Research Article

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Exploring genetic variability, heritability, and trait correlations in gari and eba quality from diverse cassava varieties in Nigeria

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Abstract

BACKGROUND: Gari (especially in Nigeria) is an important West African food product made from cassava. It is an affordable, precooked, dry, easy to prepare and store food product. Eba is a stiff dough produced by reconstituting gari in hot water. Gari and eba quality is an important driver of varietal acceptance by farmers, processors, and consumers.

RESULTS: This study characterized the genetic variability, heritability, and correlations among quality-related traits of fresh roots, gari, and eba. Thirty-three diverse genotypes, including landraces and released and advanced breeding genotypes, were used in this study. In total, 40 traits categorized into fresh root quality, colour, functional, and texture properties trait groups were assessed. We observed broad phenotypic variability among the genotypes used in this study. Dry matter content had a positive ($P < 0.05$) correlation with gari%, bulk density and a negative correlation with eba hardness and gumminess. Broad-sense heritability across all environments varied considerably among the different trait groups: 62% to 79% for fresh root quality, 0% to 96% for colour, 0% to 79% for functional and 0% to 57% for texture properties.

CONCLUSIONS: The stable broad-sense heritability found for gari%, gari and eba colour, bulk density, swelling index, and hardness measured using instrumental texture profile analysis coupled with sufficient variability in the population indicate good potential for genetic improvement of these traits through recurrent selection. Also, it is possible to genetically improve gari%, bulk density, and swelling power by simultaneously improving the dry matter content of fresh roots.

Supporting information may be found in the online version of this article.

Keywords: genetic components; principal component analysis; instrumental texture profile analysis; cassava processed product quality; breeding for consumer preference traits

INTRODUCTION

Cassava (*Manihot esculenta*) is one of the oldest root crops used for food by humans and grown in over 100 countries and meets the daily caloric requirements of close to a billion people in Africa, Asia, and South America.[1] It is a major crop for food security and is an income generator for small-scale farmers because of its resilience to environmental stresses and year-round availability. Africa accounts for more than 50% (about 203×10^6 t) of the total global production, and Nigeria is the leading producer with 7.7×10^6 ha under cultivation for the crop.[2]

Cassava roots are highly perishable owing to its tendency to undergo post-harvest physiological deterioration within 48–72 h after harvest.[3] Additionally, cassava roots contain cyanogenic

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glucoside compounds (hydrogen cyanide), which need detoxification before consumption.[4] Processing cassava roots into different granulated and paste products, such as gari, fufu, and lafun, before consumption is a strategy for overcoming post-harvest physiological deterioration and hydrogen cyanide limitations.[5] Among all processed products, gari takes up the largest percentage of cassava produced in West Africa, particularly Nigeria.[6]

Gari is a toasted, pre-gelatinized dry granule, also known as 'cassava semolina' or 'Farinha de mandioca'.[7] Basic processing of gari includes peeling, washing, grating, fermenting (optional), dewatering by pressing, pulverising, dry heat roasting, grading, and packaging.[8] Gari's profitability to farmers and processors, ease of preparation for consumption, storage, and affordability for consumers make it a high-demand commodity.[9] Gari is consumed either by soaking in cold water or rehydrating in boiling water to make a stiff dough (eba). Eba is the most consumed form of gari in Nigeria and other West African countries. Basic preparation of eba includes a sprinkling of dry gari into boiling water, covering to allow gelatinization, and stirring to form a stiff dough. The stiff dough is usually consumed with vegetables or other types of soup.

Gari/eba quality traits are categorized into colour, functional, and textural properties. Colour is an organoleptic property that has been highly associated with appearance and acceptability of gari/eba.[10] A dark colour of processed products is associated with low quality and may be due to genetic and/or processing methods.[11]

Functional properties describe the behaviour of gari during preparation and cooking, and ultimately influence the product's appearance, flavour, and texture. These properties may be affected by genotype, processing method, and preservation methods of roots before processing.[5] The functional properties include bulk density (BD), swelling power (SP), solubility, swelling index (SI), pH, and particle size and have been used as criteria for predicting gari quality[12,13] and varietal acceptability.[11,14]

Granule size, colour, and resistance to stirring of gari during eba preparation have all been linked to the textural qualities of eba.[11] Consumers often associate eba texture with qualities like smoothness, firmness, stickiness, elasticity, stretchability, and mouldability.[10] These textural measures can be influenced by length of fermentation and variety.[15] Eba texture can be assessed by using rheometry, instrumental compression tests, and human sensory panel tests.

Until recently, cassava improvement in West Africa has mainly focused on increasing root yield, nutrition, and resilience to numerous biotic and abiotic constraints that affected the crop's productivity.[16] However, insufficient consideration of quality and consumer preference traits by breeding programmes has led to the disadoption of some improved varieties.[10,11,17,18] This is due to the limited understanding of their genetic control and the difficulty in assessing these traits.

To effectively consider traits related to gari/eba quality as breeding goals, it is important to assess the available phenotypic variation and determine the genetic parameters such as heritability and genetic variances required to effectively incorporate gari/eba quality traits in breeding objectives. Understanding the inheritance of these traits is crucial in designing an effective breeding approach and in predicting the genetic gain resulting from selection. Also, in order to achieve concurrent improvement in traits related to gari, eba, and root dry-matter (DM) content – a routinely measured trait in the breeding program – understanding the interrelationships between these traits is required.

The quality of gari/eba is influenced by various factors, including genotype, environmental conditions, processing methods, and their interactions. Different genotypes exhibit variations in both the quantity and quality of the final product.[19,20] As a result, it is unclear what proportion of the phenotypic variation in gari yield and quality is due to genetics, environment, or/and processing factors and their interactions. For genetic improvements, breeders are interested in the proportion of variation attributed to genotype effect. Previous studies on genotypic variation of genotypes on traits related to gari/eba quality were mainly descriptive, and assessment was done using a limited number of varieties.[9,10,20-28] For example, Almazan[25] screened 35 genotypes in two replications to study the influence of genotypes on gari quality. Though the study revealed a significant genetic variation for gari quality, it did not elucidate the nature and extent of genetic variation, heritability, and correlations with fresh root quality-related traits. The current study aimed to characterize the genetic variability, heritability, and correlations among fresh root, gari, and eba quality traits.

MATERIALS AND METHODS

Planting material and experimental design

Identifying a representative and diverse population for targeted product assessment is a critical starting point for genetic studies. The results of a cassava monitoring survey[29] were used to assemble a population that contains 33 popular landraces, released varieties, and advanced breeding lines (Supporting Information Table S1) that are cultivated in Nigeria, the leading cassava producer in the world. The population was planted at the International Institute of Tropical Agriculture (IITA) research station in Ibadan (7°49′ N, 3°90′ E), Nigeria, during the 2020–2021 and 2021–2022 planting seasons.

The trial for the first season (https://cassavabase.org/breeders/trial/7169?format=) was established on 24 April 2020 and was harvested between 20 and 23 April 2021. The trial for the second season (https://cassavabase.org/breeders/trial/11571?format=) was established on 16 June 2021 and was harvested from 13 to 15 June 2022.

Landraces are traditional farmer-preferred varieties that evolve under farmer selections, whereas released or improved varieties are the result of conventional breeding involving targeted crosses, phenotyping, and successive selection stages for agronomic, pest and disease resilience and quality. The improved varieties came from different decades, from the 1970s to 2010s, and the advanced breeding includes varieties developed through genomic selection.[30] The selection of these genotypes ensured a full representation of cassava diversity based on the target product (gari) being assessed. The year of origin for the landraces is unknown, whereas the year of origin for the released materials was between 1972 and 2012, and the advanced breeding lines have a year of origin between 2013 and 2014 (Supporting Information Table S1).

The trials were planted in a randomized complete block design with two replications. The plot dimension was 4 m × 4 m consisting of 20 stands planted at spacings of 1 m and 0.8 m between rows and within rows respectively. The trial was conducted without supplemental irrigation under standard agronomic practices, including regular weeding.

Trial harvesting, root processing, and product phenotyping

The trials were harvested 12 months after planting, and 20 kg of marketable roots from each plot were selected for gari processing, while six roots were used to determine the DM and starch

percentage. All data captured in this study was done using the FieldBook app.[31]

For DM and starch processing, the roots were peeled and shredded after removing proximal and distal ends to reduce fibrous material. After thorough mixing, 100 g samples of the root gratings were oven-dried at 95°C for 48 h until constant weight, and the DM was expressed as a percentage of fresh weight.[32]

For starch, 100 g of freshly shredded roots from the step above were weighed and fine-milled in an electrical blender (IFM-C20G crush miller; Iwatani, Osaka, Japan). The slurry was filtered through a 180 µm by 200 mm (model no. 019-214 775-01; Tokyo Screen Co. Limited, Tokyo, Japan) sieve using 8 L of water. The starch granules were allowed to settle for 4 h, and the supernatant was decanted and air-dried for 48 h until constant weight. The starch content was expressed as a percentage of the fresh weight. The starch extraction residue was oven-dried at 95 °C for 48 h until constant weight and expressed as a percentage of fresh weight.[33]

Gari processing

Gari was produced using the method described by Abass *et al.*[8] and was further optimized by the Cassava Breeding Unit at the centralized processing facility at the IITA (Fig. 1). A fixed amount of 10 kg marketable cassava roots from each plot were peeled using a stainless-steel knife in a circumferential pattern to carefully ensure complete removal of the cortex (peel), without affecting the starchy root flesh. The peeled roots were washed and grated into a mash without adding water. The resulting mash was packed in a labelled polypropylene woven sack and allowed to ferment naturally for 72 h under ambient temperature as recommended for quality gari processing.[9,26,34] The fermented mash was dewatered using a hydraulic press and pulverized before being toasted on stainless-steel pans. The toasting process reduced the moisture content of pulverized mash to the recommended amount of about 10% for quality gari.[27,35,36] The temperature of the stainless-steel pan before frying was on average 120.5 °C.[15,34] The resulting gari was allowed to cool, sieved using a 1 mm and 2 mm mesh and packed in a well-labelled container in accordance with the guidelines provided by the Codex Alimentarius Commission.[37] The samples were then stored at ambient temperature (30 ± 2 °C) in the centralized storage facility of the Cassava Breeding Unit at IITA. Throughout the study, each processing step was carefully monitored to reduce operator variation and sample batch effects. Gari (%) was estimated as a percentage of starting weight as described by Aghogho *et al.*[20]

Eba preparation

Eba was prepared following the standardized protocol outlined in Fig. 2, in accordance with the approved standard operating procedure of the RTBfoods project.[38]

Colour measurement on fresh roots, gari, and eba

Grated fresh roots, gari, and eba samples were tightly packed in a whirl pack to avoid light refraction before the colour was measured using a chromameter (CR-400; Konica Minolta, Tokyo, Japan). The colour was recorded according to the standard CIE tristimulus *L** (for brightness), *a** (for red–green) and *b** (for yellow–blue). The samples were scanned in duplicate.

Functional properties traits analysis on gari

We analysed several functional property traits of the gari, including its BD, SP, SI, solubility, pH, and particle size distribution. BD of gari refers to the heaviness of gari, which affects packaging and distribution. BD was measured using a modified method as described by Okezie and Bello.[39] A 250 mL graduated measuring cylinder was filled with gari samples and gently tapped on the laboratory bench about 50 times until they were levelled to the 250 mL mark. The weights were taken using an EJ Series value balance, and BD was expressed as grams per cubic centimetre.

The SP and SI are two ways to assess swelling capacity, which is the ability of gari particles to absorb water and swell, in hot and normal water respectively. The swelling capacity impacts several textural aspects, including the ability of eba to be shaped and the flow of gari for 'drinking'. The SP was assessed using a modified version of the method described by Leach *et al.*,[40] where 2g of gari was weighed and mixed with 30 mL of distilled water in a preweighed centrifuge tube. The mixture was heated in a water bath at 80 °C for 30 min while continuously shaking the tubes at 165 cycles per minute. The boiled samples were centrifuged at 8000 rpm for 20 min. The supernatant was collected for further analysis and the sediment mass was weighed. The SP was calculated as the percentage increase in gari sample weight.

The SI of gari was measured using the method described by Ukpabi and Ndimele,[41] where 10 g of gari samples was placed in a 100 mL measuring cylinder and the initial volume measured. Cold distilled water was added to the 100 mL mark of the cylinder

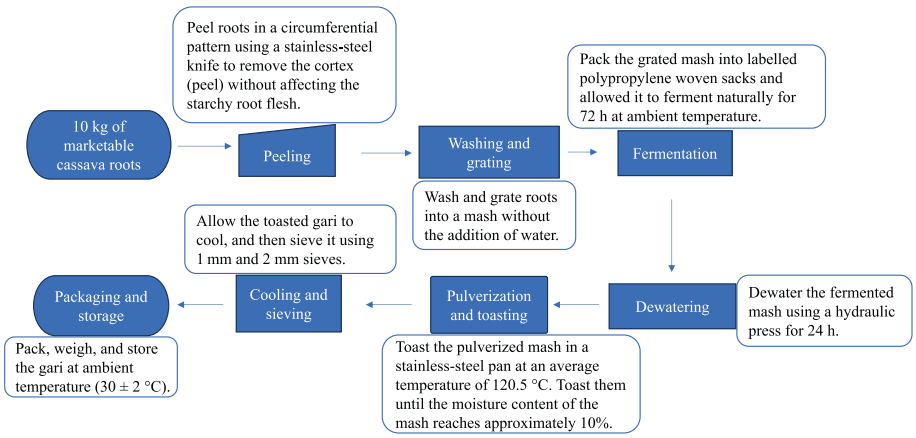

Figure 1. Schematic outlining the gari processing workflow and quality control measures.

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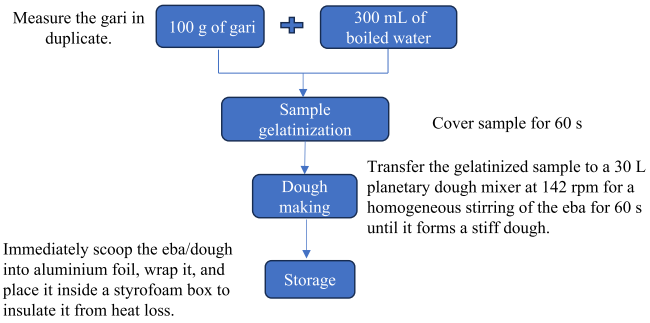

Figure 2. Schematic outlining the eba preparation for textural analysis.

and allowed to sit for 4 h before observing the final volume of gari. SI was calculated to be a multiple of the original volume.

Gari maximum rate of dissolution in a given volume of water at a given temperature is measured by its solubility. Solubility was carried out as described by Leach *et al.*,[40] with slight modification. Supernatant from SP assessment described earlier herein was oven-dried in a preweighed aluminium plate at 60 °C for 24 h. The residue was weighed and the solubility was expressed as the percentage of dried supernatant to the initial sample weight.

To measure the acidity or alkalinity of the gari samples, slurries (20% DM) of all gari were made and their pH measured using a hydrogen-ion activity meter (8606; Mettler Toledo GmbH, Greifensee, Switzerland).

Particle size distribution of gari samples was measured according to the method described by Oduro *et al.*[24] with slight modifications. A 50 g of gari sample was sieved using a four-tier arrangement in decreasing aperture size: ps800 (800 μm) for the large particles, ps500–800 (500 μm) for medium-sized particles, ps300–500 (300 μm) for small particles, and ps0–300 for the smallest particles, collected in a base pan. The sieve was covered with a tightly fitted lid and placed on a test sieve shaker (Octagon 200) and agitated for 10 min. After sieving, the different fractions of particles were weighed and recorded separately using an electronic balance (readability ±0.001) and expressed as a percentage of the initial sample weight.

Textural properties traits

Texture of food can be assessed using both instrumental (rheometry and texture profile analysis) and sensory analysis.[42] Rheometry was undertaken using a Rapid Visco Analyzer (RVA; 4500; Perten Instruments, Sydney, NSW, Australia). The gari samples were milled, passed through a 300 μm sieve, and then3 g of milled gari sample was weighed into the RVA canister containing 25 mL of distilled water. The mixture was stirred manually using a plastic paddle and the canister inserted into the tower chamber of the machine. The viscosity of gari was then measured following a previously described procedure.[12]

Instrumental texture profile analysis (ITPA) was undertaken on eba using a textural profile analyser (TA-XTplus; Stable Micro Systems, Godalming, UK) following the standard operating procedure of RTBfoods.[38]

The sensory textural profile analysis (STPA) was done according to the standard operating procedure of RTBfoods[43] based on mouldability, stretchability, stickiness, and hardness. We conducted the STPA by presenting coded and duplicate samples of the cooked eba dough to 15 trained panellists from staff and graduate students at the crop utilization laboratory at IITA, Ibadan, who consumed eba regularly.

Statistical analysis

Descriptive statistics and least significant difference among the variety status for each trait group was done using the 'pastecs' package version 1.3.21[44] and 'agricolae' package[45] in the R software.[46] We fitted the following linear mixed model using 'statgenSTA' package version 1.0.8[47] to estimate variance components and best linear unbiased predictions:

$$\mathbf{y}=\mathbf{X}\boldsymbol{\beta}+\mathbf{Z}\mathbf{u}+e$$

where $\mathbf{y}$ is the response vector of a trait for a given location, $\boldsymbol{\beta}$ is the vector of fixed effects with the design matrix $\mathbf{X}$ (relating observations to fixed effects, which include grand mean, replication number), $\mathbf{u}$ is the vector of random genetic effects with the design matrix $\mathbf{Z}$ (relating trait values to genotype, environment, genotype × environment interaction (GEI)), and e is the residual.

We calculated the broad-sense heritability on trial level and across all environments for all traits:

$$H_s^2=\frac{V_g}{V_g+\frac{V_e}{r}}$$

where H_s^2 is the trial level broad-sense heritability, V_g is the genetic variance, V_e is the error or residual variance, and r is the number of replications;

$$H_m^2=\frac{V_g}{V_g+\left(\frac{V_{ge}}{e}\right)+\left(\frac{V_e}{er}\right)}$$

where H_m^2 is the broad-sense heritability estimate across all environments, V_g is genotypic variance, V_{ge} is the variance of GEI, V_e is the residual variance, e is the number of environments, and r is the number of replications.

Pairwise correlation between traits was determined using the R function 'cor' in the 'stats' package,[46] and the correlation matrices were visualised using the complex heatmap.[48] A principal component analysis (PCA) was carried out in addition to the correlation analysis to understand the grouping of variables and genotypes. The PCA was done using the R function 'prcomp' in the 'stats' package, and visualization was done using the 'corrplot' R package.[49]

RESULTS

Variation among fresh root, gari, and eba quality traits

A total of 40 traits from the fresh root, colour, functional, and textural properties were phenotyped (Table 1). Most traits showed wide-ranging variability, with all variables exhibiting larger than twofold differences between the maximum and minimum values, except for gari BD and ITPA-cohesiveness (Table 1). These large differences indicate broad phenotypic variability within the genotypes used in this study. Notably, we observed a gradual and consistent reduction in brightness (L^*) from fresh roots, gari, and eba (91.13, 89.45, and 68.13 respectively).

A comprehensive analysis of mean values across the three classes of germplasm (landraces, released varieties, and advanced breeding genotypes) revealed differences for some traits (Table 1). For fresh-root quality traits, such as DM, starch content, starch residue, and gari%, advanced breeding genotypes outperformed both landraces and released varieties. However, traits linked to colour (chromameter L^*, a^*, and b^*) did not differ among the three groups of varieties.

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Table 1. Statistical descriptive parameters for best linear unbiased predictions of fresh root, gari, and eba quality traits

Traits name	Mean (min–max)	SD	Advanced breeding genotypes (n = 11)	Landraces (n = 10)	Released (n = 12)
Fresh root quality					
DM (%)	34.19 (22.0–44.4)	4.98	37.02a	33.53b	32.01b
Starch content (%)	27.2 (14.3–36.7)	5.15	29.5a	27.0ab	25.22b
Starch residue (%)	5.94 (3.1–10.4)	1.35	6.73a	5.47b	5.61b
Gari (%)	23.44 (12.0–30.8)	4.46	25.74a	21.85b	22.42b
Chromameter colour					
a*_fresh	−0.39 (−1.4–3.8)	0.82	−0.47a	−0.48a	−0.24a
b*_fresh	20.8 (16.1–43.6)	4.37	20.58a	20.23a	21.51a
L*_fresh	89.45 (83.5–94.3)	2.14	90.04a	89.37a	88.96a
a*_gari	1.78 (0.5–4.5)	0.82	1.78a	1.7a	1.84a
b*_gari	20.34 (14.7–35.3)	3.68	20.15a	20.27a	20.58a
L*_gari	91.13 (82.0–98.8)	5.48	91.74a	90.6a	90.9a
a*_eba	−1.14 (−6.3–4.9)	4.3	−1.08a	−1.49a	−0.96a
b*_eba	15.63 (11.5–28.7)	2.65	15.68a	15.18a	15.9a
L*_eba	68.13 (54.8–89.7)	7.46	69.07a	66.4a	68.43a
Gari quality					
Bulk density (g cm^{-3})	0.53 (0.43–0.60)	0.04	0.55a	0.52b	0.52b
pH	4.4 (3.7–5.7)	0.47	4.45a	4.32a	4.39a
Solubility (%)	9 (5.0–22.0)	3.45	9.47a	8.41a	9.02a
Swelling index	3.12 (2.3–5.0)	0.6	2.9a	3.28b	3.18ab
Swelling power (%)	647.53 (543–892)	56.33	657.6a	630.17a	650.88a
Gari particle size					
ps0–300 (μm)	10.28 (1.1–23.4)	4.32	12.45a	8.25b	9.92b
ps300–500 (μm)	25.02 (8.9–34.1)	5.46	26.9a	22.96b	24.75ab
ps500–800 (μm)	27.96 (22.4–32.1)	1.94	27.64a	28.48a	27.87a
ps800 (μm)	36.85 (18.4–67.7)	10	33.29b	40.3a	37.68ab
Gari RVA					
RVA-breakdown (RUV)	28.26 (5.6–129.5)	21.32	31.72a	24.71a	27.59a
RVA-final viscosity (RUV)	299.43 (192.4–411.6)	45.2	288.47a	309.3a	302.8a
RVA-pasting temp (°C)	76.2 (69.4–90.6)	3.38	76.71a	76.36a	75.56a
RVA-peak viscosity (RUV)	222.01 (142.6–327.4)	39.56	216.82a	222.16a	227.08a
RVA-peak time (m)	5.92 (4.7–7.0)	0.53	5.86a	5.05a	5.88a
RVA-setback viscosity (RUV)	104.49 (69.3–160.4)	18.94	102.82a	108.39a	103.09a
RVA-trough (RUV)	194.08 (119.5–282.1)	33.99	185.77a	179.68a	199.7a
Eba ITPA					
ITPA-adhesiveness (g s)	−113.83 (−579.7–143.9)	79.33	−136.6a	−95.19a	−108.07a
ITPA-chewiness (%)	61.47 (4.7–138.8)	17.98	58.27a	65.99a	60.87a
ITPA-cohesiveness (%)	0.25 (0.08–0.58)	0.17	0.24a	0.24a	0.26a
ITPA-gumminess (%)	92.27 (46.1–237.5)	41.87	86.62a	98.44a	92.62a
ITPA-hardness (g)	460.26 (164.0–907.4)	159.82	437.7a	504.33a	466.8a
ITPA-resilience (%)	5.98 (1.9–19.0)	4.68	5.66a	6.11a	6.17a
ITPA-springiness (%)	24.09 (5.5–60.8)	17.06	23.5a	23.37a	25.17a
Eba STPA					
STPA-adhesiveness	4.07 (1.1–9.8)	2.82	4.14a	3.77a	4.25a
STPA-hardness	2.81 (1.4–6.4)	1.08	2.65a	3.06a	2.77a
STPA-mouldability	4.71 (2.6–9.3)	2.2	4.62a	4.84a	4.69a
STPA-stretchability	3.41 (1.3–7.4)	1.72	3.28a	3.43a	3.5a

DM, dry matter; ITPA, instrumental texture profile analysis; RVA, Rapid Visco Analyzer; RUV, RVA units; STPA, sensory textural profile analysis.

Among the gari quality traits, BD and SI of the advanced breeding genotype were different from that of the landraces and released varieties. There were differences in all particle size distributions among the different variety statuses except for ps500–800 (μm). Gari from landraces had more larger particles (ps800 (μm)) than smaller particles (ps0–300 (μm)) compared with breeding genotypes. In contrast, there was no discernible difference among the gari RVA and the eba ITPA- and STPA-related traits.

Estimate of variance component

Figure 3 presents the percentage of phenotypic variance explained by the genotype, environment, GEI, and residual source

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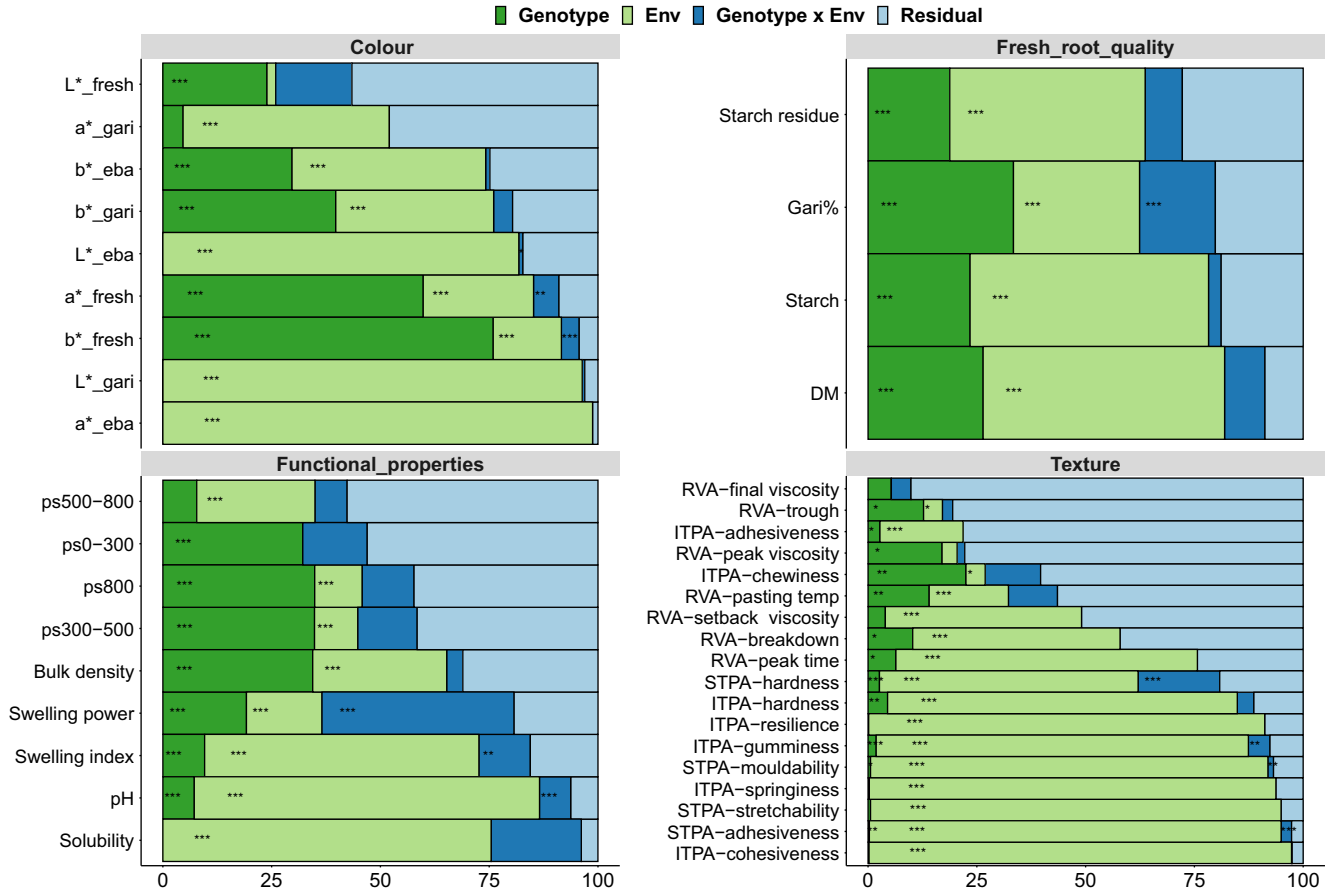

Figure 3. Percentage of phenotypic variance explained by each genotype, environment, genotype × environment interaction and residual terms for 40 gari and eba quality traits. Env: Environment. *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.

of variation for each trait. Information is sorted according to the descending residual variance component, and the level of significance (*P* value) was included. Traits with high percentages of genotypic variance are desired as they can be easily improved through recurrent selections. In the colour group, the genotypic term explained between 0% (a*_eba, L*_eba) and 75% (b*_fresh). Among colour traits, fresh root colour had the highest percentage explained by genotypes, followed by gari colour and then eba colour. This suggests that genetic improvement of colour would be more effective when measured in fresh roots and gari rather than in eba. Among the fresh-root quality traits, gari% (33.42%) had the highest percentage explained by genotype effect. Generally, traits in the fresh-root quality group have been successfully improved in the past through recurrent selection because of their high genetic variances. Traits such as BD (34.44%), ps0–300 (32.16%), ps300–500 (34.86%), and ps800 (34.9%), which have over 30% of the variation explained by the genotype term, can be considered for genetic improvement. Genetic improvement on traits like solubility (0%), pH (7.22), ps500–800 (7.78%), and SI (9.6%) may not be effective because of their low genetic variance. Among the textural traits, the RVA-related traits had between 3.97% (RVA-setback viscosity) and 17.01% (RVA-peak viscosity) of total variation attributable to genotype. In the ITPA-related traits, genotype term explained between 0.14% (ITPA-resilience) and 22.5% (ITPA-chewiness). Traits related to STPA had less than 2.62% of their variation explained by genotype, which will make improving these traits through recurrent selection difficult.

In this study, the environment variance component, which may include processing and cropping seasons, ranged from 0% (ps0–300, RVA-final viscosity) to 98.76% (a*_eba), which indicated large differences in the performance of genotypes between the two cropping seasons. However, these differences do not necessarily equate to shifts in genotype ranking (indicative of GEI), but rather signify change in means of the genotypes for each season. There was a large difference in observed response of genotypes for pH (79.34%), solubility (75.44%), and SI (63.03%), as seen by the percentage explained by environment. On the other hand, the environment explained between 0% (ps0–300) and 27.17% (ps500–800) for particle size distribution, which indicated that gari particle size did not change much between seasons. Variation among genotypes for the textural traits, especially ITPA and STPA related, were mostly explained by the environment. For example, 97.09%, 94.63%, and 93.44% of variation seen among genotypes for ITPA-cohesiveness, STPA-adhesiveness, and ITPA-springiness respectively was as a result of different planting seasons. Traits linked to RVA, such as RVA-setback viscosity, also revealed differences between seasons, with the environment explaining approximately 45.09% of the observed variation among genotypes.

Variance due to GEI is important in determining the difference in the performance and ranking of genotypes in different growing seasons. A large GEI can be a hindrance in crop improvement if it is larger than the genotypic variance. Fortunately, in this study, GEI was generally the smallest source of variation compared with the genotype and environment terms, suggesting little crossover

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in the performance of genotypes in the two cropping seasons for these traits.

The residual term explained between 1.24% (a*_eba) and 90.13% (RVA-final viscosity) of the total variation seen among genotypes. In the colour group, the residual term explained between 0.4% (a*_eba) and 57% (L*_fresh). In the fresh-root quality group, the residual term had the lowest percentage variance explained compared with other sources of variation. Solubility (4%) and ps500–800 (58%) respectively exhibited the lowest and highest percentage variance explained by residuals in the functional properties group. Among the textural-related traits, the residual variance, which represents the unexplained variation in the data, was the second largest source of variation after the environmental variance.

Genetic influence on traits expression

The trial-level broad-sense heritability H_s^2 estimates were above 25% for most traits in both planting seasons (Fig. 4). In season 2021, two colour traits (L*_eba and a*_eba) and three texture traits (RVA-peak time, RVA-setback viscosity, and ITPA-adhesiveness) had heritability estimates below 25%. Two colour traits (L*_gari, a*_eba), one functional property (solubility), and one texture trait (RVA-final viscosity) in season 2022 also had estimates lower than 25%. Broad-sense heritability estimates across all

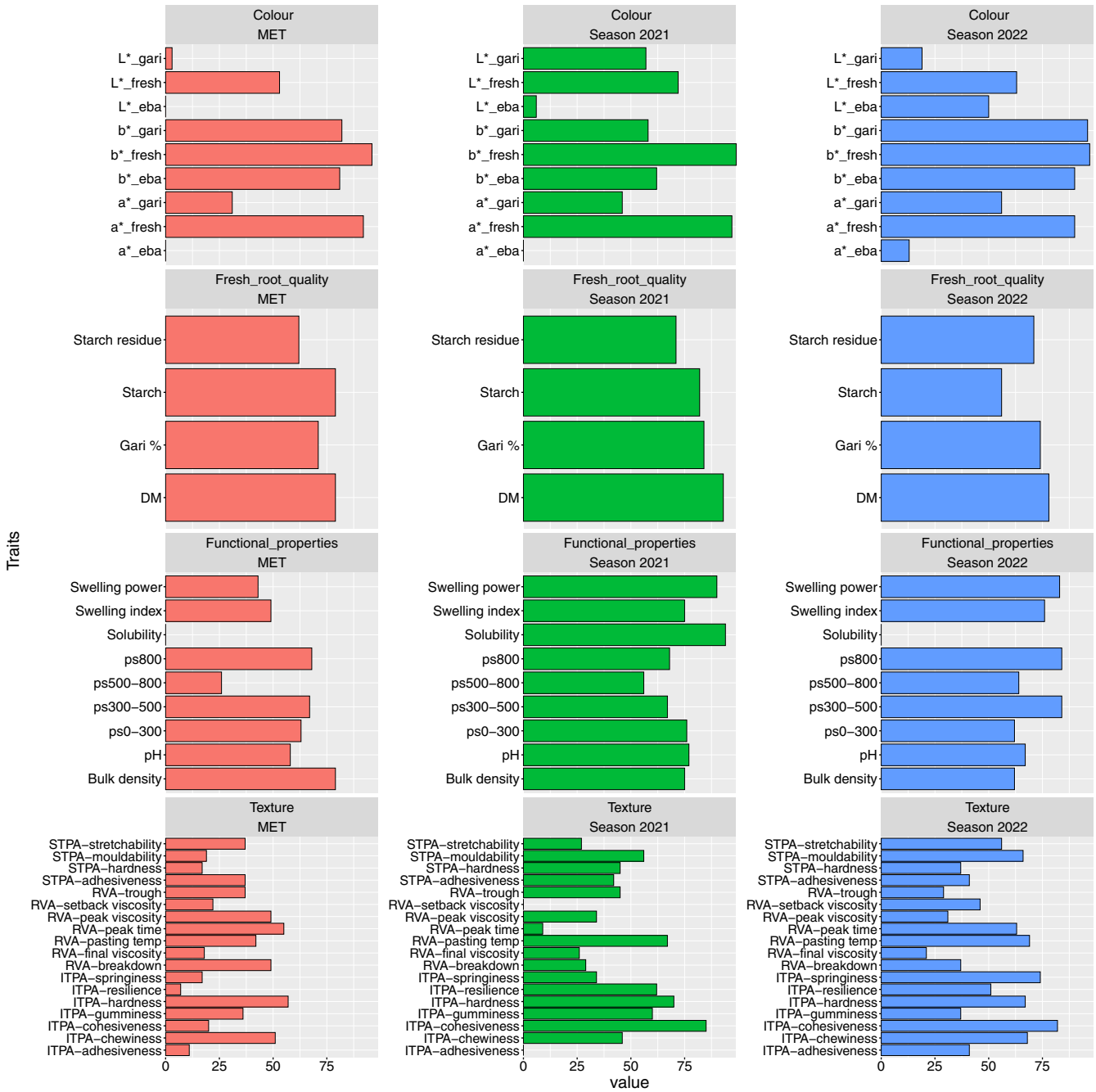

Figure 4. Broad-sense heritability estimates across all environments (MET) and trial level for 40 fresh root, gari, and eba traits. DM, dry matter; ITPA, instrumental texture profile analysis; MET, multi-environment trial; STPA, sensory textural profile analysis.

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environments H^2_m ranged from negligible (L*_eba, a*_eba, solubility) to 0.96 (b*_fresh) (Fig. 2). Heritability estimates from fresh roots were always higher than those from gari or eba (for each colour parameter). Heritability estimates for *b** were the largest, followed by those for *a** and then *L**. In the fresh-root quality categories, all traits had heritability estimates above 0.50. Similarly, in the functional property categories, most traits had heritability estimates above 0.50 with the exception of SP, ps500–800, and solubility. Among the texture-related traits analysed, only a few – namely ITPA-hardness, RVA-peak time, ITPA-chewiness, RVA-peak viscosity, and RVA-breakdown – exhibited heritability estimates above 0.50. This indicates that these specific traits are influenced more by genetic factors than by environmental factors.

Traits relationships

Because of the large differences observed between the two cropping seasons as indicated by the r^2 of the linear regression (Fig. S1) and the environmental variance observed (Fig. 3), correlation analysis (Fig. 5) was done among traits separately for each season. Further, only traits with $H^2 > 20\%$ were considered. The major purpose of the correlation analysis by season was to show the consistency of correlations among traits in terms of magnitude and direction. In both seasons, positive, negative, and negligible correlations among traits were observed. Few traits were significantly ($P < 0.001$) correlated with DM, including gari%, SI, and ITPA-hardness. Surprisingly, there were changes in correlation magnitude and sign for some traits in the two seasons (correlation between b*_gari and DM, RVA-setback and STPA-stretchability) (Fig. 5). However, in most instances where sign changes were noted, the correlation was significant in one season but not the other. In both planting seasons, b*_gari had a significant negative correlation with gari% and among the traits related to functional properties. BD and SI respectively had a positive and negative ($P < 0.05$) correlation with fresh-root quality traits. A negative correlation between DM and ITPA-hardness in both planting seasons was observed, whereas ITPA-gumminess correlated significantly with DM only in the 2020 planting season (Fig. 3). During the 2022 planting season, the correlation analysis revealed that gari pH had significant ($P < 0.05$) positive associations with gari%, b*_eba, and ps0–300, while showing negative associations with b*_gari and ps800. However, the correlation pattern for gari pH did not follow the same trend in the 2021 season. In the 2022 season, ITPA-chewiness showed a mixed correlation pattern with particle-size-related traits, with negative correlations observed for ps0–300 and ps300–500 and a positive correlation observed for ps800. This trend was similar to that observed in the 2021 season, although the correlations were not statistically significant. Also, the particle-size-related traits were significantly correlated with SI only in the 2022 planting season. In the 2022 season, there was a significant ($P < 0.05$) positive correlation between STPA-stretchability with RVA-trough, RVA-peak viscosity, and RVA-setback viscosity. However, in the 2021 season, the correlations were negative and not significant.

Other important correlations, stable across seasons, include a positive correlation between b*_fresh and b*_gari, SP and RVA-peak viscosity, and ITPA-hardness and SI, and a negative correlation between RVA-peak time and SP. Only a few traits were

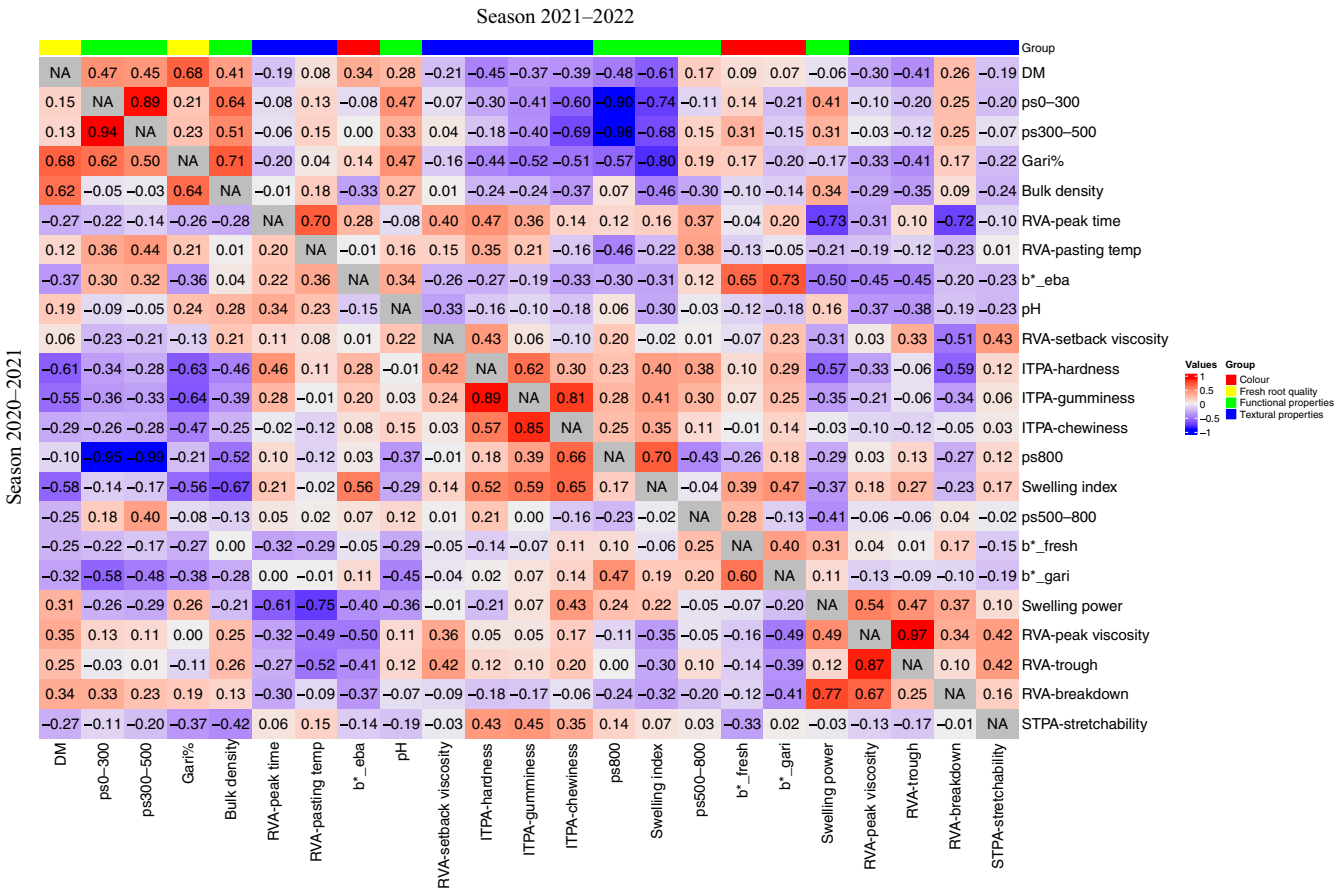

Figure 5. Correlation plot for 23 fresh roots, gari, and eba traits from two growing seasons (2021–2022 above the diagonal and 2020–2021 below the diagonal).

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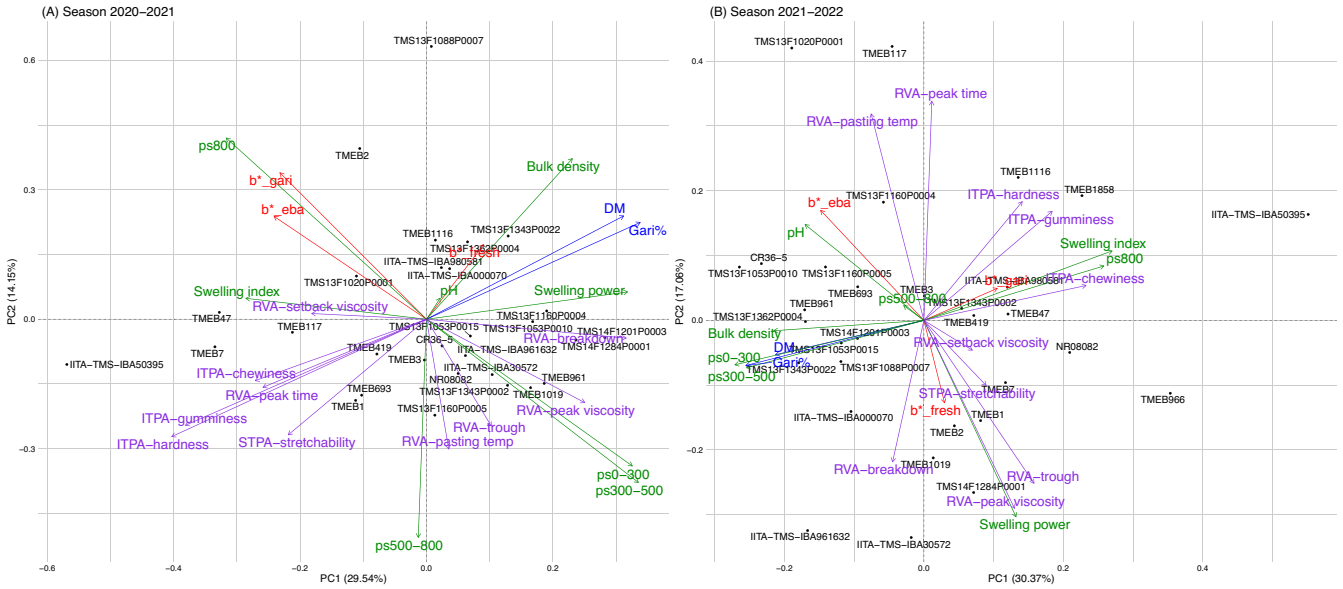

Figure 6. Principal component analysis for 23 fresh root, gari, and eba traits from two growing seasons. (A) Season 2020–2021. (B) Season 2021–2022. DM, dry matter; ITPA, instrumental texture profile analysis; STPA, sensory textural profile analysis.

found to be correlated with eba quality traits; however, they were not stable across both seasons.

Principal component analysis

The PCA was conducted for each of the two seasons' data. In the first season, the first two principal components (PCs) accounted for 43.69% of the total variance in the data (Fig. 6). PC1 explained 29.54% of the total variation, with gari% (0.27) and DM (0.25) having the highest PC loadings, whereas PC2 explained 14.15%, with b*_gari (0.27) and ps800 (0.33) having the highest PC loadings (Table S2). In the second season, the first two PCs accounted for 47.43% of the total variance in the data. PC1 explained 30.37% of the total variation, with ps800 (0.31) and SI (0.33) having the highest PC loadings, whereas PC2 explained 17.06%, with RVA-peak time (0.41) and RVA-peak pasting temp (0.38) having the highest PC loadings (Table S2). In both seasons, the biplot of the first two PCs revealed that variables such as DM, gari%, and BD, as well as SI, ITPA-hardness, ITPA-gumminess, and ITPA-chewiness, were strongly positively correlated, whereas variables such as SI and SP were negatively correlated. The landrace varieties were closely clustered together in the biplot, indicating similar values across the variables. In contrast, the released and advanced breeding genotypes were more spread out, suggesting considerable variation across the trait variables. However, four genotypes (TMS13F1053P0010, TMS13F1160P0005, TMEB3, and CR36-5) constantly clustered with each other in both seasons. The genotypes TMS13F1343P0022, TMS13F1362P0004, and IITA-TMS-IBA00070 exhibited a strong correlation with DM, gari%, and BD, indicating that these genotypes had higher values for these traits. On the other hand, the genotypes IITA-TMS-IBA50395 and TMEB47 were closely associated with textural traits such as ITPA-hardness, ITPA-gumminess, ITPA-chewiness, and SI.

DISCUSSION

Understanding the genetic variability, heritability, and correlations among fresh root, colour, functional, and textural property traits of gari and eba is a critical step towards their genetic improvement. Traits evaluated in this study were selected based on information from previous publications from the RTBfoods project.[10,11,17,18,50] The population characterized in this study displayed large phenotypic variation for most traits. The values for a few traits recorded in this study (gari%, BD, solubility, pH) were similar to those previously reported.[10,12] The range of the SI observed in this study suggests that certain genotypes produced gari capable of expanding to over three times its original volume, a characteristic highly desirable to consumers.[10,25] Advanced breeding genotypes performed better in terms of fresh-root quality traits than landraces and previously released clones did. However, for gari colour, quality, and textural traits, the three classes of genotypes were similar except for BD and SI, where landraces and released varieties performed differently from breeding genotypes.

Genetic variance is essential for selection of superior genotypes and trait improvement. We observed significant genotype effects for traits such as b*_gari, b*_eba, BD, ITPA-hardness, and ITPA-gumminess, suggesting the potential for genetic gains through hybridization and selection. Environmental variance, which explains the impact of factors such as climate, soil, biotic factors, crop management, and processing methods, was the most influential and significant component of variance for all trait groups except fresh-root quality traits.[51] Multi-season data showed that environmental and residual variances contributed more to the variation seen among genotypes than genotypic variances for all traits groups except for those in the fresh-root quality category. Encouragingly, the GEI effect contributed the least to the variation measured in the study. This finding is particularly important since significant interactions would considerably complicate the breeding efforts and reduce its effectiveness. Variations due to the residual term include all unexplained sources of variation. The residual variance can be reduced by increasing the effectiveness of the phenotyping process, the use of better breeding and experimental designs, and more appropriate statistical models.

Heritability H^2, the ratio of genetic to phenotypic variances, can range from 0 to 100%. Traits with high H^2 (>50%) suggest good potential for genetic improvement through breeding. The H^2 estimates for many traits both across all environments (H^2_m) and on

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trial-level (H_s^2) indicated promising genetic variability. Adequate genetic variation allows for trait improvement through phenotype-based recurrent selection. All fresh-root quality traits showed high heritability values ($H^2 > 0.50$). This explains the widely reported genetic gains for fresh-root quality traits in cassava, particularly for DM. On the other hand, colour, texture, and functional properties tended to have lower heritability values with few exceptions, underlining the difficulties for breeders to develop varieties meeting consumers demands. High heritability of a few traits (b*_gari and b*_eba, BD, RVA-peak time, and ITPA-hardness) is worth highlighting. These traits can be included in breeding efforts. Traits with low heritability estimates across all environments, such as solubility, L*_eba, a*_eba, and ITPA-resilience, had large environmental variance with little or no genetic variances.

Trait correlation can improve selection accuracy of complex traits through indirect selection. Negative correlations among two desirable traits would limit the simultaneous genetic progress. A significant correlation among traits may be due to the presence of genetic linkage and/or pleiotropic effects of different genes.[52] Traits correlations changed in magnitude (and in some cases even in sign) in both cropping seasons. Of note was the correlation between DM with gari% and BD. Meanwhile, other correlations agreed with those reported earlier for SP - and RVA-related traits.[12,53] The correlation observed between particle-size-related traits and SI suggests that the larger the particle size the higher the SI of gari.[14] It is not unexpected to observe a negative correlation between gari% and b*_gari because the colour of gari is determined by the quantity of beta-carotene, which is negatively associated with DM.[54] DM is a primary determinant of gari%, and hence the correlation between the two traits is expected. Also, in this study, DM was associated (either negatively or positively) with traits related to eba textural properties, which is similar to what Akingbala *et al.*[55] found. This suggests that DM content plays a crucial role in determining the textural quality of eba. Genotypes with higher DM content are likely to result in a softer and sticky eba dough. This can be attributed to their high starch content, which undergoes higher gelatinization upon contact with hot water, thereby reducing the firmness of the eba dough. Considering the high H_m^2 for DM, it would be possible to carry out an indirect selection of those traits that have low heritability but have a close association with DM.

The results of PCA from both planting seasons revealed that less than 50% of the total variation was explained by PC1 and PC2. The PCA biplot for the two seasons' data recapitulated the trait results of correlation analyses, with DM, gari%, and BD showing a strong positive relationship, and suggests the possibility of simultaneous selection and improvement for these traits. On the other hand, SI, ITPA-hardness, ITPA-gumminess, and ITPA-chewiness were correlated with each other and negatively related with the DM, gari%, and BD. An antagonistic relationship between expansion in cold water as measured by SI *versus* expansion in hot water as measured by SP was observed. When gari is added to cold water, cell wall separation is encouraged, which reduces adhesion between cells and encourages hydration.[56] Crude fibres (hemicellulose, cellulose, and lignin) are a measure of cell wall materials and are positively correlated with SI.[25,57] Therefore, genotypes with higher crude fibre content (and less DM or starch content) tend to have higher SI. In the presence of heat, starch in gari gelatinizes and swells more. In other words, gari from varieties with low DM expands more in cold water, whereas those from high DM varieties expand more in hot water because of the negative correlations between crude fibre and starch content.[58] The genotype cluster from the PCA revealed that landrace varieties were more like each other in their values across the variables, whereas the released and advanced breeding genotypes show greater variability in both seasons. These findings may have implications for the breeding and selection of cassava varieties for specific end uses. However, the results should be interpreted with caution owing to the small sample size and the fact that the experiment was repeated only in two seasons. Further research with larger sample sizes and more repetitions may be needed to confirm and expand upon these findings.

Among the 40 traits assessed in this study, 33 were specifically linked to the quality of gari and eba. Several traits, including gari%, b*_gari, b*_eba, RVA-breakdown, ITPA-hardness, SI, and BD, displayed significant correlations with DM content and had a consistent heritability estimate across all environments. It is suggested that these traits be prioritized for genetic improvement in the cassava breeding programme.

To increase the adoption of improved cassava varieties with acceptable gari and eba product quality in West Africa, it is imperative to understand the genetic basis of trait variation in the breeding germplasm. This study is a major effort to provide heritability estimates and the relationship between fresh-root quality traits, gari/eba colour, functional properties, and textural properties to support breeding decisions. It was encouraging to see the moderate to high heritability values for traits related to gari/eba colour, functional properties, and textural properties. Although a strong seasonal effect was noticed for most traits, the relative importance of GEI was generally small. The magnitude of the error in the analysis of variance of several traits, however, was high. This study identified attributes amenable to improvement through breeding, and those that having low heritability require more efficient screening protocols to reduce experimental error and/or the introduction of broader genetic variability.

AUTHOR CONTRIBUTIONS

Cynthia Idhigu Aghogho, Ismail Y Rabbi, Chiedozie Egesi, Bussie Maziya-Dixon, Elizabeth Parkes, and Peter Kulakow: design and study conceptualization. Cynthia Idhigu Aghogho, Ismail Y Rabbi, Andrew Ikpan Smith, and Siraj Ismail Kayondo: study methodology, implementation, and manuscript drafting. Cynthia Idhigu Aghogho, Racheal Abioye, Michael Adesokan, and Kayode Ogunpaimo: product processing and laboratory data collection. Cynthia Idhigu Aghogho, Ismail Y Rabbi, and Siraj Ismail Kayondo: formal data curation and analysis. Ismail Y Rabbi and Siraj Ismail Kayondo: manuscript reviewing and editing. Saviour JY Eleblu, Isaac Asante, Kayode Ogunpaimo, Ugo Chijioke, and Dominique Dufour: supervision, coordination, and fund acquisition.

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CONFLICT OF INTEREST

The authors declare no conflict of interest in this work.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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