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Assessing genetic variation, genotype-environment interactions, and genomic prediction for cassava garri quality

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Abstract

In this study, we assessed the genetic and genotype by environment interaction variation and genomic prediction of the garri quality traits of cassava (*Manihot esculenta* Crantz). The study was conducted in the National Root Crop Research Institute experimental sites in Umudike and Otobi, Nigeria, in two planting seasons of 2021 and 2022. We estimated the broad and narrow-sense heritability and correlation among measured physicochemical parameters on the garri and dried cassava roots (chips). A fivefold cross-validation scheme was used to calculate the accuracy of the genomic prediction. A significant negative correlation was observed between dry matter content, swelling index, water absorption capacity, and amylose content in garri. The swelling index had a significant negative correlation with swelling power, bulk density, amylose content of cassava chips, crude fiber, and dry matter content. Bulk density had a significant negative correlation with the crude fiber of garri and a positive correlation with the amylose content of cassava chips, the crude fiber of cassava chips, and the dry matter content. Broad-sense heritability ranged between 0 and 0.19 for garri traits and 0.02 and 0.49 for chips. Narrow-sense heritability ranged between 0 and 0.18 for garri quality traits and 0 and 0.20 for chips. A significant genotype $\times$ environment effect was observed for most of the evaluated traits of chips and garri quality. The predictability of the sugar content, swelling index, swelling power, and water absorption capacity of garri was higher than that of the amylose content, bulk density, and starch content of garri. There was low predictive accuracy for the quality traits garri studied. The sugar content, swelling power, and water absorption capacity of cassava chips averaged approximately 20%. This study

Abbreviations: AMY_ch, amylose content of chips; BLUE, best linear unbiased estimate; CF, crude fiber; CF_ch, crude fiber content of chips; DMC, dry matter content; GEBV, genomic estimated breeding value; GS, genomic selection; h^2 , narrow-sense heritability; H^2 , broad-sense heritability; NRCRI, National Root Crops Research Institute; PCA, principal component analysis; SC, sugar content; SC_ch, sugar content of chips; SNP, single-nucleotide polymorphism; STC, starch content; STC_ch, starch content of chips; TP, training population.

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provides valuable insights into assessing the genetic variation, correlation, and genomic selection within breeding programs aimed at enhancing the quality traits of cassava for end users.

Plain Language Summary

We evaluated different cassava genotypes across two locations and 2 years. We made garri from the different cassava genotypes and dried and ground some of the cassava roots (the dried roots are called the chips in this paper). The objectives were to determine the effect of cassava genotypes and locations on garri quality and whether garri quality traits can be inherited. We also used genomic prediction to predict cassava quality traits. The study was conducted in the National Root Crop Research Institute experimental sites in Umudike and Otobi, Nigeria, in 2021 and 2022. We analyzed the starch, dry matter, amylose, and crude fiber content of the cassava chips and garri. We also analyzed the bulk density, water absorption capacity, swelling index, and swelling power of garri. We calculated their broad and narrow-sense heritability and correlation among measured traits and carried out genomic prediction for the traits measured.

1 | INTRODUCTION

Cassava (*Manihot esculenta* Crantz) is a major staple in Africa, South America, and Asia (Halsey et al., 2008). It is primarily cultivated for its carbohydrate-rich roots, which serve as a dietary staple and a raw material for starch and bioethanol production (Jansson et al., 2009). Both the roots and leaves are essential components in livestock feed production: the roots are processed into pellets, while the leaves are converted into silage for livestock consumption (Parmar et al., 2017).

Unlike most crops, cassava can withstand a long period of drought, making it a valuable crop in areas with low or irregular rainfall. It exhibits adaptability to various agroecological zones and climates, making it an important crop for food security (Bechoff et al., 2018; Jarvis et al., 2012; Rabbi et al., 2014). Sub-Saharan Africa accounts for half (170 million tonnes) of the cassava produced in the world, with Nigeria leading in production with a total yield of 60 million tonnes in 2018 (FAO, 2019).

Cassava can be propagated through stem cuttings and seeds. When propagated from stem cuttings, cassava develops a fibrous root system from which some roots enlarge, accumulate starch, and become storage roots (Alves, 2002). The mature storage root consists of three main layers: the periderm, cortex, and parenchyma tissues. The parenchyma tissue, the edible part of the root, contains xylem vessels dispersed within a starch matrix (Wheatly & Chuzel, 1993).

Cassava belongs to the Euphorbiaceae family and the genus *Manihot*. The Euphorbiaceae is a large flowering plant family with 300 genera and 7500 species (Rahman & Akter, 2013), of which *M. esculenta* is the sixth most widely cultivated

food crop (Amelework & Bairu, 2022). The Euphorbiaceae family is known for producing poisonous milky latex, which serves as a defense mechanism against herbivores (Konno, 2011). This latex is distributed throughout the cassava plant and contains various phytochemicals, including diterpene esters, alkaloids, and cyanogenic glycosides (Konno, 2011). Both the roots and leaves of cassava contain significant amounts of the cyanogenic glucosides linamarin and lotaustralin. These compounds can release hydrogen cyanide (HCN) when exposed to linamarase, a naturally occurring enzyme in cassava (Cereda & Mattos, 1996). Hydrogen cyanide (HCN) is toxic to humans, and it is essential to employ processing methods that reduce its presence in food. Consuming foods with high HCN levels can lead to Konzo, an upper motor neuron disease that leads to irreversible muscle spasms (Nzwalo & Cliff, 2011).

Cassava roots are highly perishable with the formation of black, brown, and blue pigments in the roots typically leading them to become inedible 72 h after harvesting (Hahn, 1989; Wheatly & Chuzel, 1993). To avoid this postharvest physiological deterioration, cassava is processed into fermented products such as garri and fufu (Ndjouenkeu et al., 2021). Important steps such as fermentation, dewatering, heating, and drying are employed to reduce the hydrogen cyanide (HCN) concentration to a safe level (Achinewhu et al., 1998). Fermentation can alter the biochemical and nutritional properties of the starting ingredient (Sharma et al., 2020).

Cassava roots are processed into garri. In Africa, approximately 30% of the harvested cassava is consumed boiled, while the remaining 70% is processed into garri and other cassava products (Ndjouenkeu et al., 2021). Garri is produced

through a process that involves dewatering, sieving, and roasting fermented cassava mash. It is characterized by its low moisture content, extended shelf life, ease of transport, and lower hydrogen cyanide levels than other cassava products (Achinewhu et al., 1998). Garri serves as a convenient and ready-to-eat form of cassava in both urban and rural communities (Flach, 1990). It can be consumed in various ways, such as by pouring cold water over it and eating it with peanuts or by reconstituting it with hot water to create a dish known as eba.

The processing methods for cassava vary from region to region (Ndjouenkeu et al., 2021). The production of garri involves a combination of physical, chemical, and biochemical processes (Udofia et al., 2011). The quality of garri is determined by its physicochemical properties (Alaba et al., 2015).

Starch is the primary storage carbohydrate in cassava and other plants, and it consists of two glucose polymers: amylose and amylopectin (Seung, 2020). Amylose is linear and has a (1,4)-linked α -D-glucan, while amylopectin is the highly branched (1,6)-linked α -D-glucan (Kobayashi, 2012). The starch content of cassava varieties can significantly impact their taste, color, odor, feel, and physicochemical properties when used in food (Afoakwa et al., 2010). Given starch's prevalence, there is a positive relationship between dry matter and the starch content of cassava (Maraphum et al., 2021). The structure of starches is the primary attribute that affects texture (Charoenkul et al., 2011). Texture changes during processing are linked to the starch content, the amylose-to-amylopectin ratio, and the pectin content (Bechoff et al., 2018).

Amylose plays a significant role in determining the starch properties of foods (Seung, 2020). There is a direct relationship between amylose content (Juliano, 1985; Zhou et al., 2002) and cooking characteristics affecting post-cooking texture (Gandebe et al., 2017). The texture, moisture retention, gelation, and solubility are affected by the ratio of the amylose and amylopectin content of the starch (Klaochanpong et al., 2014). Natural starch consists of less than about 35% amylose. Starch with low amylose content tends to have a stickier texture than those with normal or high amylose. High amylose starch is less digestible than regular starch (Seung, 2020). Free amylose influences bulk density, swelling capacity, gelatinization, and water absorption (Achinewhu et al., 1998; Oladunmoye et al., 2014).

Swelling capacity is a critical sensory and mechanical characteristic of garri. It determines the moldability of eba and the flow of garri when mixed with water (Udofia et al., 2011). A good garri should swell to three times its volume when placed in water (Ingram, 1975). High swelling capacity is considered a good quality garri trait (Oduro et al., 2000). Swelling index and swelling power are measures of swelling capacity. Swelling power is a measure of the water-holding

Core Ideas

- Genotype by environment interaction was observed for most of the physicochemical traits studied.
- All traits studied had low broad-sense heritability except for the dry matter content (0.45).
- Dry matter content had a significant negative correlation with amylose and crude fiber content.
- There were low prediction accuracies for the physicochemical traits evaluated.

capacity of starch granules when heated in excess water. It represents the ability of starch to absorb water and swell. Swelling power is important in the gelatinization of starch (Lan et al., 2015), which determines the ability of the garri to swell (Oduro et al., 2000). Swelling index measures the volume increase of starch granules when they absorb water during gelatinization. It is typically expressed as the ratio of the volume of the gelatinized starch granules to the volume of the original dry granules.

Bulk density measures the weightiness of a product (Ngoma et al., 2019; Olapade et al., 2023) and is affected by the porosity of the product (Ngoma et al., 2019), particle size, and the moisture content of the product (Chandra & Singh, 2013). Small-scale traders often sell garri by volume using various containers, so a high bulk density may not be advantageous to them, as it would mean selling a larger weight for the same volume. However, for commercial garri sellers, products are typically sold by weight in standardized units like 20, 50, and 100 kg bags, making the bulk density less relevant to the sellers.

Water absorption capacity (WAC) is a fundamental quality characteristic (Bushuk & Békés, 2002) as it determines the amount of water required for food processing (Marikkar et al., 2021). WAC represents the quantity of water necessary to achieve the optimal dough consistency (Rakszegi et al., 2014). WAC affects starch degradation, spoilage, and a product's ability to retain moisture (Bala et al., 2020). WAC of garri tends to decrease as particle size decreases (Laya et al., 2018). There are positive correlations between water absorption, swelling capacity, and the texture experienced during chewing (Adinsi et al., 2019). This highlights how WAC impacts not only processing but also the sensory attributes of the final product. A high WAC is indicative of the presence of hydrophilic components within the food (Chandra et al., 2015).

Measuring food quality traits can be labor-intensive, especially at early stages of the breeding program where a substantial number of materials are evaluated. Genomic selection (GS) may reduce labor by enabling the prediction

of quality traits rather than requiring their measurement. GS assesses the genetic value of an individual by regressing the genome-wide array of genetic markers on specific phenotypic values (Bhat et al., 2016). The prediction model is constructed in GS using the genotype and phenotype data from a training population (TP). This model is then employed to calculate genomic estimated breeding values (GEBVs) for all individuals within the breeding population (BP), utilizing their genomic profiles (Meuwissen et al., 2001). Genomic prediction has been used to predict dry matter, starch, and total carotenoid content in cassava (Ikeogu et al., 2019; Rogerio Braatz De Andrade et al., 2019; Wolfe et al., 2016).

Currently, there is limited knowledge of the relationship between cassava genotypes and the quality of garri produced from their roots. In addition, it is still being determined if there is a genotype-by-environment effect on garri quality and if GS models can predict garri quality traits. Further research is needed to explore these aspects and gain a deeper understanding of how cassava genotype impacts the characteristics of garri.

The objectives of the study were to:

1. determine the extent of genetic variation and assess the heritability of garri quality in diverse cassava genotypes;
2. investigate genotype by environment interaction effects on the physicochemical properties of cassava;
3. measure correlations between garri quality traits to understand them better; and
4. employ genomic predictions to predict the physicochemical attributes of garri.

2 | MATERIALS AND METHODS

2.1 | Germplasm

The planting materials used in this study were sourced from the NRCRI-NextGen GS cycle 2A population. These materials are the offspring of the TP described initially by Ikeogu et al. (2019). The cycle 2A population represents the second cycle of GS, as outlined by Wolfe et al. (2016). The experiment was conducted across two growing seasons: 2020/2021 and 2021/2022, with trials conducted in Umudike (5°29' N, 7°24' E; mean annual rainfall of 2200 mm; annual temperature of 22–31°C; altitude of 120 m above sea level; humid forest zone) and Otobi (7°20' N, 8°41' E; mean annual rainfall of 1500 mm; altitude of 319 m above sea level; yearly temperature of 24–35°C; southern Guinea savannah zone). The experimental design employed was an alpha lattice design with two replications of 204 genotypes in Umudike and 196 genotypes in Otobi. The physicochemical analysis was carried out in the biotechnology teaching and research laboratory of the

National Root Crops Research Institute (NRCRI) in Umudike.

During processing and sampling for the physicochemical analysis, cassava roots were harvested from the two replicates, replicates bulked by genotype, and subsequently processed into garri and chips. 193 genotypes were processed into chips, while 192 genotypes were processed into garri.

2.2 | Processing cassava roots to garri

The cassava processing procedure involves several steps, including peeling of the roots, washing, grinding, bagging of the ground root, fermentation, dewatering, sieving, and roasting (James et al., 2012). The roots were harvested from each plot, and the number harvested was recorded. The garri was processed using the method described by James et al. (2012) with slight modifications. The cassava roots were peeled and washed. The cleaned roots were fed into a grinding machine to produce a mash. The mash from different cassava genotypes was placed in separate jute bags. The mash was left to ferment for 48 h. The bags containing the fermented mash were placed in a dewatering machine, with a weight placed on the bags of wet mash, and the weights were pressed down to remove moisture and solidify the cassava mash. The resulting hardened cassava cake was sieved to reduce its particle size and eliminate any lignin or uncrushed roots that might still be present. This step was crucial for ensuring the quality of the final product.

Roasting was carried out in batches using a cast iron pot placed over a source of heat. The pot was heated to an average temperature of 70°C. Initially, sieved garri was added to the pot and stirred until it reached a gelatinized state without forming large particles. More sieved garri was gradually added, and the roasting process continued until no more steam emanated from the garri in the pot. At this stage, the garri achieved an even dryness and a free-flowing consistency at an average temperature of 116°C. The temperature was then lowered to prevent any charring. The garri was carefully removed from the pot and spread thinly on a flat surface. This allowed it to cool and dry thoroughly, ensuring the quality of the product.

2.3 | Production of cassava chips

The peeled cassava roots were washed and chopped into small pieces of less than 1 cm³, called chips, with sharp stainless-steel knives. They were dried in the oven at 45°C for 24 h (Tran, 2019). The dried cassava chips were then allowed to cool before being milled into flour using an electric milling machine (Fadar plus FD-988).

2.4 | Data collection

2.4.1 | Genotyping data

For each clone, leaf tissue was collected in 96-well plates and submitted to Diversity Arrays Technology for genotyping by sequencing a reduced representation library, the DArTseq protocol: <https://www.diversityarrays.com/services/dartseq/>. DArTseq identified 27,206 markers. These were used to impute allele dosages at further loci based on a panel combining DArTseq markers and genotyping by sequencing markers obtained from an ApeKI restriction enzyme-based genome complexity protocol (Hamblin & Rabbi, 2014). Imputation resulted in 16,384 single-nucleotide polymorphisms (SNPs). To enhance the association power and address potential sequencing errors, an additional filtering step was applied to the combined marker dataset. Genotypes with more than 10% missing data and SNPs with over 5% missing data or minor allele frequency below 5% were removed. After filtering, a total of 14,523 SNP markers were obtained for downstream analyses.

2.4.2 | Physicochemical data

For the physicochemical analysis, cassava roots were harvested from the two replicates and processed into garri. The analysis of garri and chips samples was carried out in the biotechnology teaching and research laboratory of the NRCRI in Umudike. The following physicochemical traits were collected on both garri and chips: Water-absorbing capacity (WAC), swelling index, swelling power, bulk density, total sugar content (SC), STC, crude fiber (CF), and amylose. For traits measured on chips, all values were converted to a fresh weight basis by multiplying by the dry matter content (DMC) of the sample.

DMC

The oven-dry method was used to determine the DMC (Ikeogu et al., 2017). Ten grams of chopped fresh cassava roots were placed inside a moisture can and subjected to drying in an oven set at 105°C until a consistent weight was achieved. The DMC was then calculated by dividing the weight of the dried sample by the weight of the original fresh sample.

Swelling index

The swelling index was determined using the method described by Felber et al. (2016). One gram of the garri sample was placed in a calibrated falcon tube. Subsequently, 15 mL of water was added to the sample, and the mixture was immediately stirred. The initial volume of the sample was recorded, and after 4 hours, the final volume was mea-

sured. The swelling index was determined by dividing the final volume by the initial volume.

Swelling power

Swelling power was determined using the method described by Leach et al. (1959) with slight modifications. One gram of sample was weighed into a centrifuge tube, and 15 mL of distilled water was added and stirred. The centrifuge tube was heated in a water bath for 40 min at 80°C with constant stirring. The sample was centrifuged at 2200 rpm for 20 min. The swelling power was calculated as the percentage increase in weight of the sediment relative to the garri sample.

Bulk density

Bulk density was determined using the method described by Ashraf et al. (2012). Thirty grams of the garri sample was placed into a measuring cylinder. The cylinder containing the sample was tapped on a flat table for 60 s. The final volume of the sample in the cylinder was then recorded. Bulk density was calculated by dividing the weight of the sample by the final volume, expressed in g/mL.

Water-absorbing capacity

WAC was determined using the method of Ashraf et al. (2012) with slight modifications. One gram of sample was placed into an empty centrifuge tube, and 15 mL of distilled water was poured into the tube. This was stirred and allowed to stand for 10 min. The sample was centrifuged at 2200 rpm for 20 min, and the supernatant was decanted into calibrated falcon tubes. The final reading of the volume of water was recorded. The weights of the sediment and tube were also recorded. Water absorption is the weight of water absorbed by 100 g of the sample.

Amylose content

The amylose content of the samples was determined by the method employed by Williams et al. (1970) and Sudheesh et al. (2019) with a slight modification. 0.1 g of the sample was weighed into a test tube, and 1 mL of 95% ethanol and 9 mL of 1N NaOH were added to the sample. The sample was heated for 10 min in a boiling water bath to gelatinize the starch. It was allowed to cool, and 9 mL of water was added to the boiled sample. An aliquot of 0.5 mL of digest was collected, and 0.1 mL of acetic acid solution and 0.2 mL of iodine solution were added to the aliquot. Note that 9.2 mL of distilled water was added to the whole solution. The sample was left for 20 min to develop color before vertexing. The absorbance was read at 620 nm.

Sugar content

The sugar and starch content of the samples were determined using the method described by Otegbayo et al. (2019). To determine sugar, 0.02 g of the sample was weighed into centrifuge tubes, and 1.0 mL of 95% ethanol, 2.0 mL of distilled

water, and 10 mL of hot ethanol were added to the sample. The sample was vortexed and centrifuged for 10 mins at 2000 rpm. The supernatant was decanted into a test tube, and 7 mL of distilled water was poured into the test tube. An aliquot (0.2 mL) was collected, 0.8 mL of distilled water and 0.5 mL of phenol were added to the aliquot, and vortexed. Note that 2.5 mL of concentrated sulfuric acid was slowly added, vortexed, and allowed to cool down. The absorbance was read at 490 nm.

Starch content

7.5 mL of perchloric acid was added to the residue from the sugar analysis and was allowed to stand for 1 hour. It was diluted with 17.5 mL of distilled water and made up to the 25 mL mark and filtered. Note that 0.05 mL of the filtrate was collected and diluted with 0.95 mL of distilled water; it was vortexed and ready for assay. The absorbance was recorded at 490 nm.

CF

The CF content of the samples was determined using the AOAC method 962.09 (AOAC, 1990). Three grams of the sample was defatted using 50 mL of petroleum ether in a conical flask. Note that 200 mL of 1.25% sulfuric acid was added to the defatted sample, and a few drops of anti-foaming agent were added to the beaker and boiled for 30 min. It was allowed to stand for 1 min and filtered through a Buchner funnel. The residue was washed with boiling water to remove the acid. Note that 200 mL of 1.25% sodium hydroxide solution was added to the residue and boiled again for 30 min. After boiling, it was allowed to stand for 1 min and filtered. The residue was washed with boiling water, followed by 1% hydrochloric acid, and with boiling water until it was free of acid. It was washed with alcohol and ether, transferred into an ash dish, and dried at 100°C to a constant weight. The ash was incinerated at 600°C for 30 min, cooled in a desiccator, and weighed. The difference in weight between oven-dry weight and the weight after incineration was taken as the fiber content of the sample.

2.5 | Data analysis

2.5.1 | Data wrangling and visualization

Data wrangling was done using the tidyverse (Wickham, 2019) package in R (R Core Team, 2023). The distribution of observed traits across different environments and years was visualized using the ggplot2 package (Wickham, 2016) in R (R Core Team, 2023).

2.5.2 | Trait correlations

Outliers were removed from the data using the boxplot stat function in the base R package. Pearson correlations were

computed for all the traits studied using the Agricolae package (De Mendiburu, 2023) in R, while the psych package in R (Revelle, 2024) was used to make the correlation plot for the traits.

2.5.3 | Linear mixed model

To estimate variance components, broad-sense heritability, and narrow-sense heritability, the observed traits were fitted with a linear mixed model using the lme4 package (Bates et al., 2015). The outcome of the estimate from the lmer function was used to estimate the broad-sense heritability.

The model equation used was:

$$y_{ijk} = \mu + G_i + L_j + Y_k + Y * L_{jk} + G \times Y_{ik} + G \times L_{ij} + e_{ijk} \quad (1)$$

where:

- y_{ijk} is the observation of the i th genotype in the j th location and for the k th year.
- G_i is the effect of the i th genotype.
- L_j is the effect of the j th location.
- Y_k is the effect of the k th year.
- $Y \times L_{jk}$ and $G \times L_{ij}$ are the effects of the interactions,
- G_i , Y_k , L_j , $G \times Y_{ik}$, $Y \times L_{jk}$, $G \times L_{ij}$ were all set as random effects.
- e_{ijk} is the random noise.

Broad-sense heritability:

Broad-sense heritability (H^2) was calculated using the formula below, which accounts for genetic, environmental, and interaction variances.

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_{gl}^2}{nl} + \frac{\sigma_{gy}^2}{ny} + \frac{\sigma_e^2}{nl \cdot ny}} \quad (2)$$

where ny is the number of years, nl is the number of locations, σ_g^2 is the genetic variance, σ_e^2 is the residual variance, σ_{gl}^2 is the variance due to the genotype by location interaction, and σ_{gy}^2 is the variance due to the genotype-by-year interaction.

2.6 | Narrow-sense heritability

The mmer function in the sommer package (Covarrubias-Pazaran, 2016) was used to estimate the variance component, which was used to estimate the narrow-sense heritability using the additive relationship matrix as a covariate. The additive relationship matrix, $\mathbf{K}$, was produced from the SNPs data using the A.mat (additive genetic relationship matrix)

function in the rrBLUP package in R (Endelman, 2011) and $G \sim N(0, K\sigma^2_g)$. For detailed information on the additive relationship matrix, refer to Figure S1.

Narrow-sense heritability was estimated as a ratio of the additive genetic variance divided by phenotypic variance, using Equation (2) as for the broad-sense heritability, but replacing the genetic variance with the *additive* genetic variance as estimated by mmer.

2.7 | Principal component analysis (PCA)

The scaled values of the best linear unbiased estimates (BLUEs) for each trait were used for the principal component analysis (PCA) analysis for both the garri and chips samples. The PCA biplot was produced using the fviz_pca_biplot function in factoextra (Kassambara & Mundt, 2020). PCA was also done on the SNPs data using the ASRgenomic package (Gezan et al., 2022). The PCA analysis was done to visualize the population structure.

2.7.1 | Genomic prediction

The BLUEs values of the genotypes were estimated using Equation (3) by considering genotype as a fixed effect and used to evaluate genomic prediction accuracy.

$$y_{ijk} = \mu + G_i + L_j + Y_k + e_{ijk} \quad (3)$$

where y_{ijk} is the observed value of the i th individuals at j th location and k th year, G_i is the effect of the genotype, L_j is the effect of the location, Y_k is the year effect, and e_{ijk} is the random noise. In this model, we considered genotype and location as fixed effects. To fit the model, the lme4 package of R was used (Bates et al., 2015).

The genetic estimated breeding values for the genotypes were obtained by fitting the following genomic best linear unbiased prediction model.

$$Y = 1\mu + Zg + e$$

where Y = the BLUE of the genotypes from Equation (3), μ is the grand mean, and g is the vector of the additive genetic effect of the genotypes. e is the vector of the error variance, $g \sim N(0, K\sigma^2_g)$. Where K is the additive relationship matrix as for the narrow-sense heritability calculation above, and $e \sim N(0, I\sigma^2_e)$.

To estimate the accuracy of the genomic prediction, a fivefold cross-validation scheme was employed where the population was divided into five equal folds, of which four folds were used as a training set, while the other onefold was used as a testing set (Wolfe et al., 2017), and cross-validation was iterated 25 times. The genomic prediction accuracy of

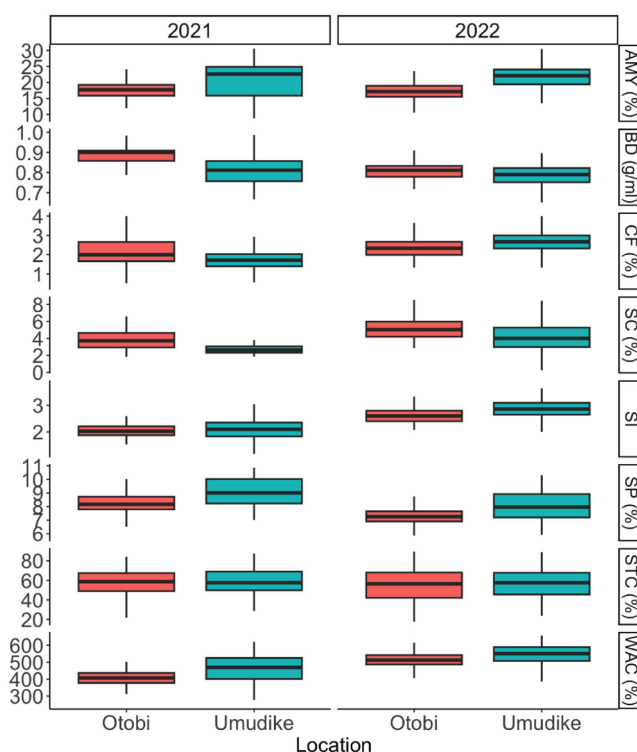


FIGURE 1 The distribution of garri amylose, crude fiber, water-absorbing capacity (WAC), swelling power, swelling index, and bulk density. AMY, amylose; BD, bulk density; CF, crude fiber; SC, sugar content; SI, swelling index; SP, swelling power; STC, starch content.

each cross-validation was estimated as a correlation between the predicted GEBVs and the BLUEs of the genotypes (Yan et al., 2022).

3 | RESULTS

3.1 | Phenotypic distribution

The physicochemical parameters of garri across all years exhibited approximately normal distributions (Figure 1). Amylose content, swelling power, swelling index, and WAC consistently showed higher values in Umudike than in Otobi. On the other hand, bulk density and SC were higher in Otobi than in Umudike.

The chemical parameters of cassava root chips exhibited an approximately normal distribution for most traits in both years, except for crude fiber content of chips (CF_ch) in 2022 (Figure 2). In 2021, Otobi had higher means for amylose content of chips (AMY_ch), DMC, and sugar content of chips (SC_ch), while Umudike had higher means for CF_ch and starch content of chips (STC_ch). In 2022, Otobi had higher means for STC and DMC, while the means for AMY_ch, CF_ch, and SC_ch appeared to be similar (Figure 2).

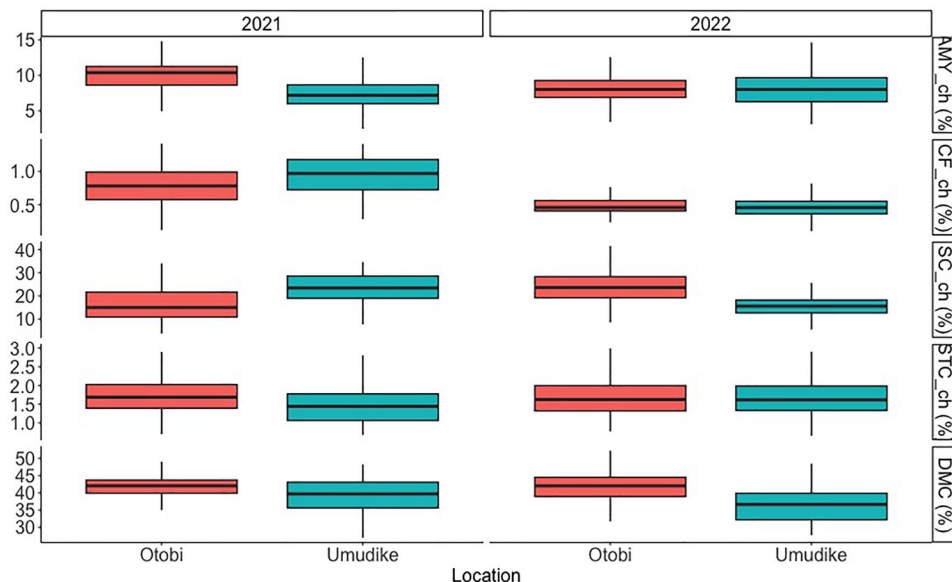


FIGURE 2 The distribution of amylose, crude fiber, starch, and free sugar in cassava chips. Abbreviations are as follows: AMY_ch = amylose of chips, CF_ch = crude fiber of chips, STC_ch = starch content of chips, SC_ch = sugar content of chips, DMC = dry matter content of the roots. AMY was consistently higher than AMY_ch. CF_ch was consistently lower than CF. Mean STC was generally higher than STC_ch across all years and locations, except for 2021 in Umudike, where they were the same.

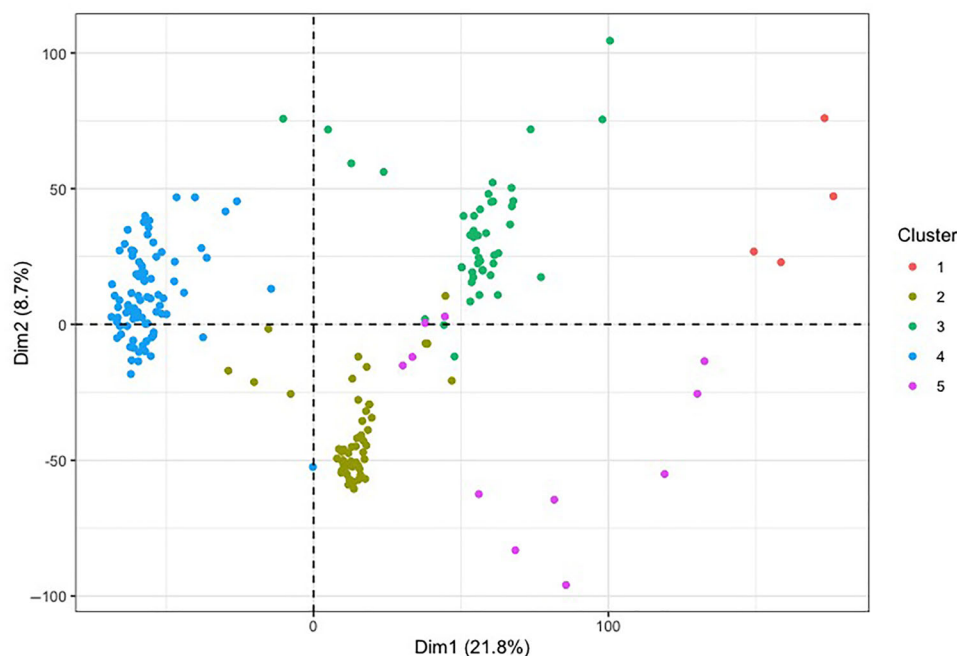


FIGURE 3 Principal component analysis (PCA) plot of the cassava clones in the C2a population, showing its population structure.

3.2 | Principal component analysis

PCA was employed to elucidate the population structure of cassava genotypes based on SNP data. Five distinct clusters of genotypes were identified (Figure 3). The analysis also showed that the first two components explained 21.8% and 8.7% of the total variation, respectively (Figure 3).

The PCA biplot of cassava garri traits showed the observed scaled scores of the two principal components. SC, SP, STC, and amylose were in the upper left quadrant. CF was found in the upper right quadrant (Figure 4). Genotypes in the upper right quadrant had high scores for CF and include G134, G91, G188, G152, G122, G127, G156, G14, G158, G139, and G113 WAC, and swelling index were in the lower right

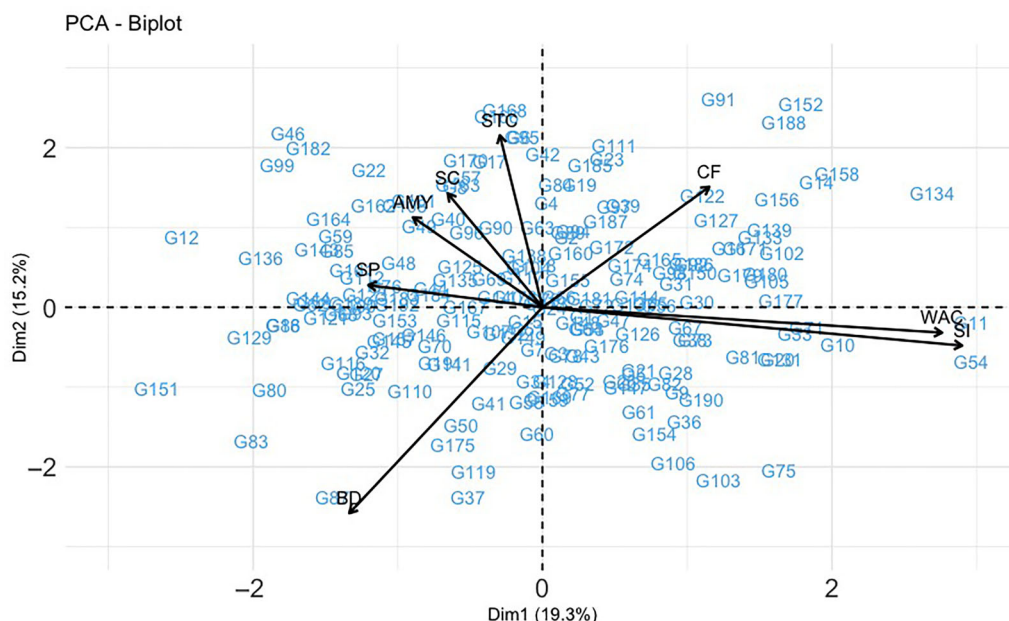


FIGURE 4 Principal component analysis (PCA)-biplot of the garri quality traits. The name of the genotypes indicated as G1, G2, G3...G192 (Table S1). AMY, amylose content; BD, bulk density; CF, crude fiber; SC, sugar content; SI, swelling index; SP, swelling power; STC, starch content; WAC, water-absorbing capacity.

quadrant but at the extreme right of the x -axis. This includes genotypes with the codes G10, G11, G109, G54, and G124 (Figure 4).

The PCA biplot of cassava root chip traits showed the observed scaled scores of the two components. Genotypes represented with the codes G143, G53, G115, G3, G111, G109, G122, G32, G42, G29, and G187 found in the upper right quadrant had high scores for DMC, STC_{ch}, and SC_{ch}. G106, G141, G89, and G2 had high CF_{ch} and AMY_{ch} scores (Figure 5). All the traits measured were observed to cluster toward the DMC because all measurements were converted to fresh weight basis using the DMC value (Figure 5).

3.3 | Correlation among traits

The result of the correlation of the physicochemical parameters of the chips and the garri obtained from different cassava genotypes showed that DMC had a significant negative correlation with swelling index, WAC, amylose, and CF at $p < 0.001$ and a significant positive correlation with bulk density, STC_{ch}, AMY_{ch}, CF_{ch}, and SC_{ch} at $p < 0.001$ (Figure 6). Swelling index had a significant ($p < 0.001$) negative correlation with SP, bulk density, AMY_{ch}, CF_{ch}, and DMC. Swelling index also had a positive correlation (significant at $p < 0.001$) with WAC and CF (Figure 6). Swelling point had significant ($p < 0.001$) negative correlations with WAC, SC, and CF at $p < 0.05$. Significant ($p < 0.001$) positive correlations were observed between swelling point and amylose, and swelling point and CF_{ch} (Figure 6). There were

negative correlations (significant at $p > 0.001$) between WAC and bulk density, WAC and AMY_{ch}, and WAC and CF_{ch}, and WAC was positively correlated with CF (Figure 6). Bulk density had a significant ($p < 0.001$) negative correlation with CF and a positive correlation with AMY_{ch}, CF_{ch}, and DMC. Amylose was negatively correlated with SC and positively correlated with CF_{ch}. Amy_{ch} had a positive correlation with CF_{ch}; the result was significant at $p < 0.001$ (Figure 6).

The result of the physicochemical attributes of garri made from different varieties of cassava showed that σ_g^2 , σ_{gl}^2 , and σ_{gy}^2 , were low for all the traits while, σ_p^2 was high for all the traits, leading to a corresponding low heritability for all the traits studied (Table 1). σ_{gl}^2 effect was observed on swelling index, swelling power, WAC, amylose, CF, STC, and SC of garri. σ_e^2 was observed to be higher than the other variance components for all the traits measured (Table 1).

The mmer method gives narrow-sense heritability, while the lmer method gives broad-sense heritability. The result of the heritability estimates of the chemical characteristics of cassava chips on a fresh weight basis showed that σ_{gl}^2 was observed for DMC, STC_{ch}, and AMY_{ch}. σ_{gy}^2 was also observed for DMC, STC, CF_{ch}, and SC_{ch}. The results also showed σ_g^2 , σ_{gl}^2 , and σ_{gy}^2 were lower than σ_{ph}^2 and σ_e^2 , thereby resulting in low heritability estimates for all the traits (Table 2). The broad-sense heritability (H^2) was higher than the narrow-sense heritability (h^2). DMC had a narrow-sense heritability of 0.2 and a broad-sense heritability of 0.45. Amylose had a narrow-sense heritability of 0.2 and a broad-sense heritability of 0.16 (Table 2).

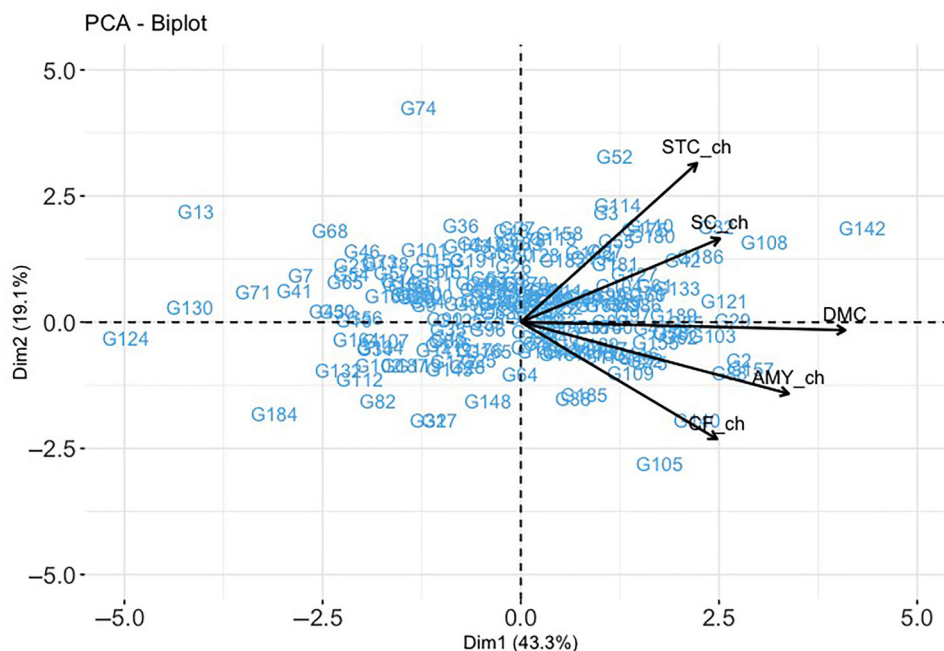


FIGURE 5 Principal component analysis (PCA) biplot of the cassava chips. AMY_ch, amylose of chips; CF_ch, crude fiber of chips; DMC, dry matter content; SC_ch, sugar content of chips; STC_ch, starch content of chips. The names of the genotypes are indicated as G1, G2, G3...G193 (Table S2).

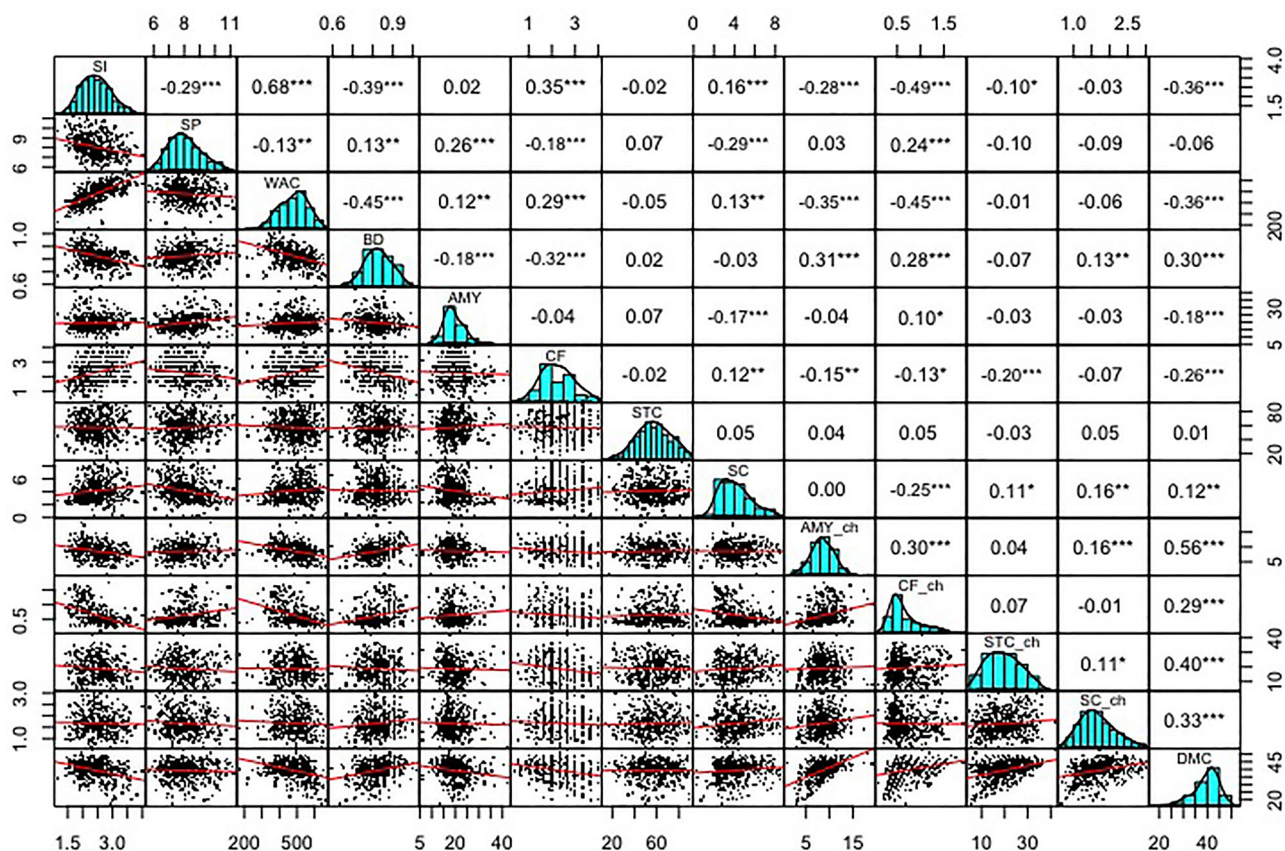


FIGURE 6 The correlation plot of the physicochemical attributes of garri and cassava chips. AMY, amylose of garri; AMY_ch, amylose of chips; BD, bulk density; CF, crude fiber of garri; CF_ch, crude fiber of chips; DMC, dry matter content; SC, sugar content of garri; SC_ch, sugar content of chips; SI, swelling index; SP, swelling power; STC, starch content of garri; STC_ch, starch content of chips; WAC, water-absorbing capacity.

TABLE 1 Variance components and heritability estimates of the physicochemical properties of garri for 2 years and two locations.

Trait	Method	σ_g^2	σ_{gl}^2	σ_{gy}^2	σ_e^2	σ_{ph}^2	Heritability
SI	h^2	0.01	0.01	3.5e-3	0.10	0.03	0.15
	H^2	0.00	0.01	0.01	0.09	0.03	0.00
SP	h^2	0.02	0.09	0.00	0.67	0.23	0.09
	H^2	0.00	0.10	0.01	0.67	0.22	0.00
WAC	h^2	197	126	287	2671	1070	0.18
	H^2	204	701	253	2733	1049	0.19
BD	h^2	4e-05	2.8e-4	0.00	7.8e-4	2.4e-3	0.05
	H^2	1.5e-04	1.7e-4	0.00	8.4e-4	2.4e-3	0.18
AMY	h^2	0.00	2.38	0.92	9.01	3.90	0.00
	H^2	0.00	2.38	0.91	9.01	3.90	0.00
CF	h^2	0.02	0.04	0.02	0.35	0.13	0.13
	H^2	0.01	0.04	0.03	0.34	0.13	0.09
STC	h^2	1.24	37	0.00	209	72	0.02
	H^2	0.00	14	0.00	215	61	0.00
SC	h^2	0.06	0.24	0.00	1.61	0.58	0.10
	H^2	0.00	0.29	0.00	1.62	0.55	0.00

Abbreviations: AMY, amylose; BD, bulk density; CF, crude fiber; h^2 , narrow-sense heritability; H^2 , broad-sense heritability; LMER, linear mixed effects model; mmer, mixed model equations for R; SC, sugar content; SI, swelling index; SP, swelling power; STC, starch content; WAC, water-absorbing capacity; σ_e^2 , variance due to environment effect; σ_g^2 , genetic variance; σ_{gl}^2 , variance due to genotype by location effect; σ_{gy}^2 , variance due to genotype by year interaction; σ_{ph}^2 , phenotypic variance.

TABLE 2 Variance components and heritability estimates of the physicochemical properties of cassava chips for 2 years and two locations.

Trait	Method	σ_g^2	σ_{gl}^2	σ_{gy}^2	σ_{ph}^2	σ_e^2	Heritability
DMC	h^2	1.66	6.62	2.01	8.38	9.62	0.20
	H^2	4.13	4.18**	0.72	9.24	10.61	0.45
STC_ch	h^2	2.12	3.83	2.08	13.82	35.00	0.15
	H^2	0.24	5.04	3.93	13.12	33.60	0.02
AMY_ch	h^2	0.32	1.01	0	1.63	3.23	0.20
	H^2	0.25	1.02**	0	1.57	3.22	0.16
CF_ch	h^2	0	7e-5	0.01	0.01	0.04	0
	H^2	1.2e-3	0	3.4e-3	0.01	0.04	0.09
SC_ch	h^2	6.5e-3	2e-3	0.02	0.07	0.20	0.10
	H^2	0.01	0	0.01	0.07	0.2	0.20

Abbreviations: AMY_ch, amylose of chips; CF_ch, crude fiber of chips; DMC, dry matter content; h^2 , narrow-sense heritability; H^2 , broad-sense heritability; LMER, linear mixed effects model; mmer, mixed model equations for R; SC_ch, sugar content of chips; STC_ch, starch content of chips; σ_e^2 , variance due to environment effect; σ_g^2 , genetic variance; σ_{gl}^2 , variance due to genotype by location effect; σ_{gy}^2 , variance due to genotype by year interaction; σ_{ph}^2 , phenotypic variance.

**Significance of the full model over the restricted model.

3.4 | Genomic prediction

The prediction accuracy of garri chips varied across traits. The predictability of SC, swelling index, swelling power, and WAC was higher than that of amylose, bulk density, and STC. There was no prediction for CF. The predictability ranged between −0.1 and 0.48 for SC, −0.1 and 0.46 for swelling index, −0.12 and 0.43 for SP, and −0.1 and 0.5 for WAC (Figure 7).

The prediction accuracy for cassava chips varied across traits. The prediction accuracy for AMY_ch ranged between

−0.28 and +0.36, and prediction accuracy of DMC ranged between −0.36 and +5.4, whereas for STC_ch, it ranged between −0.3 and +0.16, and for SC_ch, it ranged between −0.38 and 0.18 (Figure 8).

4 | DISCUSSION

Evaluation of cassava product quality at an early breeding stage is not a common practice. This is because of the large number of clones available at the early breeding stage, which

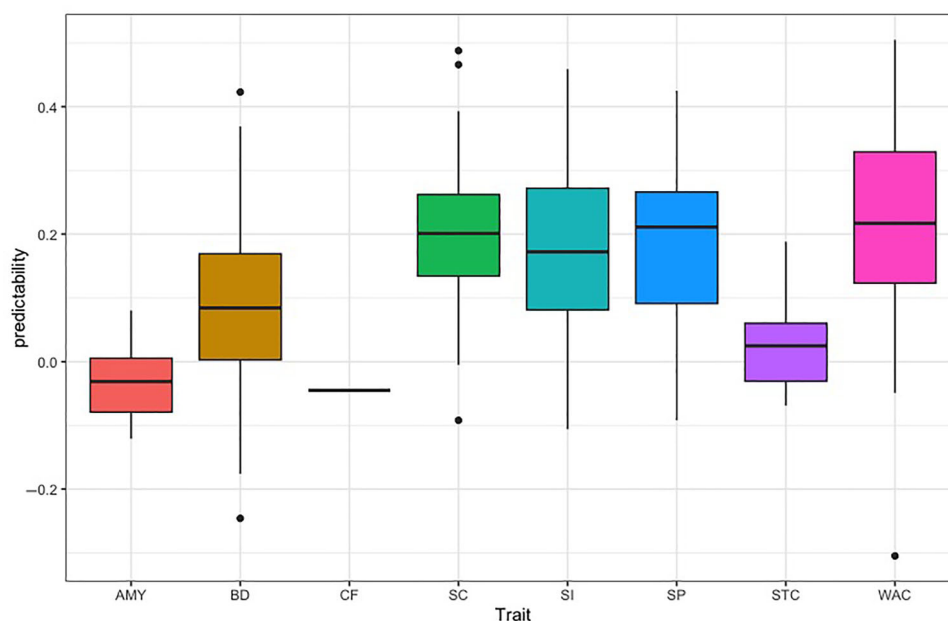


FIGURE 7 Genomic prediction of the physicochemical traits in garri. AMY, amylose; BD, bulk density; CF, crude fiber; SC, sugar content; SI, swelling index; SP, swelling power; STC, starch content; WAC, water-absorbing capacity.

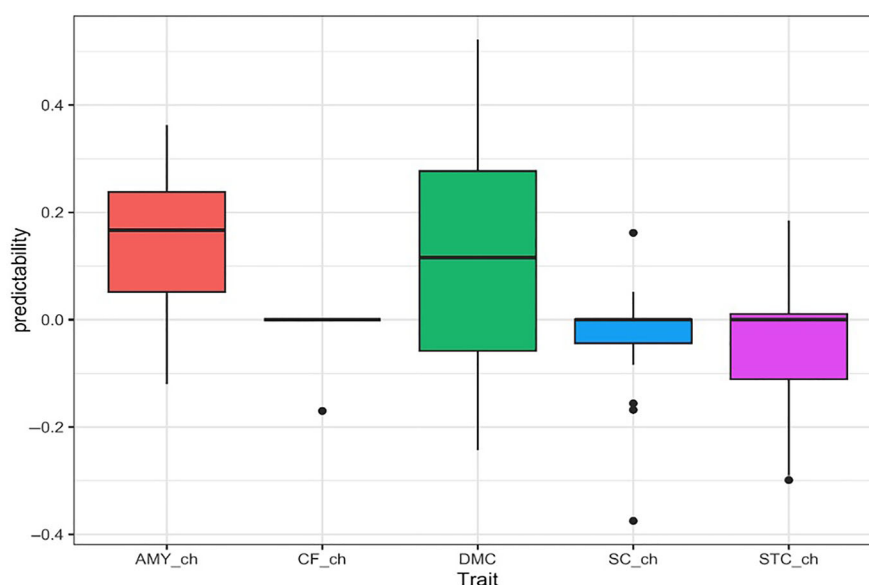


FIGURE 8 Genomic prediction of the physicochemical traits in cassava chips. AMY_ch, amylose of chips; CF_ch, crude fiber of chips; DMC, dry matter content; SC_ch, sugar content of chips; STC_ch, starch content of chips.

makes it expensive to evaluate quality traits. Therefore, breeders usually focus on selecting product quality traits toward the end of the breeding cycle, where the number of varieties to be evaluated is significantly reduced. However, this approach has its limitations. Not assessing the product quality traits at the early breeding stage could lead to the loss of cassava varieties with excellent garri quality.

By evaluating these traits early in the breeding process, we aim to improve the overall garri quality of the cassava

varieties and improve the efficiency of breeding programs. This research evaluates and identifies potential materials with superior product qualities that can be maintained throughout the breeding cycle.

There were differences in the range of the physicochemical parameters measured across genotypes, locations, and product types (garri and chips). These observed differences showed the possibility of the GEI effect on the physicochemical traits studied. It was observed that there were changes

in the chemical composition of garri and cassava chips. These changes differ based on the genotype and the location. The amylose of garri was higher than that of chips. This is because the starch in garri had undergone pre-gelatinization. Pre-gelatinization involves heating and moisture treatment of the samples, causing the starch granules to absorb moisture and swell (Aktaş & Gerçekaslan, 2019). The swelling of the starch granules makes amylose molecules more available for assessment. The CF of garri was higher than that of chips. When the samples were made into garri, all the roots were crushed during the grinding stage. Although sieving reduced the quantity of the large particles, including the xylem vessels present, some xylem vessels were finely ground and could pass through the sieve. Roots with too many woody filaments were not collected when samples were selected for CF evaluation. The SC increased in garri compared to the cassava chips. This is because fermentation increases the soluble SC until 36–48 h and drops at 60 h (Oyewole & Ayo Odunfa, 1989).

Understanding how different traits correlate can provide valuable insights into the composition, characteristics, and behavior of food quality traits. The positive correlations observed between CF, swelling index, and WAC were due to the hydrophilic nature of CF. CF contains cellulose; cellulose has a free hydroxyl group (Oh & Park, 2022). The free hydroxyl groups on the cellulose molecules can form hydrogen bonds with water molecules and other hydroxyl groups (Xiu et al., 2012). This interaction makes cellulose highly hydrophilic and contributes to its ability to absorb and hold water. Cellulose can absorb water and expand but does not dissolve in the water (Kobayashi, 2012).

A negative correlation was observed between swelling power and swelling index, swelling power, and WAC. The result was similar to Aghogho et al. (2023), who recorded a positive and a negative correlation between the swelling index and swelling power for their study in 2021 and 2022, respectively. Swelling power involves heating the samples, leading to swelling of the starch granules to form a gel. More water is absorbed during hot swelling than in cold swelling (Lefkir et al., 2017). The swelling power depends on the non-starch constituents of flour (Farooq et al., 2021). Hot water swelling breaks down the amylose of the starch-forming gel upon solidification. In cold water, starch granules are insoluble but swell in a liquid medium when heated (Escobedo-Avellaneda et al., 2020; Mesquita et al., 2018).

The negative correlations between bulk density and CF of garri mean that the more fiber is present in the sample, the less the bulk density. The irregular shape of the fibrous particles present in the sample could affect the bulk density and reduce its packing efficiency, hence the negative correlation observed. Smaller fiber particles are shown to have a higher bulk density and may lower the ability of the fiber to absorb water (Huang et al., 2009). CF contributes volume to food by aiding in regulating bowel movements and reducing the

likelihood of constipation. CF supports weight management (Miketinias et al., 2019) by promoting a sense of fullness and helping control appetite and calorie intake, making it an asset for weight loss goals.

The negative correlation observed between bulk density, WAC, and swelling index of garri is influenced by the physical and structural properties of the garri samples. Higher bulk density indicates that the garri particles are more densely packed. The compact nature of the particle leaves less space for water to be absorbed and lowers the swelling capacity. Bulk density is also a function of the particle size and shape. Fine particles compact better when tapped compared to samples with large particle sizes. The larger the particle size, the more space there will be in the sample and the lower the bulk density (Goula et al., 2004; Savlak et al., 2016). Varieties with high bulk density are preferred by consumers because more quantity of product is purchased per unit volume compared to varieties with low bulk density. The swelling of starch granules contributes to the overall swelling index of garri. When garri particles are densely packed, the starch granules may have limited space to swell during gelatinization. This restriction leads to a lower swelling index and WAC. Also, garri with coarser particles may have lower bulk density, allowing for more water absorption and a greater swelling index.

The significant positive correlation between amylose of garri with swelling index, amylose of garri with swelling power, and amylose of garri with WAC was due to the linear chains of amylose that can form a more organized structure, and as water is absorbed, these chains can interact with each other and with water molecules more effectively. Also, starch undergoes gelatinization when hydrated and heated. The more water the garri absorbs, the more gelatinization it can undergo (Lefkir et al., 2017). Furthermore, garri starch undergoes pre-gelatinization during processing and gelatinization in hot water during swelling power analysis and during centrifuging in WAC analysis. Heating causes samples of the starch granules to swell. Aktaş and Gerçekaslan (2019) recorded higher water absorption in pregelatinized starch compared to native starch. Strong positive correlations observed between DMC, starch of chips, amylose in chips, CF_ch, and starch content and SC of chips agree with the findings of other scientists (Abebe et al., 2012; Daemo et al., 2022; Silva et al., 2023). This is because the traits were converted to the fresh weight basis using the DMC.

The PCA biplots reiterate the correlation between the swelling index, amylose, starch, and SC of garri, and they showed the possibility of simultaneous selection of these traits. The positive correlations between DMC, amylose, starch, CF, and sugar of the cassava chips also showed the possibility of simultaneous selection of these traits.

Genotype by environment interaction (GEI) studies are essential for selecting varieties that adapt well to different

growing conditions, ensuring productivity and stability. GEI provides insights into the specific conditions where certain genotypes excel, enabling breeders to tailor their programs to optimize performance in target environments. GEI exists in most of the traits measured. Genotypic variance was low for all the traits, leading to their low heritability. The low heritability could also be because garri production involves many production steps, and the processing of the different varieties might be different. This could lead to noise that will affect the data downstream. During processing, the processor always tries to maintain a particular texture and flow of the product by regulating the temperature and stirring time to meet the condition of that genotype being processed. This usually results in a homogeneous product that is recognized and accepted by the consumers. Heating is one of the crucial steps in the processing steps; it has a great effect on the quality of the final product. Regulating the temperature is complicated. Some varieties may require higher temperatures, while other varieties require low but steady heat. These factors were carefully considered and controlled to ensure the production of an optimal product. A fixed temperature or processing time may not translate into a good product.

Heritability estimates for traits evaluated using the chips were higher than traits evaluated on garri. Different scientists have observed that variability in heritability estimates for traits like starch and DMC across different studies can arise due to several factors, including the method of evaluation and the experimental design (Aghogho et al., 2023; Bakare et al., 2022; Rabbi et al., 2022). The heritability of amylose was low, result on par with Oliveira et al. (2014), who recorded a low broad-sense heritability for amylose. Low heritability for quality traits does not mean traits cannot be improved, but more records are needed to achieve genetic gain when compared to traits with high heritability. Heritability can change over time because the different variance components are not constant (Wray & Visscher, 2008).

Low genomic predictions were observed for all the quality traits recorded. Hayes et al. (2017) observed low accuracies of genomic predictions for the wheat grain end-use traits such as milling traits, baking, grain, and dough rheological traits. The low prediction accuracy could be due to the low population size of the training set. Wolfe et al. (2017) recorded low heritability and prediction for root number, root weight, and shoot weight for some breeding programs. Wolfe et al. (2017) also observed that predictability varies across cycles of GSs. Yonis et al. (2020) also recorded low predictability for the number of roots, shoot weight, root weight, and other root traits from a population that was made up of offspring of the first genomic cycle C1. Evaluating these agronomic traits is easier than assessing food quality traits, which require different processing steps. A large reference or training set is needed to ensure accurate genomic predictions (Hayes et al., 2017), but there is a need for more precise phenotyping (Wolfe et al.,

2017), which is important for garri because of the many steps in the production process which might increase the uniformity of the end-product and might also include little differences in the processing of each genotype. The presence of population structure could also be the reason for the low predictability. GS models assume that individuals in the target population share a similar genetic background with those in the TP (Spindel et al., 2015). If this assumption is violated due to population structure, prediction accuracy may be affected (Bayer et al., 2017). De Andrade et al. (2019) observed a reduction in the prediction accuracy of the GS model when there was population structure. The population used for the experiment was at the preliminary yield trial (PYT) breeding stage, an F1 population with high variability. Although the quality traits had low predictive ability, this does not mean that GS is useless for product quality traits. The selection of cassava varieties for food quality traits over several GS cycles could improve, as was observed in cassava yield (Ozimati et al., 2022; Wolfe et al., 2017). Sandhu et al. (2021) observed an increase in the predictive ability of some wheat bread quality traits over the years.

5 | CONCLUSION

Most economically important traits are inherited in a complex and quantitative manner, influenced by multiple genes with intricate interactions, and their expressions can be modulated by environmental conditions. The presence of GEI in the physicochemical parameters evaluated shows the need to prioritize the evaluation of genotypes in environments that are most relevant to the target production regions. This will ensure that the developed varieties meet the specific needs and challenges of the environments where they will be cultivated.

With the presence of a positive correlation among the quality traits, it becomes easier to improve multiple traits at the same time. Improvement of one trait will lead to improvement in the correlated traits. Breeders can target a few traits with known positive correlations, streamlining the decision-making process. This will lead to a reduction in the cost of running the breeding program.

However, using the PYT population for the garri quality study led to lower prediction accuracy due to its population structure and low heritability. While heritability was generally low for most quality traits, it is important to note that these traits influence end-users' preferences. Evaluation of genotypes for food quality traits should include more years and more samples in the TP to increase the predictive ability of the genomic prediction model. Evaluating large samples for garri quality traits might not be feasible because of the process involved in the production of garri, a high throughput phenotyping approach such as Near Infrared Spectroscopy can

be used to predict quality traits which can further be used in Genomic prediction models (Hayes et al., 2017).

A laboratory garri production machine should be developed to standardize the production process from start to finish. This machine would reduce variation in the different stages of production, thereby reducing error and unnecessary sample uniformity.

AUTHOR CONTRIBUTIONS

Chinedozi Amaefula: Conceptualization; data curation; formal analysis; investigation; validation; visualization; writing—original draft; writing—review and editing. **Tesfahun Alemu Setotaw:** Formal analysis; methodology; writing—review and editing. **Justice Obinna Okoronkwo:** Formal analysis; investigation; methodology. **Ugo Chijioke:** Resources. **Lydia Chidinma Ezenwaka:** Resources. **Joseph Onyeka:** Conceptualization; funding acquisition; project administration; resources. **Ismail Y Rabbi:** Funding acquisition. **Hale Ann Tufan:** Conceptualization; funding acquisition; project administration; supervision. **Chiedozie Ngozi Egesi:** Conceptualization; funding acquisition; project administration; resources; supervision. **Jean-Luc Jannink:** Conceptualization; formal analysis; funding acquisition; investigation; methodology; project administration; supervision; validation; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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