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Comparative analysis of variation in African Bambara groundnut [*Vigna subterranea* (L) Verdc.] landraces assessed through seed traits[☆]

Charles U. Uba[a,*], Happiness O. Oselebe[b], Abush A. Tesfaye[c], Christian U. Agbo[d], Wosene G. Abtew[a]

[a] *Department of Horticulture and Plant Science, Jimma University, Ethiopia*
[b] *Ebonyi State University Abakalilki, Nigeria*
[c] *International Institute of Tropical Agriculture, Ibadan, Nigeria*
[d] *University of Nigeria, Nsukka, Nigeria*

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ABSTRACT

Bambara groundnut [*Vigna subterranea* (L.) Verdc.] originated from the African continent and plays social-economic roles in regions where it is consumed. This study examined 297 landraces of African Bambara groundnut from four African regions (West, Central, East, and Southern) to estimate the extent of diversity in each population, identify useful seed traits for differentiation in the population and estimate association among seed quantitative traits using eight qualitative and seven quantitative seed traits. The result of seed qualitative traits showed considerable diversity in the African Bambara groundnut population with West African regions having the highest diversity (0.71) followed by Central Africa (0.64), East Africa (0.62), and Southern Africa (0.61). Heatmap analysis on the distribution of seed qualitative traits revealed that all the regions shared similarities in reference to the phenotypic classes of the traits with greater similarity found within the group. These groups were West and Central Africa as group A; while East and Southern Africa as group B. The descriptive statistics on seed quantitative traits revealed a wide range of variations within each population. Significant ($p < 0.05$) genetic variation was recorded among the landraces within each region for the most studied traits. Moderate heritability accompanied with high genetic advance was obtained on hundred seed weight in most of the studied regions. Factor analysis of mixed data (FAMD) in principal component analysis revealed that seed coat colour had strong discriminatory power in the crop characterization. FAMD in cluster analysis grouped the germplasm into three clusters with cluster II showing superiority for seed-related (seed length, seed width, and seed thickness) traits. The overall results confirmed that Bambara groundnut can be classified through seed morphology and considerable seed diversity depicted among the population that can be utilized in the future genetic improvement of Bambara groundnut.

1. Introduction

Bambara groundnut [*Vigna subterranea* (L.) Verdc.] is an indigenous African legume grown mostly by smallholder farmers in sub-Sahara Africa (Mubaiwa et al., 2018) and intercropped widely with cereals, root and tuber crops (Olukulo et al., 2012). Bambara groundnut adapts to less fertile areas when compared with other legumes, and plays an important role in food diversification because it is rich in carbohydrate and protein with relatively low fat making it an ideal crop for rural communities where animal protein are not affordable for consumption (Khan et al., 2021). Bambara groundnut seeds are used as food for diabetic patients because it promotes insulin hormones and rich in potassium (K: 1723.25 mg) with other minerals like Ca: 260 mg; Fe: 3.6 mg, and Na: 75.25 mg for each 100 g seed dry weight (Chandra et al., 2017). It is mainly produced for its dry seed that is consumed like any dry vegetable or used for the production of vegetable milk comparable to soya milk (Gbaguidi et al., 2018). The seeds are consumed alone or combined with other cereal crops, like maize.

The prospect of using seed morphological characters for seed taxonomy has been recognized in several plants group for providing important information for their systematic classification (Liu et al., 2013). Seed morphology is useful in genotype discrimination (Daniel et al., 2012), and the analysis of taxonomic relationships in a wide variety of plant species families and genus has been achieved through it (Cervantes et al., 2016). The analysis of seed phenotypic traits is essential for seed characterization in a population and designing its improvement method. Plants worldwide have a

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[☆] Edited by: E. Balazs
[*] Corresponding author.
E-mail address: charlesuba192@gmail.com (C.U. Uba).

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startling diversity among species for seed size (Cervantes et al., 2016). Seed size is an important determinant of seed dispersal and probable loss, moisture imbibitions, germination of seeds, and grain grading quality (Adewale et al., 2010). Hence, variations in seed traits are very important aspects of a population's survival and genetic diversity during evolution.

In spite of the importance of Bambara groundnut and various application of seed morphology or phenotypes in the classification of several crops, there is still a paucity of information on the diversity of seed morphology as a basis for selection and systematic crop improvement in Bambara groundnut (Mohamed et al., 2016). The lack of characterization of Bambara groundnut germplasm through seed phenotypes has restricted its utilization for commercial seed production and consequently reduces the identification of potential genotypes with desirable seed traits for breeding programmes. This has partly resulted in limited breeding opportunity for cultivar development and lack of nationally and internationally value chains for the crop. Mubaiwa et al. (2018) reported lack of commercial seeds as a key constraint facing Bambara groundnut farming and hence, developing best performing varieties with desirable seeds traits is identified as an important step towards preliminary breeding programs to screen for drought tolerance and increased yields. Most available literature on Bambara groundnut variability based on seed phenotypic traits is mainly focused on seed length and seed width, with few studies on the seed qualitative traits. Hence, a good description of the Bambara groundnut seed traits is lacking, resulting in poor germplasm conservation and seed improvement. Mohammed et al. (2016) used 58 seed lots, which are smaller number of accessions, compared with the present study to characterize Bambara groundnut based on the seed morphology. Although, Olukola et al. (2012) used higher numbers of accessions and studied the frequency of seed patterns of Bambara groundnut accessions, only based on the qualitative traits. None of these research combined qualitative and quantitative seed traits to study the extent of variation that existed among the germplasm. Furthermore, information on diverse landraces germplasm that are sourced from different regions to elucidate their variability through seed morphology is unavailable.

Phenotypic characterization of germplasm through morphological markers is among the methods used for assessing diversity within and between plant populations because they are simple, direct, easy, and cheap. The usefulness and importance of this approach in developing countries where scientific and technological support is poor and infrastructure is lacking have been highlighted (Hsu et al., 2005; Alake and Alake, 2016). They have aided in understanding the diversity of a population and guided in the improvement process as well as setting priorities for future germplasm collection expeditions. The use of quantitative seed morphological trait is one common approach utilized to estimate the relationships between genotypes and their selection. Bambara groundnut landraces possess distinguishable morphological identities based on seed phenotypes that could be used for characterization (Abu and Buah 2011; Mohammed et al., 2016). Bambara groundnut seed showed variations for morphological features such as seed shape, seed eye, seed coat colour, hilum colour and testa pattern (Abu and Buah, 2011; Mohammed et al., 2016). The variation in Bambara groundnut seed coat colour preferences differs between countries or regions, and the dominant colour depends mostly on farmers' or consumers' preferences. In Botswana (central and southern district) consumers prefer white and cream seed coat colours, while in Zimbabwe (northern zone) red seed coat colour are most desirable (Mubaiwa et al., 2017). Dominant colours planted in Indonesia are black, dark red, dark brown, and dark purple (Makanda et al., 2009). Consumers in Ghana that use Bambara groundnut for flour prefers red-colored seeds (high in tannin); while cream-colored (low in tannin) seeds are preferred by those that boil it (Ofori et al., 2001). Arteaga et al. (2019) characterized 24 landraces of common bean (*Phaseolus vulgaris* L) using quantitative and qualitative traits. Therefore, clarifying the amount and nature of genetic variation available for seed phenotypic traits in a population and analysing their genetic relationships are of strategic importance for the genetic improvement of Bambara groundnut. This research aims to investigate the amount of diversity present in each African Bambara groundnut population through seed phenotypic traits, identify useful seed traits for differentiation in the population and estimate association among seed quantitative traits.

2. Materials and methods

2.1. Plant material and experimental site

A total of two hundred ninety-seven (297) Bambara groundnut accessions were used in this study, with 287 accessions collected from gene bank of the International Institute for Tropical Agriculture (IITA), Ibadan, Nigeria, and ten accessions from Crops and Soil Science Research Farm in Bunda, Malawi (Supplementary Table 1). The accessions were representatives of four regions of Africa (East, West, Central, and South). The grouping of the African region as sources of the accessions was based on African union grouping of the different African countries into regions (https://au.int/en/member_states/countryprofiles2). Among the studied accessions, the majority of were West African accessions (52%), followed by Southern (28%), Central (15%), and East (5%) as shown in Fig. 1. The experiment was conducted in the year 2019 and 2020 at experimental farm of Jimma University, College of Agriculture and Veterinary Medicine, Jimma Ethiopia. The field experiment was planted one seed per hill in a single row with inter and intra-row spacing of 0.5 m × 0.3 m, respectively. The area is classified as a mid-altitude sub-humid agro-ecology (7° 42 N latitude

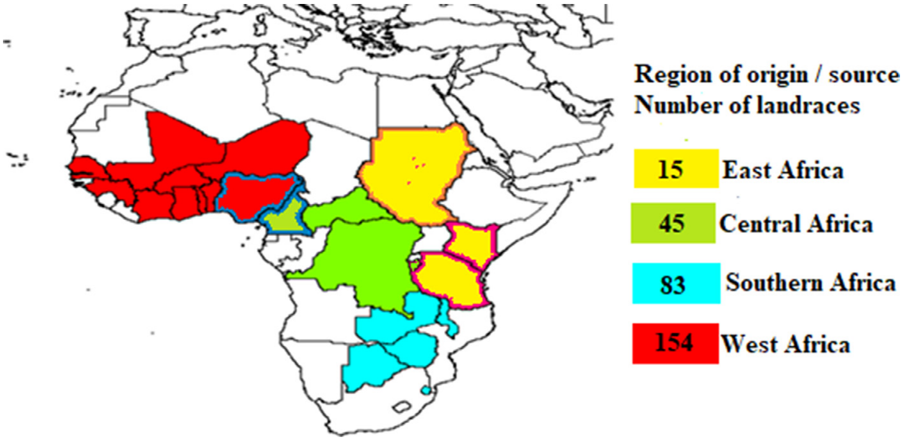

Fig. 1. Geographical distribution of the sampled accessions of Bambara groundnut constructed using Diva-gis software (Hijmans et al., 2001).

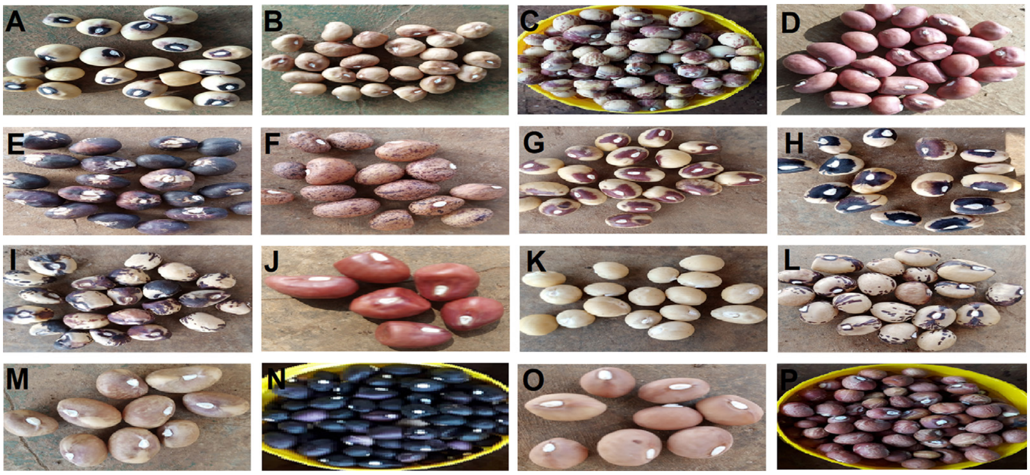

Fig. 2. Bambara groundnut showing variation in their seed coat color, eye pattern and testa pattern. A = cream coat colour with two thick eye lines on both sides of the hilum; B = Light brown coat colour with a thin eye; C = cream coat colour with two thin eye lines and marble testa pattern; D = light red seed coat colour with a thin eye; E = purple seed coat colour with two thin eyes and much rhomboid spotting testa pattern; F = dark brown seed coat colour and entire testa pattern; G = cream coat colour with butterfly eye; H = cream coat colour with a shapeless eye; I = cream coat colour with little rhomboid on both sides; J = dark red coat colour with a thin eye; K = cream coat colour; L = cream colour with two thin eyes and little rhomboid spotting on one side; M = brown seed colour and butterfly eye; M = purple coat colour, O = light brown colour; P = dark brown coat colour with two thin lines and stripped testa pattern.

and 36° 50 E longitude) with an altitude of 1710masl. Also, receives an average annual rainfall of 1250 mm, and has an average maximum temperature of 26.2 °C. The soil of the experimental site contains 0.98% organic carbon, 0.04% total nitrogen, 30.6 ppm available phosphorus and 52.04 μS/cm electrical conductivity (Sintayehu et al., 2015).

All the standard operation practice for Bambara groundnut production was observed according to Jonah et al. (2012).

2.2. Seed phenotyping

At maturity, the pods were harvested and cleaned from sands or other unwanted materials. The clean pods were dried before threshing. Care was taken to avoid damage to the seeds during threshing. The seeds were then cleaned and dried until the moisture content was maintained at 12%. The seed qualitative traits were recorded using visual observation (Fig. 2) from the seed lot of the accessions based on the descriptors of Bambara groundnut, while the quantitative traits were laid out in a completely randomized design with three replications and the metric traits determined. Ten (10) seeds in three replicates were randomly selected from each seed lot of 297 accessions.

2.3. Data collection

The seed phenotypic traits for the eight qualitative and seven quantitative traits (Table 2) were collected using the IPGRI/IITA/BAMNET (2000) descriptor list of Bambara groundnut. The qualitative traits (hilum colour, seed eye, seed shape, eye colour, seed coat colour, eye shape, number of colour and testa pattern) were assessed visually; while the quantitative traits (seed length, seed width, seed thickness, seed length/width ratio, seed length/thickness ratio, seed width/thickness ratio and hundred seed weight) were measured on selected fully developed undamaged seeds.

2.4. Statistical analysis

Shannon–Weaver's diversity index (H') was calculated for the qualitative traits to assess their phenotypic diversity for each descriptor, according to Shannon and Weaver (1963). To describe the

Table 1
Description of qualitative and quantitative traits used for seed phenotypic assessment.

Character	Code	Phenotypic scale
Hilum Colour	HC	1 = White, 2 = Chalk white
Seed eye	SE	1 = Absent, 2 = Present
Seed shape	SS	1 = Round, 2 = Oval
Eye colour	EC	0 = No colour/Absent, 1 = Pinkish, 2 = Purple, 3 = Black, 4 = Cream
Seed coat colour	SC	1 = Cream, 2 = Gray, 3 = Light red, 4 = Dark red, 5 = Light brown, 6= Dark brown, 7 = Dark purple
Eye shape	ES	0 = No eye/ Absent, 1 = Eye as thin circle around hilum, 2 = Eye as 2 thin lines on both sides of hilum, 3 = Eye as 2 thick lines on both side of hilum, 4 = Eye forms an almost triangular shape, 5 = Large eye more shapeless becoming frayed, 6 = Eye lines like butterfly, 7 = Mottled eye
Number of colour	NC	1 = Single, 2 = Mixed colour
Testa pattern	TP	0= No pattern, 1 = Entire line, 2 = Striped, 3 = Marbled, 4 = Dotted, 5 = Little rhomboid spotting only on one side of hilum, 6 = Little rhomboid spotting only on two side of hilum, 7 = Much rhomboid spotting on both sides of hilum, 8 = Holstein pattern
Seed length (mm)	SL	Measured as the distance between the two ends of the seed, parallel to the hilum using vernier caliper
Seed width (mm):	SW	Measured as distance from hilum to the keel (i.e. from hilum to the opposite side) using vernier caliper
Seed thickness (mm)	ST	Measured as the distance perpendicular to the seed length
Seed length/width ratio	L/W	Calculated as the ratio of the seed length to width
Seed length/thickness ratio	L/T	Calculated as the ratio of the seed length to thickness
Seed width/thickness ratio	W/T	Calculated as the ratio of the seed width to thickness
Hundred seed weight (g)	HSW	Measured using electronic weighing balance for 100 seeds randomly selected from the seed lot

Table 2
Shannon-Weaver diversity indices of seed qualitative traits for the Bambara groundnut germplasm.

REGIONS **Traits**	**Central Africa**	**Southern Africa**	**East Africa**	**West Africa**
Hilum colour	0.16	0.37	0.09	0.32
Seed eye	0.36	0.45	0.54	0.54
Seed shape	0.93	0.86	0.81	0.90
Eye colour	0.81	0.77	0.77	0.75
Seed coat colour	0.60	0.62	0.54	0.72
Eye shape	0.72	0.79	0.72	0.86
Number of colour	0.93	0.75	0.96	0.91
Testa pattern	0.59	0.27	0.51	0.64
Mean	**0.64**	**0.61**	**0.62**	**0.71**

relative abundance of Bambara groundnut genotypes for seed qualitative traits in each region we constructed a heatmap using ClustVis tools (https://bio.tools/clustvis). Before pooling the means of the years, we tested for homogeneity of error variances of each year using Bartlett's test. Data collected for quantitative traits were subjected to two-way analysis of variance (ANOVA) using R software (R Core Team, 2017). The descriptive statistics (minimum, maximum and mean) and genetic parameters (phenotypic coefficient of variation (PCV), genotypic coefficient of variation (GCV), genetic advance (GA) as percentage of mean and broad-sense heritability) were computed to understand the overall variability in the germplasm using the package "variability" in R (Raj et al., 2020). The estimated values were categorized for PCV, GCV and GA as low (0–10%), intermediate (10–20%) and high (≥20%) while broadsense heritability was categorized as 0-30% for low, 30–60% for intermediate and greater than 60% as high according to Khan et al. (2021). Factor analysis of mixed data (FAMD) that combined both the qualitative and quantitative variables was used to perform analysis on all the seed traits for principal component analysis (PCA) with "FactoMineR" package (Lê et al., 2008) and cluster analysis "factoextra" R packages (Kassambara and Mundt, 2017). The PCA was performed to reveal the most influential seed traits that discriminated among the genotypes, while cluster analysis was used to determine the relationship between the genotypes. Spearman's correlation was computed to understand the relationship among the seed quantitative traits using the chart. Correlation () function of the "PerfomanceAnalytics" package (Peterson et al., 2018).

3. Results

3.1. Qualitative seed diversity index

The Shannon diversity index values for the studied eight qualitative seed traits ranged from 0.09 to 0.96 (Table 2). The West African region was the most diverse, with the highest mean value (0.71) of diversity index, followed by Central Africa (0.64), East Africa (0.62) and Southern Africa (0.61). The Shannon diversity index values for seed qualitative traits of the Central African region germplasm ranged from 0.16 (hilum colour) to 0.93 (seed shape/number of colour), while ranged from 0.27 (testa pattern) to 0.86 (seed shape) in the Southern Africa germplasm. The East African region ranged from 0.09 (hilum colour) to 0.96 (number of colour); while the West African region showed 0.32 (hilum colour) to 0.91 (number of colour). Furthermore, among the eight qualitative traits West African region exhibited the highest diversity in testa pattern, eye shape and seed coat colour; while the East African region showed the highest diversity index for number of colours. The Central African region had the highest diversity values on traits, like as seed shape and eye colour, while the Southern African region recorded the lowest values of diversity index of seed testa pattern.

3.2. Distribution of seed qualitative traits in Bambara groundnut germplasm

The heatmap analysis was conducted to show the abundance or frequency of the seed qualitative traits in each region (Fig. 3, Supplementary Table 2). The regions of the Bambara groundnut landraces are represented in the horizontal direction, while the seed qualitative traits are represented in the vertical direction. The dendrogram results revealed that the regions are classified into two major groups, which include the West and Central African regions as group A; and the East and Southern African regions as group B. The relative abundance distribution of each seed qualitative trait varies across regions, with the East African landraces showing higher abundant distribution on oval seed shape, cream eye colour, a thin circle eye shape, little rhomboid one side testa pattern, dark purple seed coat colour, mixed colour and marbled testa pattern. Most of the Southern African landraces had high abundance of traits like triangular eye shape, absent hilum colour, black eye colour, single seed colour, butterfly eye shape, dark red seed coat colour, gray seed coat colour and no testa pattern. In the West African landraces, light red coat colour, dotted testa pattern, much rhomboid testa pattern, two thick circles, no eye shape, and stripped testa pattern had higher abundance. The Central African landraces manifested high abundant distribution of white hilum colour, present seed eye, shapeless eye shape, holstein testa pattern, round seed shape, purple eye colour, mottled eye shape and entire line testa pattern. All these regions revealed that seeds of Bambara groundnut landraces showed considerable variation in the crops which could be used in its classification.

3.3. Variability and genetic components of the seed quantitative traits in each region

The descriptive and genetic parameters of the studied traits in each region are summarized in Table 3. The results revealed that most of the seed quantitative traits studied exhibited greater ranges within each region. Among the studied regions, Southern African landraces showed the highest maximum values in seed length (17.50 mm), seed width (11.43 mm), seed thickness (9.67 mm) and seed length width ratio (1.78); while the West African landraces had the highest maximum value of hundred seed weight (126.00 g). Moreover, the mean values showed that the Southern African region had the highest mean values in all the studied traits; except seed width thickness ratio and seed length thickness ratio.

The West African region displayed low PCV values for seed length width ratio (6.38%), seed width thickness ratio (5.23 %) and seed length thickness ratio (7.90%); intermediate for seed length (12.42%), seed width (10.60) and seed thickness (12.69%); while hundred seed weight (29.48%) was high. Furthermore, the GCV values for all the studied traits within this region were low (less than 10), except for hundred seed weight (20.07%) with intermediate GCV values. Broadsense heritability within the West African population showed moderate heritability for most of the studied traits, except seed length (61.00%) with high heritability and seed width to thickness ratio (4.00%) with low heritability. Low PCV, GCV and GA (0–10%) values were obtained for most of the traits studied in the Southern African region, except seed length that recorded intermediate PCV (10.56%) and GA (11.54%) values. Also, hundred seed weight had intermediate GCV (16.45%), high PCV (25.48%) and high GA (22.69%) values in this region. In the Central African region, the GCV values for all the studied traits was low (0–10%), except hundred seed weight with intermediate values (GCV = 16.38%) and high PCV (25.61%) values. Also, the GA values (21.58%) in this region were high for hundred seed weight and intermediate for seed length (14.16%) and seed thickness (13.41%). Broadsense heritability in this population showed high heritability for seed length (63.00%), moderate for seed width (51.00%), seed thickness (57.00%) and hundred seed weight (41.00%), while

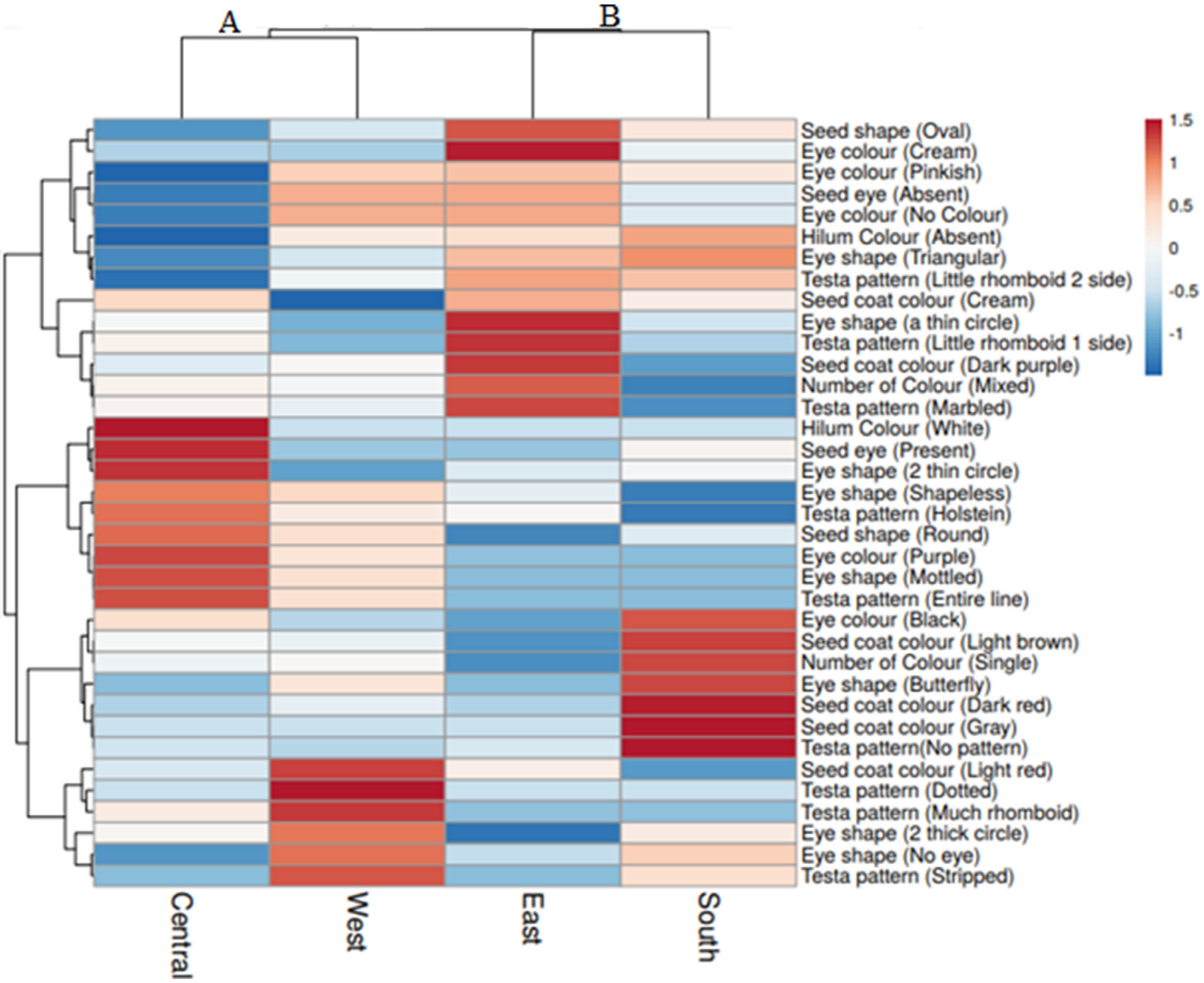

Fig. 3. The heatmap plot analysis depicting the relative seed qualitative trait abundance of each region (columns) within each qualitative trait (rows). The color code (blue to dark red) displays the row z-score: red color indicates high abundance while blue color low abundance.

low for seed length width ratio (3.00%), seed width thickness (24.00%) and seed length thickness ratio (24.00%). The East African germplasm displayed low GCV values (0–10%) for all the studied traits. The PCV values for most of the traits within this region were low (0–10%), except for hundred seed weight (22.17%) that had a high value. However, GA values for all the traits are low, except for seed length (14.43%) with an intermediate value. The heritability results showed low heritability for seed length width ratio (11.00%), seed width thickness ratio (6.00%) and hundred seed weight (4.00%); while high heritability were recorded for seed length (68.00%), and moderate heritability for seed width (50.00%) and seed thickness (56.00%).

4. Principal component analysis

Factor maps for the first five dimensions (principal components) for seed phenotypic (quantitative and qualitative) traits obtained from FAMD showed the percentage variation for PC1 to PC5 as 12.12%, 9.61%, 7.13%, 6.91%, 5.67%, respectively (Table 4). Principal component 1 (PC1), which accounted 12.12% had high loadings for seed length, seed width, seed thickness, hundred seed weight and seed coat colour; while PC2 is associated with eye colour, eye pattern, seed eye, seed coat colour and seed length:thickness ratio accounting 9.6 1% of the total variation in the germplasm. PC3 had 7.13% of the total variation and displayed differences based on testa pattern, the number of colours, seed coat colour, seed length:thickness ratio and seed length:width ratio. Furthermore, 6.91% of the total variation was detected for PC4 and had high loading on eye colour, eye shape and seed coat colour. The PC5 accounted for 5.67% of the total variation and was associated with testa pattern, seed coat colour, eye shape and seed length:width ratio. Interestingly, among the studied

Table 4
Contribution of seed phenotypic traits to variation in the African Bambara groundnut landrace.

Traits	PC1	PC2	PC3	PC4	PC5
Seed length (mm)	0.89548	0.00195	0.05027	0.00625	0.00058
Seed width (mm)	0.84257	0.00731	0.00004	0.01374	0.04190
Seed thickness (mm)	0.84613	0.04113	0.00387	0.02948	0.03930
Seed length/width ratio	0.15575	0.07731	0.27740	0.00183	0.22244
Seed width/thickness ratio	0.19638	0.27430	0.04828	0.07391	0.00679
Seed length/thickness ratio	0.00803	0.26104	0.32673	0.03485	0.18946
Hundred seed weight (g)	0.73939	0.01998	0.00228	0.04702	0.00490
Hilum colour	0.00060	0.00515	0.04298	0.04651	0.00031
Seed eye	0.00003	0.59719	0.03969	0.17808	0.00013
Seed shape	0.06838	0.07277	0.18959	0.05036	0.01358
Eye colour	0.04013	0.76879	0.13527	0.67513	0.19472
Seed coat colour	0.31452	0.37599	0.28725	0.4868	0.41109
Eye shape	0.15790	0.76087	0.14153	0.5914	0.25498
Testa pattern	0.14935	0.17751	0.56894	0.18491	0.54800
Number of colour	0.05632	0.01952	0.45306	0.06753	0.11266
Eigenvalue	4.37	3.46	2.56	2.49	2.04
Percentage variance	12.14	9.61	7.13	6.91	5.67
Cumulative variance	12.14	21.75	28.89	35.80	41.47

Table 3
Descriptive statistics and genetic estimates for the quantitative traits studied.

Region	Trait	Min	Max	Mean	GCV	PCV	H_b	GAM	F-tab
West Africa									
	SL	6.93	15.57	11.14	9.73	12.42	61.00	15.68	***
	SW	5.61	11.29	8.46	8.15	10.60	59.00	12.91	***
	ST	4.17	9.53	6.85	9.11	12.69	51.00	13.48	***
	SLWR	1.07	1.56	1.32	3.72	6.36	34.00	4.49	***
	SWTR	0.84	1.59	1.23	0.02	5.23	4.00	1.20	NS
	SLTR	1.14	2.18	1.63	4.16	7.97	27.00	4.47	***
	HSW	24.00	126.00	51.75	20.07	29.48	46.00	28.15	***
Southern Africa									
	SL	9.18	17.50	12.84	7.69	10.56	53.00	11.54	***
	SW	7.60	11.43	9.69	5.26	7.09	55.00	8.04	***
	ST	5.54	9.67	8.00	5.36	8.35	41.00	7.10	***
	SLWR	1.15	1.78	1.33	3.54	6.96	26.00	3.71	**
	SWTR	1.12	1.43	1.21	0.01	3.40	3.00	1.11	NS
	SLTR	1.36	2.01	1.61	4.03	7.52	29.00	4.46	**
	HSW	33.00	117.00	71.49	16.45	24.58	49.00	22.69	***
Central Africa	SL	9.02	17.00	12.72	8.66	10.90	63.00	14.16	***
	SW	6.84	12.29	9.46	6.85	9.55	51.00	10.12	***
	ST	5.11	10.53	7.76	8.59	10.33	57.00	13.41	***
	SLWR	1.14	1.60	1.34	3.24	5.95	3.00	3.64	*
	SWTR	1.04	1.38	1.23	2.00	4.08	24.00	2.02	NS
	SLTR	1.37	1.90	1.65	3.27	6.68	24.00	3.30	NS
	HSW	24.00	122.40	68.55	16.38	25.61	41.00	21.58	**
East Africa	SL	9.10	15.29	12.26	8.51	10.33	68.00	14.43	**
	SW	7.65	10.42	9.27	5.40	7.61	50.00	7.32	*
	ST	6.19	8.67	7.53	5.49	7.35	56.00	8.43	*
	SLWR	1.17	1.47	1.32	2.00	5.90	11.00	1.40	NS
	SWTR	1.17	1.36	1.23	0.01	3.15	6.00	0.43	NS
	SLTR	1.43	1.85	1.63	3.83	6.13	39.00	4.92	NS
	HSW	33.00	90.00	60.38	4.41	22.17	4.00	1.81	NS

SL: seed length; SW: seed width; ST: seed thickness; SLWR: seed length/width ratio; SLTR: seed length/thickness ratio; HSW: hundred seed weight; Min: minimum; Max: maximum; and PCV: phenotypic coefficient of variation; GCV: genotypic coefficient of variation; H_b: Heritability in broadsense; GA: genetic advance; F-tab: F-tabulated

traits, seed coat colour showed considerable loading in all the principal components (i.e. PC1 to PC5).

However, the contribution of each of the qualitative trait was represented in the graph divided into upper and lower quadrants (Fig. 4, Supplementary Table 3). Traits with positive values are at the top dimension or axis; while negative values were at the bottom dimension. However, among the studied qualitative traits, PC1 accounted for 12.12% of the total variation and displayed differences based on eye shape (a thin circle), seed coat colour (Dark red), seed coat colour (Light brown) and seed shape (Round). PC2 accounted for 9.6% of the total variation and had high loading on seed coat colour (Cream), eye colour (Black), seed coat colour (Dark purple), seed shape (Round), seed eye (Present), eye shape (Triangular), seed coat colour (Dark red) and seed coat colour (Light red).

4.1. Clustering analysis of landraces

The result of FAMD in cluster analysis performed using dendrogram on the Bambara groundnut landrace for the seed phenotypic traits grouped the genotypes into three clusters with a varied number of genotypes (Fig. 5). The highest number of landraces was found in cluster 3 (143 landraces), followed by cluster 2 (124 landraces); while the least was cluster 1 (30 landraces). The mean of each cluster group plotted in a boxplot analysis displayed significant differences for all the studied seed quantitative traits (Fig. 6). Cluster 2 had the highest mean value for seed length, seed width, seed thickness and hundred seed weight; while cluster 3 had the lowest for these traits. Cluster 1 had the highest mean values for seed length width ratio, seed width thickness ratio and seed length thickness ratio; while cluster 2 had the lowest only for seed width thickness ratio.

4.2. Relationship among the seed quantitative traits

The Pearson correlation coefficient among the studied seed quantitative traits of Bambara groundnut germplasm ranged from 0.007 to 0.97 (Fig. 7). There was strong significant and positive association between seed width and seed thickness ($r = 0.97$; $p < 0.001$). Conversely, negative and significant relationship were found between seed length and seed width thickness ratio ($r = -0.36$; $p < 0.001$), seed width and seed width thickness ratio ($r = -0.31$; $p < 0.001$), seed thickness and seed width thickness ratio ($r = -0.56$; $p < 0.001$), seed width thickness ratio and hundred seed weight ($r = -0.45$; $p < 0.001$), and seed thickness and seed length thickness ratio ($r = -0.20$; $p < 0.001$). Hundred seed weight was positively and significantly correlated with seed length ($r = 0.82$; $p < 0.001$), seed width ($r = 0.82$; $p < 0.001$), seed thickness ($r = 0.84$; $p < 0.001$) and seed length thickness ratio ($r = 0.28$; $p < 0.001$). Seed length was significantly and positively correlated with seed width ($r = 0.91$; $p < 0.001$), seed thickness ($r = 0.97$; $p < 0.001$), seed length width ratio ($r = 0.54$; $p < 0.001$), seed length thickness ratio ($r = 0.29$; $p < 0.001$) and hundred seed weight ($r = 0.82$; $p < 0.001$). Seed width was positively and significantly correlated with seed thickness ($r = 0.97$; $p < 0.001$), seed length width ratio ($r = 0.15$; $p < 0.05$), and hundred seed weight ($r = 0.82$; $p < 0.001$).

5. Discussion

5.1. Diversity in seed qualitative traits

The knowledge of genetic diversity in germplasm enhances the efficiency of its conservation and improvement (Bonny et al., 2019a).

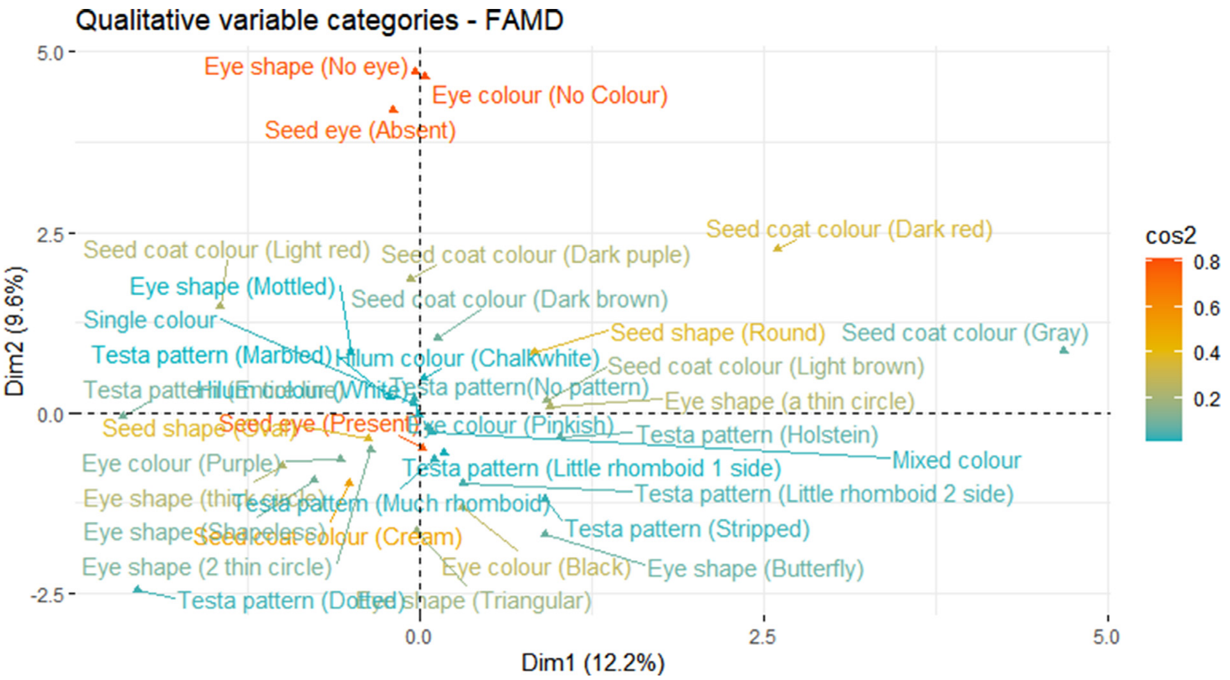

Fig. 4. Factor maps for the first two dimensions obtained from the FAMD used for PCA analysis for seed qualitative traits. The colour code (sky-blue to red) red indicates high contribution while sky-blue colour low contribution.

Bambara groundnut landraces in different populations or regions in this study have shown a remarkable level of diversity through their seed qualitative traits with the overall high diversity in each population. The Shannon diversity result showed that the diversity index values among African Bambara groundnut landraces ranged from 0.61 to 0.71. This implies that Bambara groundnut landraces are composed of heterogeneous mixtures of diverse seed morpho-types and vary greatly. Characterization of variation in geographical pattern is important for efficient conservation strategy and use of agricultural genetic resources (Dulloo et al., 2010). This variability obtained from the qualitative seed traits could be used as a selection strategy in the conservation of genetic resources of Bambara groundnut. Also, it will provide opportunities for the selection of novel landraces that can be utilized for cultivar development and deployment based on consumer preferences. Therefore, the identification of desirable landraces from the Bambara groundnut germplasm used in this study could be achieved for seed traits improvement. Variation in seed morphological characters, like seed testa colour, shape, eye, testa pattern and hilium has been previously reported (Massawe et al., 2005; Abu and Buah, 2011; Mohammed et al., 2016). Furthermore, the Shannon diversity index values obtained among traits and between populations varied revealing the important genetic diversity of Bambara groundnut has been preserved through seed conservations. Uba et al. (2021) and Somta et al. (2011) have reported that Bambara groundnut accessions had high genetic diversity. The genetic diversity within accessions and population is vital for breeding, germplasm conservation and utilization of Bambara groundnut (Khaliqi et al., 2021). The West African region showed a higher diversity (H′ = 0.71), when compared with the other regions indicating higher chances of selecting consumers' desirable seed traits that could be used for commercial production. Olukola et al. (2012) reported higher diversity in West African accessions for seed qualitative traits, when compared with the Central African and East African accessions. Furthermore, the distribution of seed qualitative traits revealed that the regions shared strong similarities in reference to all phenotypic classes for these traits. The shared similarities could be due to Bambara groundnut landraces having common ancestors, seed exchange between farmers, new introductions and human immigration. Ntudu et al. (2006) noted that annual seed exchange in Tanzania is 44% from farmers' own fields, 39% from other farmers and 5% from other regions. The spatial distribution of populations is vital for the long-term maintenance of genetic variation (Cruzan, 2001; Bonny et al., 2019b). Therefore, evidence of considerable diversity observed from the seed phenotypic traits studied from different populations in Africa reveals the ability to use seed qualitative traits for the classification of Bambara groundnut or the usefulness of studying genetic diversity through seed morphology. Also, it has shown that

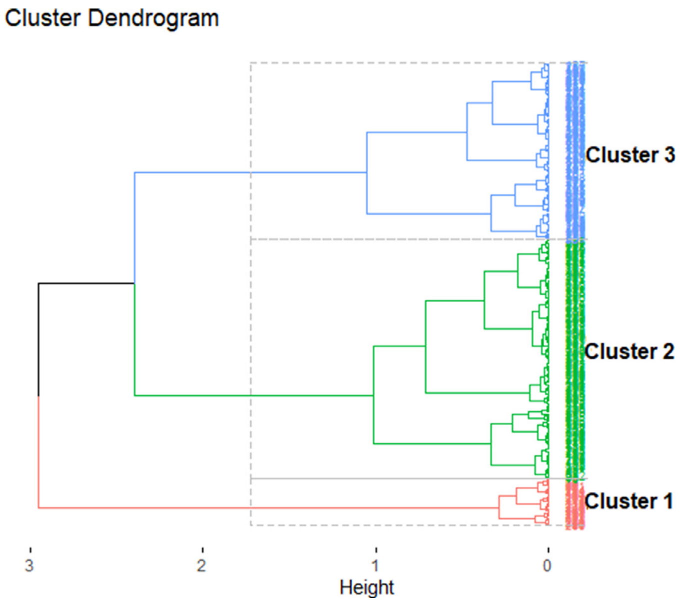

Fig. 5. FAMD on cluster dendrogram analysis showing number of phenotypic groups in the germpaslm.

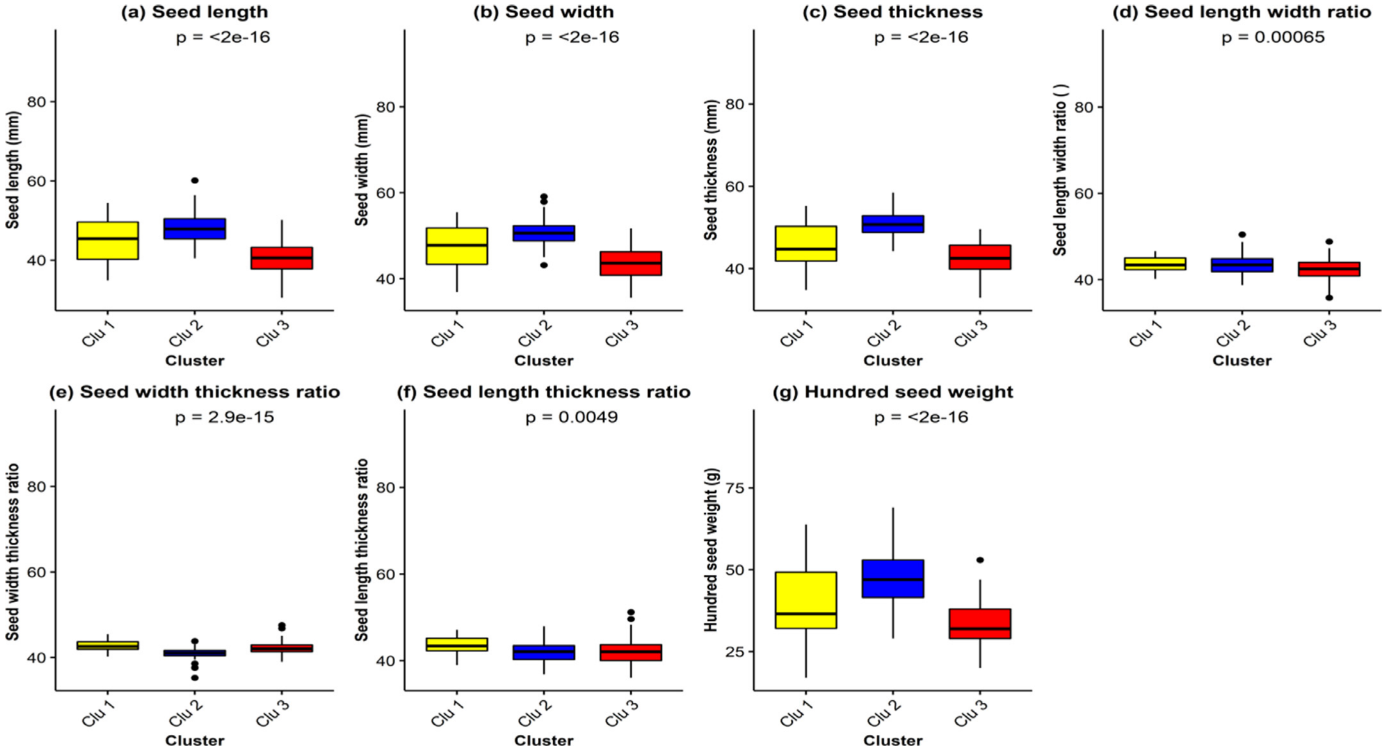

Fig. 6. Boxplot showing the mean of identified seed quantitative traits for each cluster in Bambara groundnut germplasm (yellow = cluster 1, blue = cluster 2 and red = cluster 3).

the current Bambara groundnut germplasm maintained in the gene banks has adequate diversity and was not mismanaged (e.g. cases of genetic shift, spread of seed-born disease because of poor plant quarantine). The characterization of seed traits variation within and among species through structural diversity is useful (Dong et al., 2016; Ocampo et al., 2014) and can be an advantage in comparison with other plant organs because seeds are easy to collect and store (Grillo et al., 2010).

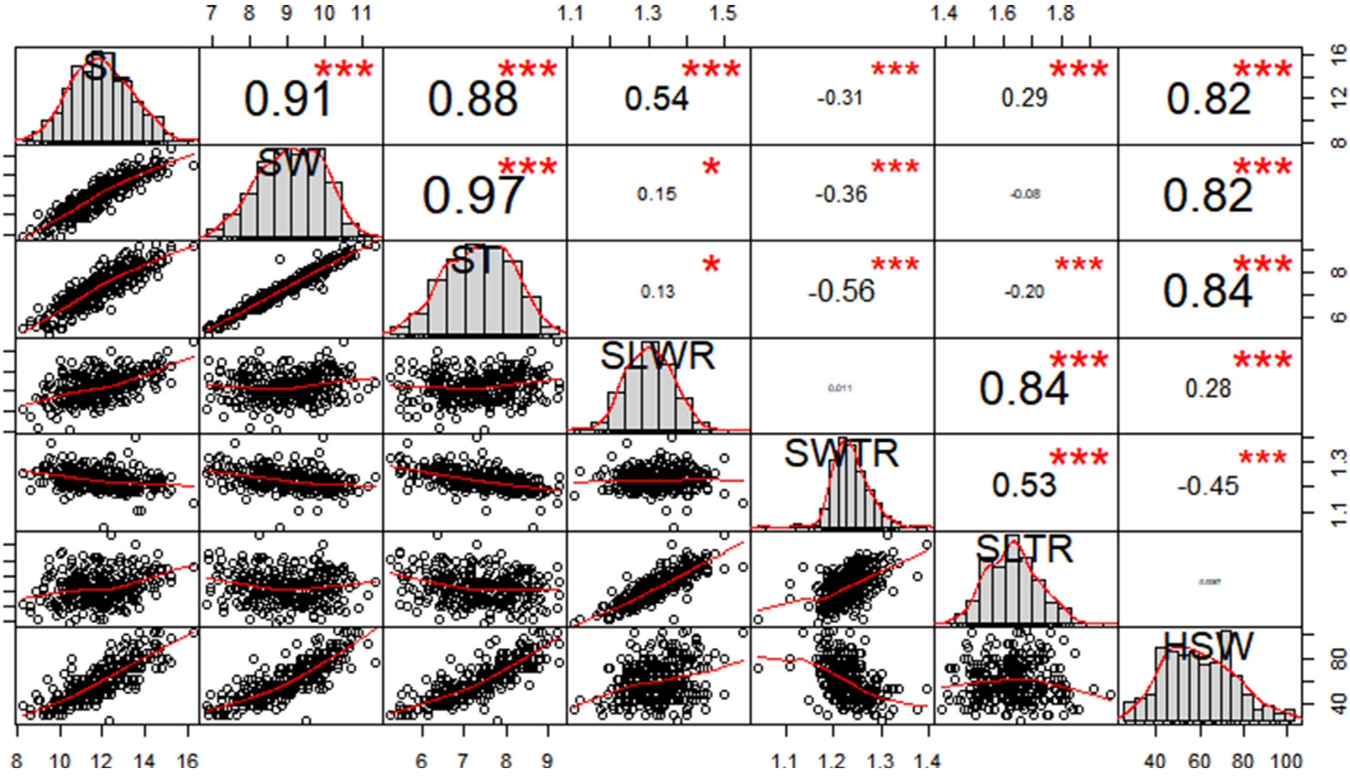

Fig. 7. Mixed correlogram based on seed quantitative traits of the Bambara groundnut. On the main diagonal histograms are presented for each trait, the upper triangle contains correlation coefficients with significance value from a correlation test and the low. SL = seed length, SW = seed width, ST = seed thickness, SLWR = seed length width ratio, SWTR = seed width thickness ratio, SLTR = seed length thickness ratio, HSW = hundred seed weight.

5.2. Variability and genetic components of quantitative seeds traits

The significant ($p < 0.05$) genotypic variation obtained among the landraces within each region for most of the studied quantitative traits indicates the existence of genotypic variability among the studied germplasm that can be utilized for breeding purposes. Jonah et al. (2012) reported variations among accessions on the studied seed quantitative traits. The mean value of the Southern African region on seed length, seed width, and seed thickness was higher when compared with other regions. Larger seed sizes obtained within the population could be as a result of differences in natural selection pressure by farmers in the areas of cultivation. In Botswana (Southern African region), farmers have selected a limited amount of larger seed sizes of landraces with cream pericarp (Brink et al., 1996; Manthe et al., 2001; Karikari and Tabona, 2004). The values of PCV and GCV with narrow differences among each other for most of the seed quantitative traits indicate less influence of the environmental factors on the expression of these traits. Khan et al. (2021) reported that a trait with lower difference between PCV and GCV indicates that direct selection would be effective and provides desirable output for crop improvement. Heritability in association with genetic advance gives more reliable selection value in a breeding programme. Moderate heritability accompanied with a high genetic advance for hundred seeds weight in most of the studied regions indicates that the inheritance in this trait was due to additive gene actions, which also indicates the effectiveness of selection to improve the trait in the crop. Mazid et al. (2013) and Khan et al. (2021) reported high heritability coupled with high genetic advance for hundred seed weight in Bambara groundnut. Seed width, seed thickness, seed width thickness ratio, seed length width ratio and seed length thickness ratio exhibited moderate to low heritability in conjunction with a low genetic advance in most of the regions indicating the expression of these traits is highly influenced by environment, and selection might not be effective. Thus, improvement of these traits could be achieved through heterosis breeding. Khan et al. (2021) have reported low heritability coupled with low genetic advance for seed width traits in Bambara groundnut. High heritability along with moderate genetic advance for seed length in most of the regions implies the traits have potential in the selection process because of low environmental influence. Khan et al. (2020) studied 150 Bambara groundnut accessions sourced from the local market in Nigeria and reported high heritability combined with high genetic advance for seed length.

5.3. Principal component and cluster analysis

The principal component is used to determine traits that account for maximum variability in germplasm and the total variation that existed in various components (Khan et al., 2020). Interestingly, the PCA result revealed that seed coat colour had considerable loading in all the principle components (i.e. PC1 to PC 5). This implies that seed coat colour is important as Bambara groundnut descriptor and could be utilized most effectively to characterize the crop. The principal component analysis has been used to determine traits that contributed to more variations existing in germplasm for crops, like Bambara groundnut (Olukola et al., 2012; Mohammed et al., 2019; Khan et al., 2020) and common bean (Nadeem et al., 2020). Cluster analysis was used to group the genotypes into three different groups based on their genetic differences and similarities. The inability to group all the genotypes of the same origin in the same group reflects a lack of regional differentiation, probably caused by the transport of seeds by humans and seed exchange between farmers. Several authors have reported a similar pattern of grouping of genotypes on Bambara groundnut (Ntundu et al., 2006; Aliyu and Massawe, 2013; Odongo et al., 2015). Cluster 2 showed superiority for seed length, seed width and seed thickness, indicating the suitability of these landraces as donor parents in areas with a harsh environment. Large-seeded species develop seedlings that tolerate environmental stresses during plant establishment compared to small-seeded species (Dong et al., 2016). Furthermore, genotypes with large seed sizes could meet the preference of Bambara groundnut farmers and consumers. Doumbia et al. (2013) noted that cowpea landraces with a big seed size would meet the expectation of consumers and often have good technological qualities. Hence, the selection of genotypes from Cluster 2 with a larger seed size could be beneficial for future Bambara groundnut breeding programme, after verifying their consistencies over different environments.

5.4. Relationship among traits

The correlation analysis established the association between traits and helps in the selection of suitable traits**.** Also, the selection of genotypes would require the screening and identification of traits that are strongly and positively correlated with seed yield (Khan et al., 2022). The associations between seed width and seed length imply that an increase in one increases the other traits, and this was similar to those reported in African yam bean (Adewale et al., 2010). The positive association between different traits and the existence of correlation could result from genetic linkage or epistatic effect among various genes (Ozer et al., 2010). The significant positive correlation obtained between hundred seed weight and seed length, seed width and seed thickness indicates that selection of any of these traits as a surrogate would significantly improve the hundred seed weight of Bambara groundnut landraces. Jonah (2012) has reported a positive and significant association between hundred seed weight and seed quantitative traits in Bambara groundnut. A negative and significant relationship was found between seed length and seed width thickness ratio, seed width and seed width thickness ratio, seed thickness and seed width thickness ratio and seed thickness and seed length thickness ratio implying improvement in any of these traits will significantly lower the length thickness and the width thickness ratios of the seeds. Adewale et al. (2010) reported the correlation of seed traits in African yam bean accessions and observed a negative correlation with similar traits.

6. Conclusion

The African Bambara groundnut population, through seed traits, revealed considerable diversity that would be useful for Bambara groundnut seed improvement. Among the populations based on the seed qualitative traits, West and Central Africa are closely related and form group A; while East and Southern Africa show a closer relationship and form group B. The seed coat colour trait is an important descriptor used for the characterization of Bambara groundnut population. The hundred seed weight trait could be improved through direct selection, and its inheritance predominantly due to the additive gene actions. Also, Bambara groundnut landraces with superior seed size (seed length, seed width and seed thickness) traits could be selected from cluster 2. The overall results have shown that Bambara groundnut can be classified through seed phenotype and considerable seed diversity was depicted among the African Bambara groundnut population.

Declaration of competing interest

The authors declare no competing interests.

Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.sajb.2022.06.060.

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