively stable compared to other genotypes. For dry matter content, genotype UGY16071 was the best performer but very unstable across the six test environments. For total yield of yam, genotype UGY16070 was the least impressive performer, though it was relatively stable compared to other genotypes. This shows that the genotype (UGY16070) responded positively to favorable environmental conditions and performed well under less favorable

settings, implying particular adaptation characteristics. Yam mosaic viruses have been reported to be widespread in all yam-producing countries around the world. The observed strong negative correction of yam mosaic virus with yield in the current study was desirable since healthy plants produce optimum assimilates which are translocated to the root and stored in tubers as starch [48]. This suggests that the tuber yield can be increased by simple selection of healthy plants. Adeniji et al. [49] observed that tuber yield in white yam could be reduced up to 92.8% after inoculation with yam mosaic virus. Yam plants infected with yam mosaic virus become unhealthy and chlorotic, and these plants do not produce optimally due to distorted chlorophyll content [50]. However, a positive correlation was observed for the relationship between dry matter content and yam mosaic virus.

Certain types of genotypes would be ideal for high-input agriculture under favorable environmental circumstances. The optimal temperature for the growth of yam is between 25 °C and 30 °C, depending on the species. The average annual temperature for the test environments ranged from 18.8 °C to 29.2 °C which is within the range of the optimal temperature required for yam growth and development during the crop growing period. According to Srivastava et al. [51], nitrogen stress serves as the most serious growth constraint for yam production and they strongly recommend the necessity of including this management factor in the assessment of climate impacts on crop yields. In the current study, the test environments were within the range of critical nutrient requirements for yam. Literature defines certain genotypes as being resistive to environmental situations, and they continue to be the best insurance for farmers under difficult situations. Furthermore, certain genotypes tend to respond well to favorable environments while maintaining moderate yields, dry matter content, and disease resistance under hard conditions. Such genotypes are often chosen for specific settings where they may fully realize their production potential. The yields of locally cultivated genotypes such as UGY16085 and UGY16012 remained highest in the current investigation, despite being unstable across the six environments. The dry matter content of genotypes UGY16022 and UGY16064, on the other hand, remained considerably high across environments, while disease-resistant genotypes throughout the six test environments were UGY16020, UGY16034, UGY16042, and UGY16080. This was obviously reflected in the performance of the genotypes across the various environments. Further, similar observations were drawn from the relationship between dry matter content and total yield of yam where a non-significant weak negative correlation was observed.

5. Conclusions

This study revealed significant GEI effects for yam mosaic virus, total yield of yam, and dry matter content in the yam genotypes evaluated, and significant genotypic variation for studied traits. These findings are an important resource for making selections targeting yam genetic improvement through hybridization. Genotypes UGY16022 and UGY16066 were the most stable, with relatively high dry matter content across test environments.

The six test environments used for the study were excellent for research and development of yams. In general, genotypes UGY16020, UGY16034, UGY16042, and UGY16080 had high tolerance to yam mosaic virus disease and were relatively high yielding, hence are considered good candidates for improving other genotypes in the future. For a combination of all three traits (virus resistance, dry matter content, tuber yield), genotypes UGY16022 and UGY16066 showed best stability, closest to the ideal genotype. These genotypes presented high yields with substantial dry matter content and yam mosaic virus resistance. There is a need for more evaluation with participation of farmers, targeting official variety release in Uganda.

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