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RESEARCH ARTICLE OPEN ACCESS

Genetic Variability of Water Yam (*Dioscorea alata* L.) Tubers From Côte d'Ivoire Based on Agromorphological and Culinary Traits

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ABSTRACT

Assessment of the genetic diversity within existing germplasm is essential for the sustainable management of plant genetic resources, and the development of improved cultivars. *Dioscorea alata* is considered as one of the most widespread root and tuber crop species in tropical regions, and significantly contributes to enhancing the income of small-scale producers and improving food security. This study was conducted to profile the genetic variability within a panel of 205 *D. alata* accessions using 15 key yam tuber traits. Multivariate analysis revealed high variability among the accessions for the evaluated traits. Based on the clustering methods, the accessions were grouped into four main clusters with different genetic performance. Furthermore, silhouette (Si) analysis indicated that tuber quality-related traits clustered the accessions more distinctly than tuber quantitative traits, with the highest coefficient of 0.58. A subset of traits, including flesh color, flesh oxidation, and tuber shape, emerged as the most relevant variables for cluster differentiation based on tuber quality. Meanwhile, yield, circumference, and length were the key quantitative traits that best defined the clusters. Among the relevant variables identified by PLS-DA, only tuber circumference and tuber length significantly predicted tuber yield, with regression coefficients of 0.55 and 0.35, respectively. Tuber browning was the trait that reduced cooking quality, and multi-trait genotype–ideotype distance index (MGIDI) analysis identified genotypes performing better within each cluster defined by tuber quantitative traits for water yam breeding programs. This study provides reliable and valuable insights into the genetic variability within Côte d'Ivoire's water yam germplasm and constitutes a reliable source for genetic improvement.

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1 | Introduction

Yam species are mainly grown in tropical and subtropical areas of Africa, Asia, the Caribbean Islands, Oceania, and Latin America for their starchy underground tubers [1, 2]. Unlike other root and tuber crops such as cassava, cocoyam, and sweet potato, yam is considered the most energy-efficient food crop [3]. It primarily contains carbohydrates with substantial amounts of protein, making it one of the most important and valuable tuber crops worldwide [4, 5].

The genus *Dioscorea* in the family Dioscoreaceae includes more than 600 tuber-bearing plant species, but only about 10 are true edible crops with significant potential for food security, energy, and economic development [6]. Among them, *D. alata* (L.), *D. rotundata* (P.), and *D. cayenensis* (Lam.) are the most widely cultivated and economically important species in Africa [7, 8].

In 2023, yam production in Africa reached 87.645 million metric tons, accounting for 98.09% of the world's total production of 89.345 million metric tons, with 85.375 million tons (95.55%) coming from West Africa [9]. Côte d'Ivoire is the second-largest yam-producing country after Nigeria, contributing ~7.967 million metric tons in 2023 [9]. In Côte d'Ivoire, yam is the largest food crop, and *D. alata* represents 60% to 70% of the total yam production [10, 11], owing to its high yield potential, ease of propagation, rapid growth that suppresses weed competition, and the long postharvest conservation ability of its tubers [12, 13].

Vegetatively propagated crops such as yam face several constraints that could lead to the abandonment or loss of important genetic resources. In fact, yams are often neglected in favor of more economically important crops and face competition from plant species such as cotton, maize, and cassava [14]. It has also been reported that poor yam quality attributes, including high tuber flesh oxidation, poor taste, and low market value, contribute to varietal loss, and the abandonment of some landraces in Togo [15]. Similarly, studies in the Mbe plains of Cameroon reported that a single yam variety grown for commercial purposes accounted for more than 80% of the cultivated area, significantly reducing varietal diversity [14].

Germplasm collections are essential for the conservation and sustainable management of plant genetic resources. They help to mitigate the loss of genetic diversity caused by genetic erosion, climate change, the disappearance of wild relatives, and habitat degradation. Currently, important yam germplasms are conserved worldwide in vivo, in vitro, and as seed collections [11]. The largest collections are found in West Africa, particularly in Nigeria and Côte d'Ivoire. Several studies have focused on the morphological characterization of accessions from these African yam germplasms [16–21].

The morphological traits of *D. alata* are highly polymorphic and subjected to environment conditions, making it difficult to establish clear phenotypic relationships between accessions. Furthermore, the informal trade and exchange of planting materials by farmers often lead to the duplication and variation of varietal names across ethnic groups and regions. Assessing the intraspecific genetic variability of crop plants is essential for identifying traits associated with desirable biological functions, which can be strategically used to develop new varieties [22]. Therefore, a thorough characterization of *D. alata* genetic resources is necessary

to enable their sustainable and efficient management for breeding programs aimed at improving yield and productivity [23]. Genetic diversity in *D. alata* accessions is usually assessed using both vegetative traits and tuber characteristics [18–20, 24, 25]. However, as tubers are the most economically important part of the plant, their characteristics deserve to be studied separately from other agromorphological traits.

The main objective of the present study is to assess the genetic variability among yam accessions maintained in vivo at the National Agronomic Research Centre in Côte d'Ivoire, using agronomic and culinary traits of the tubers. The work also aims to provide plant breeding programs with reliable data to support the selection of plant materials for developing improved cultivars with higher productivity and enhanced resilience to pests and environmental stresses.

2 | Materials and Methods

2.1 | Plant Materials

The plant materials consisted of 205 *D. alata* accessions from the Centre National de Recherche Agronomique (CNRA's) yam germplasm collection. These accessions were partially collected through surveys conducted across different cities and villages in the major yam-growing areas of Côte d'Ivoire (South, Center, and North) between 2008 and 2013. They represented different variety groups, including landraces (148 accessions) and offspring varieties (57 accessions). The landraces included betebete (56 accessions), brazo (10 accessions), double (16 accessions), florido (41 accessions), and nza (25 accessions).

2.2 | Experimental Design

The experiment was conducted under field conditions using a Fisher block design [26] with a plot size of 60 m × 42 m (0.2520 ha), comprising two completely randomized blocks spaced 2 m apart. The first trial was established during the 2018 growing season at the experimental site of CNRA, located in Bouaké, central Côte d'Ivoire, at latitude 7°44' N and longitude 5°04' W. In 2019, the trial was replicated both in Bouaké and Gagnoa. The second city is located in the southwest, at latitude 6°08' N and longitude 5°56' W, in moist evergreen forest areas with annual precipitation ranging from 1200 to 1700 mm and temperatures ranging from 25 to 27°C [27]. Replicating the trials in two locations was intended to account for genotype-environment interaction (G×E) and increase the reliability of the results. Each plot consisted of five plants from whole tubers, with a weight of 300 to 400 g per accession, and a spacing of 1 m between and within rows. When the tuber weight exceeded these values, a single large tuber was sliced into several uniform fragments, each with an equivalent weight as specified earlier. The accessions were planted after ploughing and clearing the experimental plot. No fertilizer was applied, and manual weeding was done regularly to keep the plot free of weeds.

2.3 | Data Collection

The 205 *D. alata* accessions were characterized using 15 variables recorded according to the yam crop ontology [28], a dichotomous key for water yam identification [29], and a visual color chart

from CIRAD. The variables included: (1) tuber morphological and culinary traits such as tuber shape, appearance, hairiness, tuber branching, circumference, length, width, phelloderm color, and flesh cooking quality; (2) flesh color, flesh oxidation or browning, flesh texture, and flesh dry matter content (DMC); and (3) yield and anthracnose disease severity. Tuber shape (oval, round, cylindrical, irregular, or pyriform), appearance (smooth or rough), digitation (absent, shallow, or deep), and hairiness (absent, slight, moderate, or high) were assessed on all the tubers of each accession immediately after harvesting. Tuber flesh and phelloderm color (white, yellow, orange, or purple), flesh texture (thin, moderate, or coarse), and flesh oxidation were determined on two halves of tubers from each accession. Flesh cooking quality was evaluated according to the following criteria: very good (no color change and very low water content), good (slight color change and low water content), and poor (noticeable color change and high water content). Flesh oxidation (absent, slight, moderate, or high) was assessed after exposing the peeled tuber to open air for 10 to 30 min. Tuber length, width, and circumference were measured on five tubers of each accession. Flesh DMC was determined from 100 g of fresh flesh from two tubers, dehydrated for 72 h at 70°C in a drying room. Anthracnose disease severity was recorded 2 months after planting and then monthly until complete senescence of the plants, using a 1–5 rating scale as described by Asala et al. [30] and Kolade et al. [31].

2.4 | Data Analysis

The phenotypic data were first separately analyzed based on the quantitative and qualitative agromorphological traits from tubers of the 205 assessed accessions, and then a single data matrix was generated as the numeric combination of the two matrices [32]. Quantitative data was used to estimate genotype and location effects, as well as interaction genotype x environment effects, using a two-way analysis of variance (ANOVA) computed with *rstatic* packages [33]. Prior to the ANOVA, the condition of normality was verified to avoid potential bias from undesirable values in the dataset, ensuring the reliability of the results. Consequently, a Q-Qplot graphic was generated to identify observations falling outside the general scope or the expected distribution, and any detected outlier values were removed from the dataset. The *gamem_met* (*Genotype-environment analysis by mixed-effect models*) function in the *metan* (*Multi Environment Trials Analysis*) package was used to calculate the best linear unbiased predictor (BLUP) values of each quantitative trait of yam tubers [34]. In the model, the genotype (accession) effect was considered as a random effect. Extracted BLUP values for each trait were standardized and used as input data to identify the most relevant quantitative tuber traits through principle component analysis (PCA), using the *Factoshiny* package [35]. A multiple correspondence analysis (MCA) was performed using the *Factoshiny* packages in R to identify the traits with the highest discriminative power. Each relevant qualitative trait was then coded based on the scaling codes in the yam crop ontology [28]. The generated data matrix was transformed into semiquantitative data using the *log-rat* function in Excel 2013, and the BLUP values for each accession were computed based on a one-way linear mixed model using the *mixmeta* R packages [36]. Clustering analysis was then performed to group the accessions into distinct homogeneous groups. A genetic distance matrix was generated through the Euclidean method, and ward.D2 approach was

used for cluster analysis using the *ape* and *dendextend* packages implemented in R [37–39]. A clustering validation method was applied to evaluate how well the population under study is clustered, using silhouette (Si) analysis [40, 41]. Si coefficients estimate the average distance between clusters. Si values close to 1 indicate that the population is well clustered, while values close to –1 suggest poor clustering. The *fviz_silhouette* function from the *Factoextra* package was used to calculate the Si coefficients of each grouping pattern [39]. The most discriminative variables contributing to the clustering patterns were identified using partial least squares-discriminant analysis (PLSDA) with standardized data, as reported in several studies [41–43]. The optimal number of linear discriminants to be retained was determined based on eigenvalues greater than 1 [41]. The most discriminant variables were selected using the variable importance in projection (VIP) of the accessions at a threshold of 1.0 (≥ 1.0). The reliability of the test was assessed by calculating the accuracy of the PLSDA model. The area under curve and receiver operating characteristic (AUROC) operator is commonly used as a diagnostic statistic for PLSDA models. AUROC values range from 0 (<0.5, no discrimination) to 1 (perfect discrimination) of classes [44]. So, AUROC values were computed, and the *mixomics* package was used to generate plots for supervised classification of the accessions [45]. ANOVA was then applied to characterize the grouping patterns using the *lm* function implemented in R software, with the relevant quantitative tuber traits identified by PLSDA analysis. In addition, path analysis was performed to determine the direct and indirect effects of relevant PLSDA-identified traits on tuber yield and cooking quality for selection purposes, using the *lavaan* and *semPlot* packages [46, 47]. The multi-trait genotype–ideotype distance index (MGIDI) was computed to identify genotypes with superior performance within each cluster defined by tuber quantitative traits, using the *metan* packages [34].

The concordance of accession assignments to the different groups based on the three matrices (qualitative, quantitative, and the combined) was assessed using a nonparametric Mantel test by estimating Spearman's rank correlation coefficients (ρ). Correlation coefficients and their significance levels were determined using 9999 permutations with the *vegan* package implemented in R [48]. A Venn diagram was used to assess the concordance of accession affiliations within each group defined by the agromorphological traits of water yam tubers.

3 | Results

3.1 | Variability in Tuber Quality-Related Traits

Quality attributes related to water yam tuber quality were highly polymorphic, with some attributes being more frequently observed across the entire population (Table S1). White (59.02%), orange (20.49%), purple (13.17%), and yellow (7.32%) were the major tuber flesh colors observed in the total population, while for tuber phelloderm colors like white (1.95%), orange (22.44%), yellow (52.68%), and purple (22.93%) were recorded. Tuber shapes included oval (1.95%), cylindrical (66.83%), round (19.02%), pyriform (2.44%), and irregular (9.76%). For starch grain size variables such as thin (24.88%), moderate (63.90%), and coarse (11.22%) were mainly observed among the 205 *D. alata* accessions. Quality attributes associated with tuber flesh oxidation or browning were high (6.34%), moderate (12.20%), low (20%), and absent (61.46%). Tuber branching was absent in 55.12% of the accessions, shallow in

30.24%, and deep in 14.64%. Tuber appearance was generally smooth (54.63%) or rough (45.37%), while tuber hairiness was absent in 12.20% of the accessions, slightly absent in 61.46%, and highly present in 26.34%. Attributes of flesh cooking quality were poor (3.90%), good (80.98%), and very good (15.12%).

3.2 | Genotype, Location, and Genotype x Location Interaction Effects on Tuber Quantative Traits

All the assessed tuber quantitative traits were strongly influenced by both genotype and location effects (Table 1). However, genotype x location interaction effects revealed significant differences among genotypes for four tuber traits, including tuber length, tuber circumference, tuber DMC, and anthracnose disease severity score (ADSS). The interaction effects were not significant only for tuber yield and tuber width. The generalized eta squared (GES), which indicates the size of the effect the factor could have on the dependent variable, showed that genotype effects were stronger than those of location and genotype x location interaction, with the highest values for all the tuber quantitative traits. In addition, mean square values for genotypes were higher than those for the genotype x location interaction for all tuber traits. Furthermore, the coefficient of variation for all tuber traits was above 10%. The highest value was 44.27% for tuber yield, while the lowest value (12.33%) was observed for tuber DMC (Table 1).

3.3 | Phenotyping Traits Correlation

Tuber flesh color was positively correlated with tuber appearance ($r=0.31$, $p=0.004$) and tuber flesh browning ($r=0.28$, $p=0.018$). However, the correlation coefficient between flesh color and hairiness was negative ($r=-0.26$, $p=0.006$). Phelloderm color was negatively correlated with flesh color ($r=-0.46$, $p<0.001$) and tuber appearance ($r=-0.37$, $p<0.001$), and positively correlated with hairiness ($r=0.36$, $p<0.001$). The correlation between tuber appearance and tuber hairiness was negative ($r=-0.41$, $p<0.001$, Table S2).

Quantitative traits such as tuber width were positively correlated with yield ($r=0.72$, $p<0.001$) and tuber circumference ($r=0.97$, $p<0.001$), while tuber circumference was also strongly associated with yield ($r=0.69$, $p<0.001$). In contrast, ADSS were negatively correlated with yield ($r=-0.57$, $p<0.001$), tuber width

($r=-0.50$, $p<0.001$), tuber circumference ($r=-0.52$, $p<0.001$), and DMC ($r=-0.31$, $p<0.001$). Thus, all the traits were considered relevant for the clustering analysis of the 205 *D. alata* accessions.

3.4 | Multivariate Analysis of Agromorphologic and Culinary Traits

Based on their contributions to the determination of factorial components in multiple component analysis (MCA) and principal component analysis (PCA), all the agromorphological traits of the tubers were relevant in discriminating the 205 *D. alata* accessions. For qualitative traits, the first 10 components of the MCA explained 64.88% of the total variability, with eigenvalues ranging from 0.11 to 0.32 (Table 2). The first component explained 13.21% of the total variation and was primarily determined by yellow tuber phelloderm, white and orange tuber flesh, tuber appearance (smooth and rough), and high tuber hairiness. Purple tuber phelloderm and tuber flesh, along with orange tuber phelloderm, contributed significantly to the second component, which accounted for 7.93% of the total variability. Irregular and cylindrical tuber shapes, along with shallow tuber branching, mainly determined the third component, explaining 6.90% of the total variation. Low oxidation of tuber flesh was the only characteristic determining the fourth component, which explained 6.08% of the total variation. Component five was mainly due to coarse tuber texture, yellow tuber flesh, moderate oxidation, poor cooking quality of tuber flesh, and pyriform tuber shape, accounting for 5.94% of the total variance. The absence of tuber branching, shallow tuber branching, and oval tuber shape were the main characteristics contributing to the variability explained by component six, which accounted for 5.45% of the total variance. Component seven explained 5.16% of the total variation and was mainly due to the very good cooking quality of tuber flesh, deep tuber branching, and the absence of hairiness on the tuber. Moderate tuber texture and high tuber hairiness mainly determined component eight, explaining 4.97% of the total variation.

Component nine explained 4.74% of the total variance and was defined by white tuber phelloderm and high oxidation of tuber flesh. Component 10 accounted for 4.49% of total variability and was primarily determined by thin tuber texture and irregular tuber shapes.

TABLE 1 | Mean square, generalized eta squared, and coefficient of variation for tuber quantitative traits of 205 *D. alata* accessions.

Tuber trait	Genotype			Location			Genotype x location			CV (%)
	Mean Sq	GES	Df	Mean Sq	GES	Df	Mean Sq	GES	Df	
Length (cm)	54.40***	0.622*	204	2622.60***	0.298*	1	24.70**	0.417*	198	23.64
Yield (t ha ⁻¹)	42.20***	0.531*	204	2158.40***	0.242*	1	24.20 ^{ns}	0.375 ^{ns}	198	44.27
Width (cm)	15.00***	0.654*	204	459.80***	0.219*	1	5.00 ^{ns}	0.376 ^{ns}	198	18.69
Circumference (cm)	71.70***	0.682*	204	908.30***	0.141*	1	24.80*	0.411*	198	18.46
ADSS	0.23***	0.679*	204	3.52***	0.120*	1	0.181***	0.597*	198	17.61
Dmc (%)	30.82***	0.991*	204	93.79***	0.340*	1	12.70***	0.973*	198	12.33

Note: *, **, *** significant at p -value thresholds of 0.05, 0.01, and 0.001, respectively.

Abbreviations: ADSS, anthracnose disease severity scores; CV, coefficient of variation; Df, degree of freedom; Dmc, dry matter content; ges, generalized eta squared; Mean Sq, mean square; ns, not significant.

TABLE 2 | Percentages of variance explained by components of the MCA and the PCA, eigenvalues, and variables contribution of 205 *D. alata* accessions.

Analysis	Tuber trait	Modality	Dim 1	Dim 2	Dim 3	Dim 4	Dim 5	Dim 6	Dim 7	Dim 8	Dim 9	Dim 10
MCA	Phelloderm color	White	0.30	1.17	11.60	1.16	4.46	1.64	0.00	1.16	37.76	0.07
		Yellow	9.92	0.59	0.43	1.30	0.43	0.19	0.02	0.01	0.85	0.00
		Orange	7.20	9.46	0.51	0.10	2.17	0.01	0.18	2.58	0.02	0.40
	—	Purple	5.20	20.50	0.49	2.95	1.17	0.16	0.05	1.92	0.07	0.45
	Texture	Thin	3.52	2.93	1.45	0.24	0.29	0.40	2.94	7.21	0.45	26.61
		Coarse	2.97	8.20	0.00	1.15	11.50	8.03	1.91	7.19	0.16	2.55
	—	Moderate	0.20	5.14	0.56	0.02	1.17	0.63	0.24	7.83	0.34	6.50
	Flesh color	White	7.79	0.11	0.04	0.14	1.54	0.02	0.01	1.78	0.05	1.05
		Yellow	0.00	3.29	2.92	0.14	17.00	0.00	0.18	10.10	2.58	9.64
		Orange	11.40	3.42	3.55	2.52	0.63	0.17	0.11	2.96	0.34	0.20
	—	Purple	2.88	19.10	2.32	6.17	2.06	0.71	0.02	6.80	0.00	0.17
	Oxidation	Absent	3.71	1.56	0.72	2.35	0.02	4.03	0.19	0.56	0.01	1.58
		Slight	0.07	3.39	0.12	13.00	4.86	5.84	0.02	10.70	0.59	1.85
	—	High	3.57	0.03	1.90	6.77	0.01	11.30	4.45	0.58	16.55	0.56
	—	Moderate	6.86	0.10	6.00	0.48	9.65	1.02	0.52	9.35	3.01	0.29
	Cooking quality	Good	0.01	0.40	0.50	4.44	0.03	0.85	1.96	0.00	0.90	0.63
		Poor	4.39	0.50	0.75	12.90	13.7	2.25	0.03	6.42	0.48	2.04
	—	Very good	0.62	3.35	4.29	9.32	2.12	1.88	9.91	1.79	3.40	6.59
	Shape	Round	0.27	3.74	15.10	2.24	3.50	1.02	3.03	0.18	6.53	2.22
		Cylindrical	0.38	0.13	8.32	0.02	0.16	4.95	0.04	0.47	0.89	0.35
		Irregular	2.29	6.33	0.53	0.39	0.66	10.90	0.12	1.84	4.48	17.64
	—	Oval	1.08	0.00	1.18	0.47	2.18	12.30	25.40	0.02	0.25	0.18
	—	Puriform	0.09	5.23	3.35	8.18	11.70	0.84	2.00	0.03	6.09	0.56
	Tuber branching	Absent	0.59	0.03	3.10	3.04	0.67	9.13	2.54	0.24	1.24	0.04
		Shallow	0.43	0.10	0.02	8.95	3.60	15.70	2.71	1.57	4.46	0.03
	—	Deep	0.31	0.64	10.50	0.84	1.29	0.03	29.80	0.72	0.77	0.39
	Appearance	Smooth	5.62	0.02	0.36	0.64	0.19	2.36	0.29	1.99	0.04	3.63
		Rough	6.77	0.03	0.44	0.77	0.23	2.84	0.35	2.39	0.05	4.37
	Hairiness	Absent	4.61	0.34	3.60	4.42	2.67	0.01	8.75	0.79	5.01	5.90
		High	6.41	0.19	8.05	1.67	0.38	0.63	0.06	6.56	0.51	3.49
	—	Moderate	0.49	0.00	7.31	3.18	0.10	0.23	2.18	4.29	2.14	0.02
	Eigenvalues		0.32	0.19	0.17	0.15	0.15	0.13	0.13	0.12	0.12	0.11
	Total variance (%)		13.21	7.93	6.90	6.08	5.94	5.45	5.16	4.97	4.74	4.49
	Cumulative variance (%)		13.21	21.15	2.05	34.13	40.07	45.52	50.68	55.65	60.40	64.88
PCA	Circumference (cm)		34.97	0.58	1.10	1.38	9.72	51.44	—	—	—	—
	Width (cm)		35.78	0.80	1.80	1.72	12.25	48.45	—	—	—	—
	Dry matter content (%)		0.16	3.25	77.10	19.35	0.12	0.01	—	—	—	—
	Length (cm)		0.95	46.50	14.65	27.04	10.85	0.01	—	—	—	—
	Yield (t.ha ⁻¹)		26.83	4.94	0.75	0.43	66.97	0.08	—	—	—	—

(Continues)

TABLE 2 | (Continued)

Analysis	Tuber trait	Modality	Dim 1	Dim 2	Dim 3	Dim 4	Dim 5	Dim 6	Dim 7	Dim 8	Dim 9	Dim 10
	ADSS		1.31	43.94	4.59	50.08	0.08	0.00	—	—	—	—
	Eigenvalues		2.59	1.26	1.06	0.72	0.35	0.02	—	—	—	—
	Total variance (%)		43.10	21.05	17.60	12.06	5.79	0.39	—	—	—	—
	Cumulative variance (%)		43.10	64.15	81.75	93.82	99.61	100	—	—	—	—

Note: Values in bold represent the tuber traits that contribute the most to the variation of components.

Abbreviations: ADSS, anthracnose disease severity score; MCA, multiple component analysis; PCA, principle component analysis.

For the quantitative variables and based on the PCA, the first six components explained 100% of the variability (Table 2). Tuber width and circumference were the main determinants of the first component. Component three explained 17.60% of the total variability, with DMC identified as the main variable with the highest contribution value. ADSS, tuber length, and DMC defined component four, accounting for 12.06% of the variance. Yield, tuber width, and length determined component five, which explained 5.79% of the variability.

3.5 | Grouping Patterns of Water Yam Accessions Based on Agromorphological Traits of Tubers

Based on the quantitative traits, the 205 *D. alata* accessions were grouped into four main clusters (Figure 1). Cluster 3 was the largest, with 48.78% of the accessions. It is followed by cluster 4 with 22.92%. Clusters 2 and 1 contained, in order, 22.44% and 5.85% of the accessions (Figure 1a). Si analysis, used as a clustering diagnostic, showed clearly the four main clusters with non-overlapping groups, and a high average value of the Si coefficient value of 0.49 (Figure 1b).

The whole population was mainly made of the “betebete” variety group and progenies (hybrid), with 27.32% and 27.80% of accessions, respectively. The Brazo variety group was the smallest, with 4.88% of accessions (Table 3). “douoble,” “florido,” and “nza” variety groups accounted for 7.90%, 20%, and 12.20% of the total accessions, respectively. In the grouping patterns defined by tuber quantitative traits, hybrids were the largest variety group within cluster 1, 2, and 3 with 58.33%, 36.96%, and 30% of the accessions, while the “florido” variety group was the largest within the cluster 4. The membership proportions of accessions from variety groups within cluster 1 were 16.67% (betebete and douoble) and 8.33% (nza). None of the accessions from the brazo and florido groups were allocated into cluster 1.

Tuber quality traits also affiliated the 205 *D. alata* accessions into four main clusters at about 12.5 Euclidean distance units with a silhouette coefficient value of 0.58, independently of variety groups (Figure 2a,b).

Cluster one consisted of 70 accessions (34.15%). Most of the accessions in this cluster belonged to the “betebete” (50%) and “florido” (32.86%) varieties. Cluster two contained 31.22% of the accessions (Table 4) and was primarily composed of progenies (43.75%) and accessions of the “betebete” variety (15.63%). Clusters 3 and 4 accounted for 26.33% and 8.29% of the accessions, respectively.

The combined data matrix, defined as the algebraic sum of both qualitative and quantitative data, also identified four clusters as suggested by the phylogenetic analysis of the two types of variables taken separately (Figure 3a). Cluster 1 consisted of 69 accessions (33.65%), predominantly comprising accessions of the “betebete” (52.17%) and “florido” (27.54%) varieties. Cluster 2 included 56 accessions (27.32%). The accessions in cluster two shared similar vegetative characteristics with those in cluster 1, with mainly accessions of the “betebete” (33.93%) and “florido” (26.79%) varieties. Cluster 3 contained 33 accessions (16.10%), with progenies (48.4%) and accessions of the “Douoble” variety (30.31%) being the main components of this cluster (Table 4). Cluster 4 included 47 accessions (22.93%), most of which were hybrid lines or progenies (70.21%). The Si value (0.34) was high but lower than those of the quantitative and qualitative variables (Figure 3b).

3.6 | Most Discriminating Tuber Traits for Each Cluster

The PLSDA of the cluster accessions, using qualitative traits, revealed three informative components that explained 100% of the total variance. Tuber flesh color and tuber flesh oxidation contributed significantly to these components. The first discriminant function, which accounted for 99.997% of the total variance, was most strongly correlated with tuber flesh color ($r=0.673$) and tuber flesh oxidation ($r=0.668$). Tuber shape most strongly defined the third discriminant function, with a regression coefficient value of -0.763 . Additionally, the three tuber qualitative traits (tuber flesh color, tuber flesh oxidation, and tuber shape) were the most discriminative variables, with VIP values ≥ 1 (Table 5).

For quantitative traits, the first three functions obtained from the PLSDA, explaining 97.76% of the total variance, were used to discriminate the *D. alata* accessions. Tuber circumference and tuber yield were highly and positively correlated with the first and second discriminant functions, respectively. The third component was most strongly correlated with tuber DMC ($r=-0.632$) and tuber length ($r=-0.564$). The VIP values were significant for only three variables, exceeding the threshold value of 1.0, for yield (1.165), tuber length (1.005), and tuber circumference (1.785). Thus, these quantitative traits were the most predictive variables for *D. alata* accessions (Table 5).

When qualitative and quantitative traits were combined into a single data matrix for the PLSDA analysis, three discriminant functions accounted for 97.287% of the total variance. The first

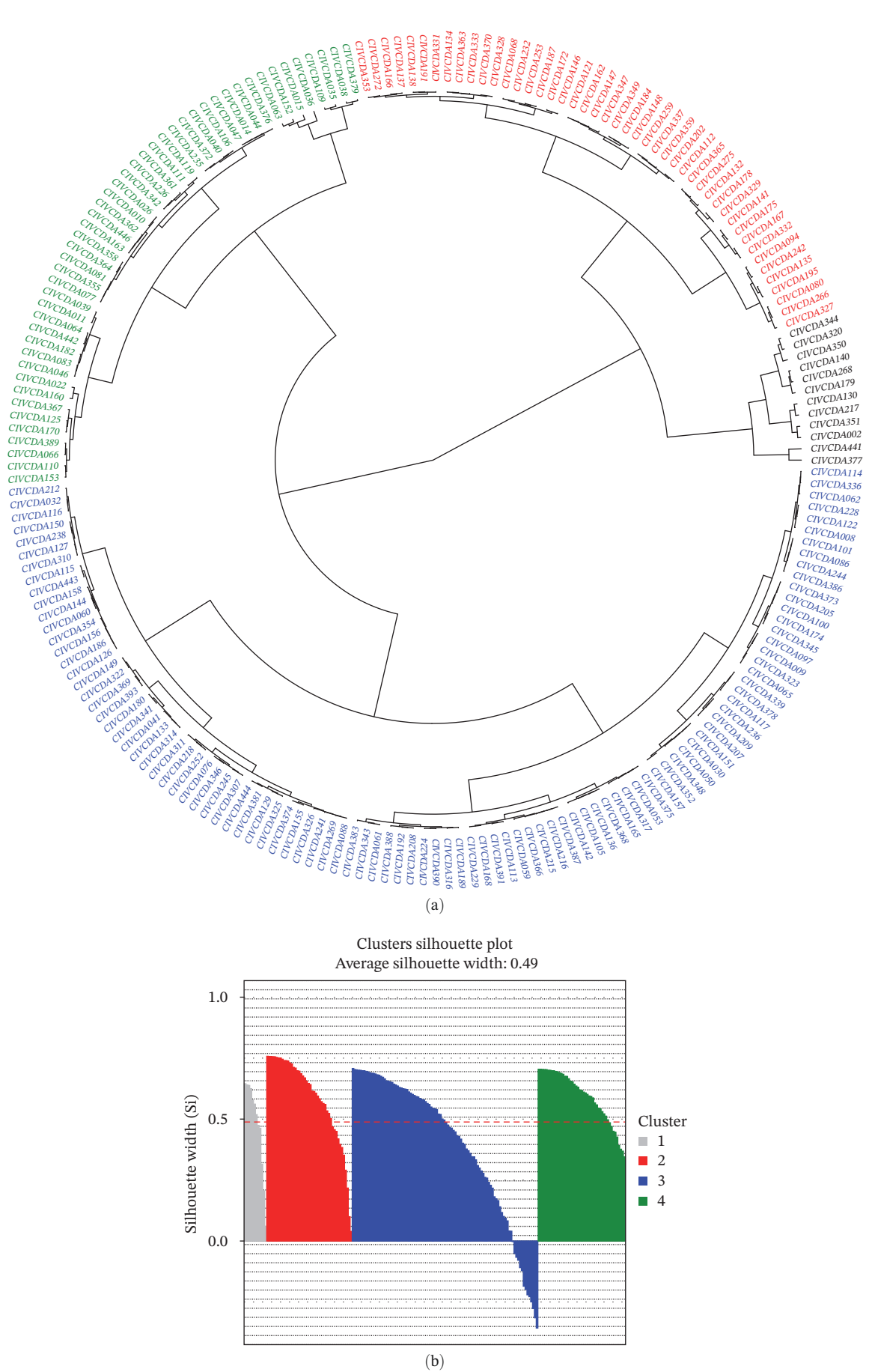


FIGURE 1 | Grouping patterns of the 205 *D. alata* accessions based on tuber quantitative traits and ward.D2 method. Cluster 1 (gray); cluster 2 (red); cluster 3 (blue); cluster 4 (yellow). (a) Phylogenetic tree of 205 *D. alata* accessions and (b) silhouette coefficients of grouping patterns.

TABLE 3 | Proportion of variety groups within clusters defined by tuber quantitative phenotypic traits.

Variety groups	Cluster 1 (n = 12)	Cluster 2 (n = 46)	Cluster 3 (n = 100)	Cluster 4 (n = 47)	Population (n = 205)
Betebete	16.67	23.91	31.00	25.53	27.32
Brazo	0.00	4.35	5.00	8.51	4.88
Douoble	16.67	2.17	8.00	10.64	7.80
Florido	0.00	15.22	17.00	34.04	20.00
Hybrid	58.33	36.96	30.00	6.38	27.80
nza	8.33	17.39	9.00	14.90	12.20

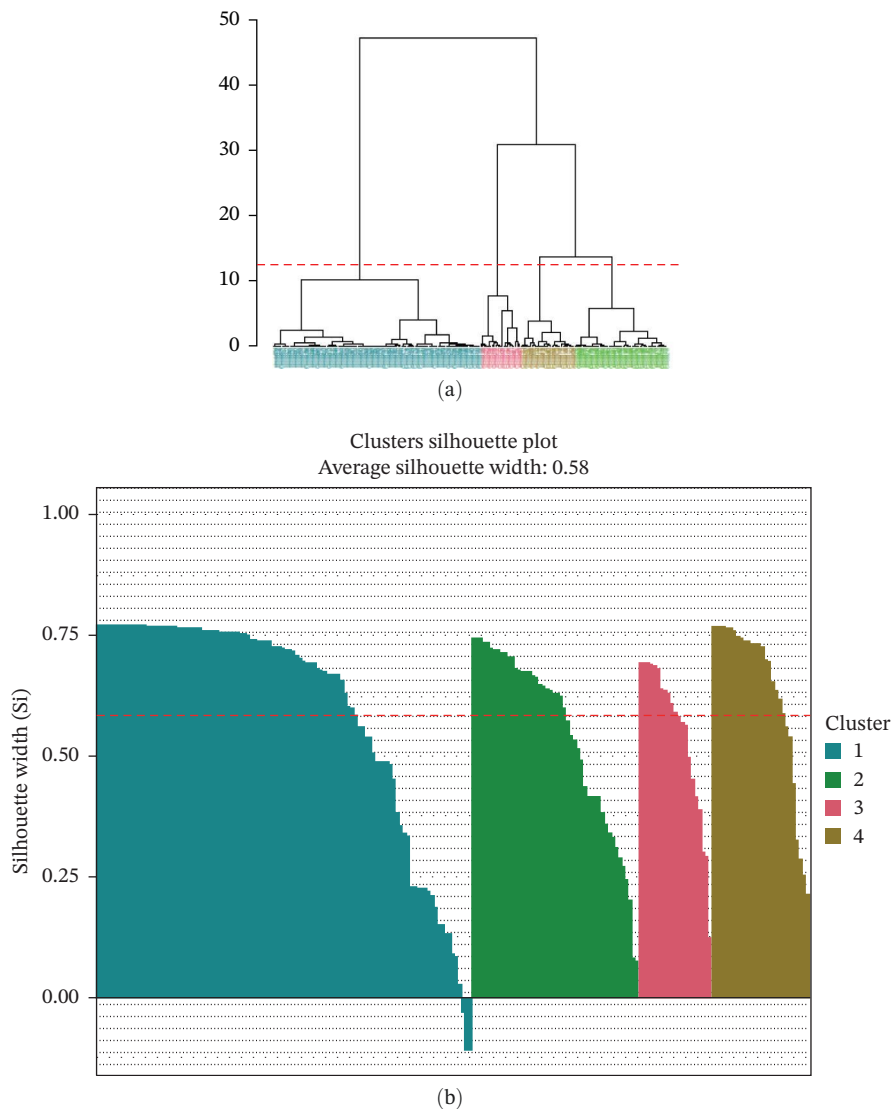


FIGURE 2 | Clustering of the 205 *D. alata* accessions using tuber qualitative traits and ward.D2 method. Cluster 1 (green); cluster 2 (blue); cluster 3 (pink); cluster 4 (dark gold). (a) Phylogenetic tree of 205 *D. alata* accessions and (b) silhouette coefficients of grouping patterns.

discriminant function was most strongly correlated with tuber circumference, while tuber yield contributed negatively to the variance explained by the second component. Phelloderm color, flesh oxidation, and flesh cooking quality were the main traits determining the second discriminant function.

The third discriminant function was primarily influenced by tuber length. Tuber circumference (VIP = 1.352), yield (VIP = 2.899), tuber length (VIP = 1.666), and tuber DMC (VIP = 1.343) were the most discriminating traits for the clusters (Table 5).

TABLE 4 | Proportions of variety groups within clusters identified by tuber qualitative traits and the combined (quantitative and qualitative) data matrix.

Variety group	Proportion of variety groups within clusters defined by tuber qualitative phenotypic traits				Proportion of variety groups within clusters defined by combined data matrix			
	Cluster 1 (n = 70)	Cluster 2 (n = 64)	Cluster 3 (n = 54)	Cluster 4 (n = 17)	Cluster 1 (n = 69)	Cluster 2 (n = 56)	Cluster 3 (n = 33)	Cluster 4 (n = 47)
Betebete	50.00	15.63	3.70	52.95	52.17	33.93	0.00	2.13
Brazo	0.00	7.81	11.11	0.00	1.45	14.29	0.00	4.26
Douoble	1.43	7.81	18.53	0.00	1.45	1.78	30.30	8.51
Florido	32.86	7.81	11.11	35.29	27.54	26.79	9.09	6.38
Hybrid	7.14	43.75	44.44	0.00	5.8	7.14	48.49	70.21
nza	8.57	17.19	11.11	11.76	11.59	16.07	12.12	8.51

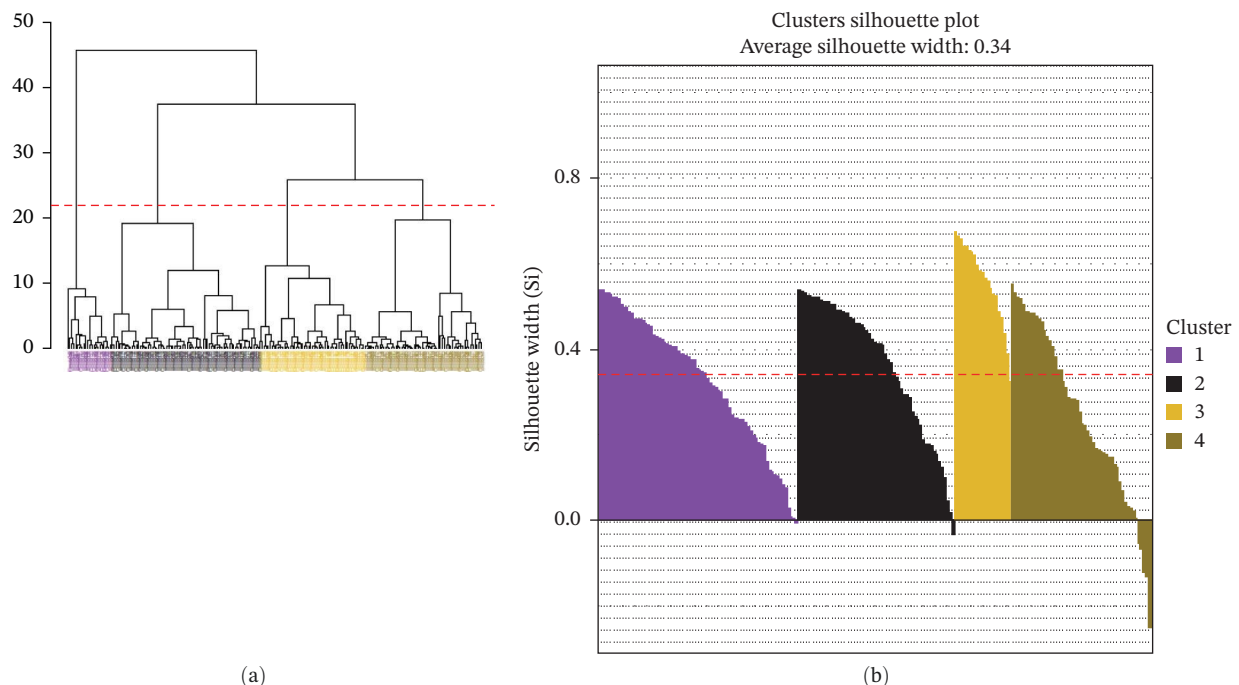


FIGURE 3 | Genetic relationships among the 205 *D. alata* accessions using the combined (quantitative and qualitative variable) tuber traits and ward.D2 method. Cluster 1 (purple); cluster 2 (black); cluster 3 (gold); cluster 4 (dark gold). (a) Phylogenetic tree of 205 *D. alata* accessions and (b) silhouette coefficients of grouping patterns.

3.7 | Characteristics of the Accessions Within the Discriminated Clusters

With the training dataset, the first two discriminant functions clearly separated the four groups of *D. alata* accessions identified by the HCA, independently of the qualitative and quantitative traits (Figure 4). The first discriminant function was more efficient in distinguishing clusters 1 and 4 when the datasets only included quantitative and combined traits, while the second function was more correlated with clusters 2 and 3 (Figure 4a). For qualitative traits, discriminant function 1 was more effective in discriminating clusters 1 and 2 as well as clusters 3 and 4, and function 2 efficiently contributed to distinguish clusters 1 and 4 from clusters 2 and 3 (Figure 4b). However, the four groups were overlapped for the combined data matrix (Figure 4c).

Posterior prediction of the groups from the validation dataset revealed error rates ranging from 4.76% for qualitative traits to 9.42% when quantitative and qualitative traits were combined as a single data matrix.

When tuber quality traits were considered, the clusters defined by the first discriminant function accounted for 56.22% of the total variability. Cluster 1 was predominantly composed of accessions with a cylindrical shape (77.78% of total accessions) and white flesh (87.96%). In addition, the tuber flesh had very good cooking quality and did not oxidize (Table 6). In contrast to cluster 1, the tuber flesh of the accessions in cluster 4 (75%) oxidized with different oxidation trends, including slight oxidation (46.43%), moderate oxidation (25%), and high oxidation (3.57%). The flesh color was predominantly orange (67.86%).

TABLE 5 | Percentages of variance explained by the first three discriminant functions, importance of the variables in the projection (VIP) and regression coefficients (*r*).

Types of traits	Variables	Partial least square coefficients (<i>r</i>)			VIP
		F 1	F 2	F 3	
Qualitative traits	Phelloderm color	−0.150	0.025	0.067	0.037
	Flesh texture	0.095	−0.016	0.043	0.020
	Flesh color	0.673	−0.532	0.553	1.338
	Flesh oxidation	0.668	0.660	−0.338	1.827
	Cooking quality	0.065	0.015	0.003	0.047
	Tuber shape	0.197	−0.499	−0.763	1.867
	Tuber branching	−0.050	−0.183	0.064	0.426
	Tuber apearance	0.085	0.150	−0.080	0.438
	Tuber hairiness	−0.121	0.018	−0.001	0.055
	Variance (%)	99.997	0.002	0.01	—
	TCV (%)	99.997	99.99	100.00	—
Quantitative traits	Yield	0.561	0.865	0.006	1.165
	Width	0.113	−0.053	0.009	0.305
	Circumference	0.677	−0.378	0.533	1.785
	ADSS	0.001	−0.0066	−0.001	0.001
	Dry matter content	0.230	−0.346	−0.632	0.592
	Tuber lenght	0.413	−0.109	−0.564	1.005
	Variance (%)	92.910	4.490	1.330	—
	TCV (%)	92.910	96.430	97.760	—
Combined traits	Phelloderm color	−0.003	0.007	0.003	0.001
	Flesh texture	0.002	−0.006	−0.002	0.001
	Flesh color	0.023	−0.066	−0.023	0.010
	Flesh oxidation	0.023	−0.067	−0.024	0.012
	Cooking quality	0.002	−0.005	−0.002	0.001
	Tuber shape	0.005	−0.015	−0.005	0.003
	Tuber branching	−0.001	0.002	0.001	0.001
	Tuber apearance	0.002	−0.004	−0.001	0.001
	Tuber hairiness	−0.003	0.008	0.029	0.002
	ADSS	0.347	0.135	0.015	0.001
	Yield	0.577	−0.788	0.158	2.899
	Tuber width	0.111	0.076	0.001	0.423
	Circumference	0.666	0.499	−0.587	1.352
	Dry matter content	0.217	0.372	−0.061	1.343
	Tuber lenght	0.409	0.226	0.798	1.666
	Variance (%)	55.017	22.040	20.230	—
	TCV (%)	55.017	77.057	97.287	—

Note: The most significant values are in bold.

Abbreviations: ADSS, anthracnose disease severity scores; TCV, total cumulative variance; VIP, variable's importance in the projection.

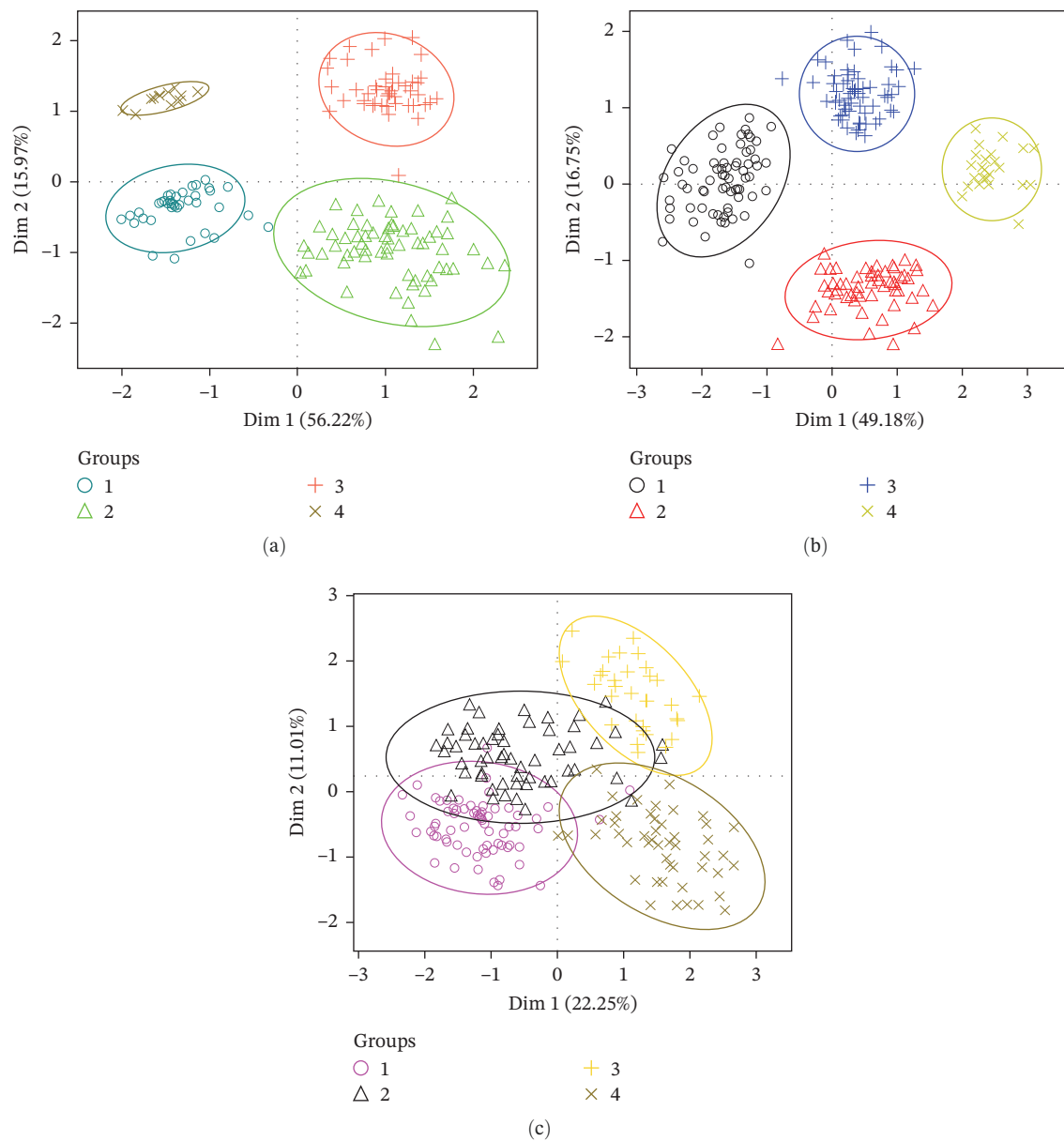


FIGURE 4 | Population genetic structure of *D. alata* accessions using partial least square discriminant analysis method. (a) Groups identified by qualitative traits; (b, c) Groups defined by quantitative and the combined traits, respectively. The dots represent the accessions, and the colors show the different groups. Dim 1: discriminant function 1 and Dim 2: discriminant function 2.

However, tuber shape was round and cylindrical, with 42.86% and 39.29% of accessions, respectively. The second discriminant function explained 15.97% of the total variability, distinguishing accessions in cluster 2. These accessions had tuber flesh that was white (45.83%) or orange (35.42%), with slight and moderate oxidation, and the tuber shape was cylindrical. The tubers of the accessions in cluster 3 were predominantly cylindrical (47.62%), round (28.57%), and irregular (23.81%) in shape, with the highest rates of yellow flesh color and flesh oxidation (Table 6).

Cluster 1, identified by tuber quantitative traits, was correlated with the first discriminant function, which accounted for 49.18% of the total variance. It included accessions producing the largest tubers, with an average circumference of 25.12 cm, the highest yields (11.54 t·ha⁻¹), and the longest tuber length (20.75 cm). In contrast, accessions in cluster 4 were mainly correlated with the

second discriminant function, which explained 16.75% of the total variance. These accessions had low yields and the smallest tubers (Table 7). Furthermore, cluster–location interaction was not significant for all the assessed tuber quantitative traits.

The AUROC, plotted as a function of sensitivity (true positive rate) and specificity (false positive rate) of the PLSDA model, showed that the first discriminant function was less efficient than the second function in distinguishing the clusters defined by quantitative traits, qualitative traits, and the combined traits (Figures S1–S3). Based on quantitative traits, the ROC curve for component 1 perfectly discriminated clusters 1 and 4, with ROC values of 98.16% and 99.70%, respectively, while clusters 2 and 3 recorded high false positive rates, with ROC values of 65.76% and 61.54%, respectively. The second component showed that all the clusters were perfectly discriminated, with the lowest ROC value of 88.59% for cluster 3, and the highest value of 99.77% for cluster

TABLE 6 | Characteristics of each cluster based on the most discriminating tuber quality traits.

Variables	Modality	Cluster 1 N = 108	Cluster 2 N = 48	Cluster 3 N = 21	Cluster 4 N = 28	Statistical test	
						Chi- ²	p-Value
Tuber flesh color	White	87.96 ^a	45.83 ^b	9.53 ^c	7.14 ^c	93.29	<0.001
	Orange	0.00 ^c	35.42 ^b	28.57 ^b	67.86 ^a	78.80	<0.001
	Yellow	0.00 ^b	0.00 ^b	47.62 ^a	17.86 ^a	67.20	<0.001
	Purple	12.04	18.75	14.28	7.14	2.34	0.504
Tuber flesh oxidation (browning)	Absent	95.37 ^a	27.08 ^b	14.29 ^b	25.00 ^b	111.83	<0.001
	Slight	1.85 ^b	50.00 ^a	9.52 ^b	46.43 ^a	62.89	<0.001
	Moderate	2.78 ^b	22.92 ^a	19.05 ^a	25.00 ^a	19.31	<0.001
	High	0.00 ^b	0.00 ^b	57.14 ^a	3.57 ^b	102.17	<0.001
Tuber shape	Round	13.89 ^b	12.50 ^b	28.57 ^b	42.86 ^a	14.74	0.002
	Cylindrical	77.78 ^a	66.67 ^{ab}	47.62 ^{bc}	39.29 ^c	18.92	<0.001
	Irregular	3.70 ^b	14.58 ^a	23.81 ^a	14.28 ^{ab}	11.13	0.011
	Oval	2.78	2.08	0.00	0.00	1.37	0.71
	Pyriform	1.85	4.17	0.00	3.57	1.43	0.69

Note: For a given parameter, the mean values followed by the same superscript letter are not significantly different at the error threshold $\alpha = 0.05$, N , number of individuals (accessions).

TABLE 7 | Mean $\pm$ standard deviation of tuber quantitative-related traits in each cluster.

Tuber traits	Cluster 1 (n = 12)	Cluster 2 (n = 46)	Cluster 3 (n = 100)	Cluster 4 (n = 47)	Statistical test	
					F	p-Value
Crc (cm)	25.12 $\pm$ 7.88 ^a	24.01 $\pm$ 7.44 ^{ab}	24.75 $\pm$ 7.40 ^a	22.73 $\pm$ 7.02 ^{ab}	3.446	0.016
Yield (t.ha ⁻¹)	11.54 $\pm$ 13.27 ^a	10.36 $\pm$ 9.40 ^{ab}	10.73 $\pm$ 10.02 ^a	8.44 $\pm$ 8.15 ^{ab}	2.722	0.043
Length (cm)	20.75 $\pm$ 7.07 ^a	18.51 $\pm$ 5.87 ^b	18.39 $\pm$ 6.80 ^b	17.15 $\pm$ 6.39 ^b	4.109	0.006
Width (cm)	9.71 $\pm$ 2.84 ^a	9.39 $\pm$ 3.08 ^{ab}	9.58 $\pm$ 2.85 ^a	8.80 $\pm$ 2.85 ^{ab}	3.264	0.020
Dmc (%)	29.59 $\pm$ 2.89 ^{ab}	29.63 $\pm$ 3.80 ^a	28.63 $\pm$ 3.54 ^b	29.35 $\pm$ 3.60 ^{ab}	3.817	0.009
ADSS	2.93 $\pm$ 0.55	2.87 $\pm$ 0.52	2.91 $\pm$ 0.52	2.98 $\pm$ 0.58	1.212	0.304

Note: For a given parameter, the mean values followed by the same superscript letter are not significantly different at the error threshold $\alpha = 0.05$, n , number of accessions.

Abbreviations: ADSS, anthracnose disease severity score; Crc, circumference; Dmc, dry matter content.

4. For water yam tuber qualitative traits, discriminant functions showed ROC values ranging from 78.57% to 99.70% (function 1) and from 93.81% to 99.94% (function 2).

3.8 | Effects of Relevant PLSDA-Identified Variables on Yield and Tuber Cooking Quality

Path analysis revealed that only tuber circumference and tuber length significantly predicted tuber yield. A one-unit increase in tuber circumference was associated with a 0.55-unit increase in tuber yield, while an increase of 0.35 in tuber yield was corresponded to a one-unit increase in tuber length (Figure 5). Furthermore, tuber browning was the only quality-related trait with a significant effect on tuber cooking quality ($R = 0.20$, $p > 0.007$). The remaining tuber traits did not have a significant effect on either tuber yield or tuber cooking quality.

3.9 | Best-Performing Genotypes From Each Cluster Based on Tuber Quantitative Traits

Based on the MGIDI, only civcda 35 and civcd 217 were selected as high-performing genotypes within cluster 1 (Figure 6a). Seven and 15 genotypes in cluster 2 and 3, respectively, recorded lower MGIDI values, and were positioned away from the centre of the selection circle, corresponding to the highest-performing genotypes for the traits under study (Figure 6b,c). Cluster 4 included seven top genotypes with superior performance (Figure 6d).

3.10 | Comparison of *D. alata* Accessions Assignment Into Clusters as Revealed by Tuber Phenotypic Traits

Fourteen accessions (6.83%) were only classified into the same groups by the three methods using the qualitative and the quantitative traits separately, and the combined data matrix.

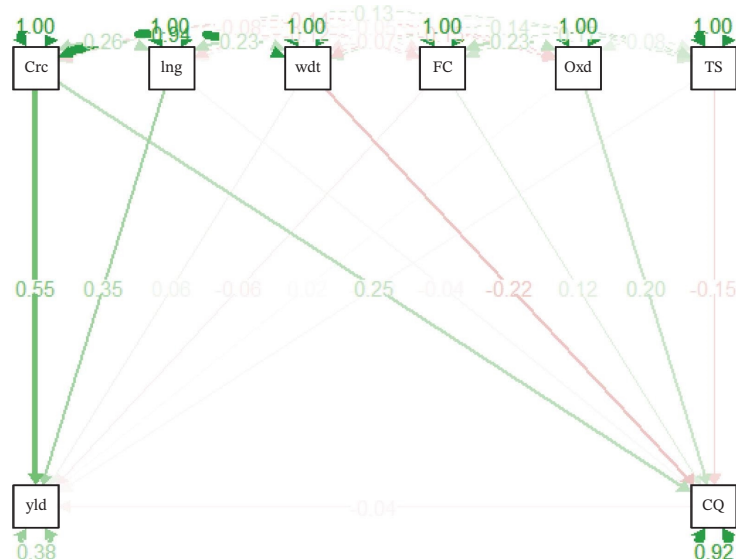


FIGURE 5 | Effects of relevant traits identified by PLDA on tuber yield and cooking quality. Crc, circumference; lng, length; wdt, width; FC, Flesh color; Oxd, oxidation (browning); TS, tuber shape; yld, yield; CQ, cooking quality.

Thirty-one accessions (15.12%) were assigned to the same groups by both qualitative and quantitative traits. The combined data matrix and qualitative traits grouped 20 accessions (9.75%) into the same clusters, while 64 accessions (31.22%) were clustered into the same groups by the combined and quantitative traits (Figure 7). Further, Mantel statistics based on Spearman's rank correlations revealed that qualitative and quantitative data matrices were weakly correlated ($r = 0.102$; p -value = 0.0004).

4 | Discussion

Genetic variability among 205 *D. alata* accessions from Côte d'Ivoire was assessed using 15 agromorphological traits of tubers. Multivariate analysis (MCA and PCA) revealed highly significant variation in the phenotypic expression of the tuber traits, which were all relevant and informative for discriminating the current set of accessions, as reported by Asfaw et al. [28].

Four main groups were identified based on the tuber's qualitative and quantitative traits, as well as the combined data matrix. Additionally, PLS-DA of the identified groups indicated that a subset of tuber qualitative traits, including flesh color, flesh oxidation, and tuber shape, as well as three tuber quantitative traits (yield, tuber length, and tuber circumference), were the most discriminative variables with the highest values of VIP when the data from qualitative and quantitative traits were analyzed separately. These tuber traits could be used to efficiently assess the genetic diversity of *D. alata* accessions. In contrast, when both qualitative and quantitative traits were combined in a single data matrix, only yield, tuber length, tuber circumference, and tuber DMC were identified as the most variable in discriminating the different genotypes from each cluster. As previously reported by several authors [28, 29, 49, 50], all these traits are important in profiling water yam accessions.

Based on the traits under study, the high variability and the grouping patterns observed among the assessed water yam accessions could be attributed to the existing natural diversity within

landrace varieties, particularly in the phenotypic expression of morphological and agronomic traits [21]. This variability may also be linked to historical events of *D. alata* domestication. In fact, this plant species was introduced into Africa from different origins along the southern border regions between Asia and Oceania in the 16th century, where it naturally outcrossed with its wild relatives, such as *D. nummularia* [51]. Furthermore, breeding lines obtained from true cross-breeding between different landraces, used as part of the accessions evaluated in this study, may have contributed to enhancing the diversity of the current material, as plant breeders typically use cross-pollination processes to broaden the genetic base of germplasms, improving tuber yield, pest resistance, and tuber quality [52].

It is noteworthy that accessions within clusters shared more similarity in exhibiting quantitative and qualitative traits compared to accessions from different clusters. This result likely reflects differences in the relevant genomic regions responsible for the variations in the phenotypic expression of tuber traits [32]. Consequently, the identified groups should be genetically divergent in expressing traits of interest that control the subsequent variation in phenotypic traits of yam tubers. These findings confirm the high level of variability within the studied population. Furthermore, the tuber phenotypic traits allocated all the accessions into four main groups. A previous study using molecular-based markers also structured a set of 188 accessions from *D. alata* genebank collection into four main groups [53], showing that phenotypic traits of water yam tubers were in perfect alignment with molecular markers in clustering the accessions. This result underlines the importance of yam tuber traits to be used for characterizing accessions and for improving genotypes through breeding programs. Several studies using both vegetative and tuber traits have also revealed highly structured populations of water yam accessions worldwide. For example, Hasan et al. [54] identified four groups among 70 *D. alata* accessions in Malaysia, based on 47 morphological variables. Adoukonou-Sagbadja et al. [18], using 17 agromorphological traits, isolated three phenotypic classes among 21 *D. alata* accessions introduced into Benin from the

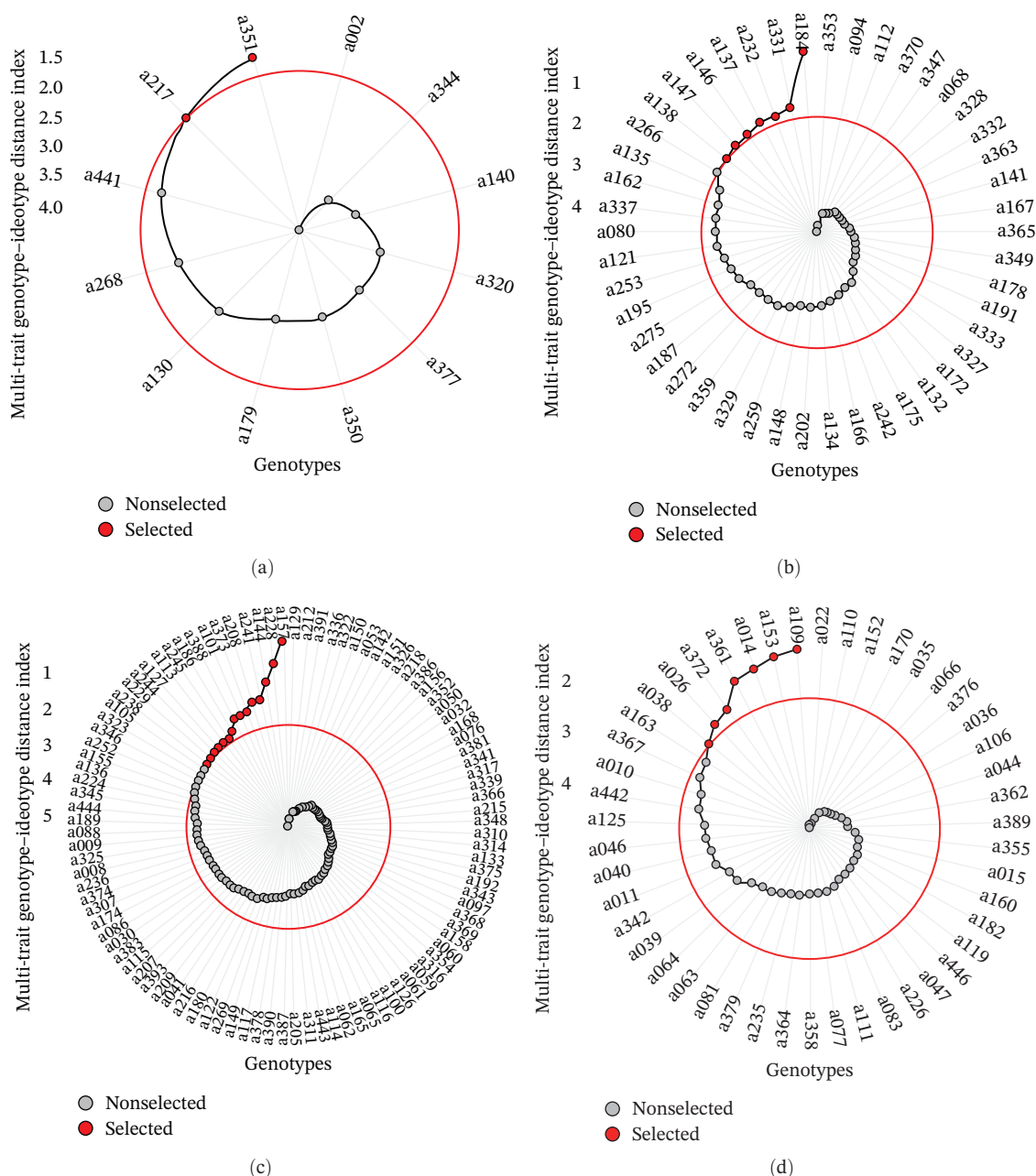


FIGURE 6 | Raking of accessions from each cluster defined by tuber quantitative traits using multi-trait genotype-ideotype distance index (MGIDI). (a) Cluster 1, (b) cluster 2, (c) cluster 3, and (d) cluster 4.

South Pacific islands. More recently, in Nigeria, 100 *D. alata* clones and cultivars were separated into two main phenotypic groups based on 24 variables [20].

Since tubers are the useful parts of yam plants, their characteristics are reliable parameters, as sustainable management of genetic resources is closely linked to a better understanding of population structure through phenotypic characterization. These studies provide tools for identifying germplasm accessions that are of agronomic, nutritional, and economic interest. Therefore, they are meaningful criteria for defining and selecting plant material with desirable traits for breeding programs [20]. Additionally, understanding the genetic relationships between accessions is essential for preserving genetic diversity and identifying

parental lines likely to be hybridized for the development of new cultivars with traits of interest to plant breeders [32].

Indeed, the analysis of both tuber qualitative and quantitative traits could provide maximum information about the diversity of the accessions due to the two different types of traits. However, in the present study, a low correlation coefficient was found between tuber qualitative and quantitative traits. The Si coefficient of the combined data was also lower than those of the quantitative and qualitative traits through cluster analysis, with overlapped grouping patterns revealed by discriminant analysis. These results further demonstrated a negligible linear relationship between the phenotypic variations of tuber quantitative traits (including yield, tuber width, tuber circumference, and

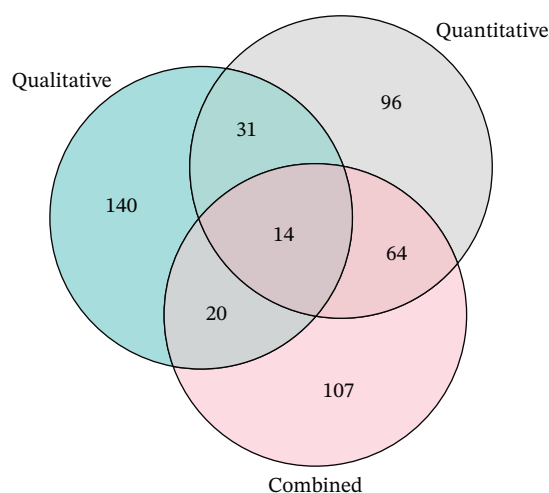


FIGURE 7 | Venn diagram showing variations in 205 *D. alata* accessions' affiliation into each cluster based on tuber phenotypic traits.

tuber length) and the tuber qualitative traits. It also suggests that the grouping patterns could not be distinctively recognized using morphological traits of water yam tubers.

It appears, therefore, that analyzing quantitative and qualitative data together in a single matrix may lead to the underestimation of some variables, while traits such as tuber flesh cooking quality, flesh color, and flesh oxidation are useful criteria for acceptance or rejection of yams by some people [55, 56]. This highlights the importance of combining phenotypic traits of yam tubers when selecting parental lines in breeding programs to account for their agromorphological performance. However, it is noteworthy that vegetative or tuber traits of many crops are often influenced by environmental factors, and their relatively low polymorphism is a limitation for detecting small differences between accessions. This limits the application of such descriptors for clear characterization of plant species [57], and they may not provide an accurate assessment of genetic variability among accessions [58, 59].

Based on only tuber quantitative traits, genotype and geographical patterns were significant factors influencing phenotypic variations in yam tubers for all variables. This result supports Bakayoko et al. [53], who assessed the variability of water yam across years, indicating high variability in yam genotypes with diverse genetic backgrounds and different agronomic performances when cultivated under various environmental conditions. The high genetic variability among genotypes highlights the opportunities to be further exploited by plant breeders for defining and developing new cultivars of water yam using contrasted genotypes through hybridization processes [51].

Genotype $\times$ location interactions of the tested quantitative tuber traits were highly significant for tuber length, tuber circumference, anthracnose disease severity, and tuber DMC, suggesting that the accessions were unstable in expressing agronomic performance. This instability could be primarily due to rainfall variability and soil conditions across multiple ecosystems, as Bouaké and Gagnoa cities are located in two different geographical areas of Côte d'Ivoire. Thus, these traits were relevant and reliable for distinguishing accessions with the highest agronomic performance. Yield and tuber width were the only tuber traits for which the genotype $\times$ location interactions were not significant,

indicating that these traits did not differ significantly among accessions across different locations in Côte d'Ivoire. Furthermore, higher mean square values for all agronomic traits, compared to those of genotype $\times$ location interaction, suggest that the variance of these traits is mainly controlled by genetic factors rather than the environment [53, 60].

The clustering of accessions based on tuber quantitative traits revealed distinct groups with contrasting agronomic performances. Cluster one exhibited the highest performance compared to the other clusters, while cluster four was less productive, showing the lowest values for all tuber traits. The presence of contrasting clusters in the current set of yam plant material suggests that accessions within each cluster were genetically similar, offering opportunities to select potential parental lines for hybridization and to form new breeding populations by crossing individuals among the four clusters [59].

5 | Conclusion

The results of this study revealed high trait performance among the 205 *Dioscorea alata* accessions from Côte d'Ivoire, as evidenced by the population stratification into four main clusters. All the evaluated tuber traits proved to be potentially relevant and reliable for distinguishing the accessions. A subset of variables, namely yield, tuber length, tuber circumference, flesh color, flesh browning, tuber shape, and tuber DMC, were particularly effective in discriminating among the groups. However, cluster membership varied depending on whether data from quantitative or qualitative traits were analyzed separately, as indicated by a low Mantel correlation between the two data matrices and poor concordance in group assignments. This study provides valuable information and useful insights for breeding programs aimed at *D. alata* improvement, as well as for the sustainable management and conservation of yam genetic resources. It also demonstrates that agromorphological and culinary traits of *D. alata* tubers can serve as meaningful criteria for assessing phenotypic diversity and genetic variability among accessions from diverse germplasm collections worldwide.

Author Contributions

Désiré N'da Pokou and Amani Michel Kouakou designed the experiment. Lassana Bakayoko, Yacouba Bakayoko, Adou Emmanuel Ehounou, Tchambi Zamble, Dogoba Coulibaly, and Akissi Rolande N'goran executed the experiment and collected field data. Désiré N'da Pokou, Amani Michel Kouakou, Boni N'zue, Konan Evrard Brice Dibi, Brice Sidoine Essis, and Patrick Olusanmi Adebola supervised the work. Lassana Bakayoko performed the data analysis. Lassana Bakayoko, Adou Emmanuel Ehounou, and Paterné Angelot Agre wrote the manuscript. Désiré N'da Pokou, Amani Michel Kouakou, and Boni N'zue edited and reviewed the manuscript. Dominique Dufour supported financially the work implementation in Côte d'Ivoire through the RTBfood project.

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Disclosure

All authors have read and approved the submitted final version of the manuscript.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The authors hereby declare that most of the data are contained within the article and supporting files, and they can submit the data at any time based on the publisher's request. Additionally, the data set used in the current study are available upon request from the corresponding author.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. ([Supporting Information](#))

The following materials are available: Figure S1. AUROC values of quantitative traits based on discriminant functions 1 and 2; Figure S2. AUROC values of qualitative traits based on discriminant functions 1 and 2; Figure S3. AUROC values of combined traits based on discriminant functions 1 and 2. Table S1. Frequency of tuber quality attributes based on 205 water yam accessions. Table S2. Pearson's correlation coefficients (r) between the 15 tuber traits of 205 *D. alata* accessions from Côte d'Ivoire.