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Genetic diversity and physicochemical variation among Sudanese onion (*Allium cepa* L.) genotypes across agro-ecological zones

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Abstract

Onion (*Allium cepa* L.) is one of the most economically important vegetable crops in Sudan, cultivated across diverse agro-ecological zones ranging from arid to sub-humid climates. The present study aimed to evaluate the genetic diversity and physicochemical variation among fifteen Sudanese onion genotypes grown across three representative zones-River Nile, Gezira, and South Kordofan-using molecular and biochemical approaches. The genotypes were analyzed for total soluble solids (TSS), dry matter, pyruvate concentration, titratable acidity, and total phenolic content. Molecular characterization was conducted using Simple Sequence Repeat (SSR) markers to assess allelic diversity and genetic differentiation. Results from two-way ANOVA revealed highly significant effects of genotype, location, and their interaction on all studied traits, indicating strong genotype \times environment influence. River Nile genotypes exhibited the highest TSS, dry matter, and pyruvate levels, while those from South Kordofan showed lower solids and pungency but higher moisture content. Principal Component Analysis (PCA) effectively clustered genotypes into distinct quality groups, identifying G03, G07, G10, and G11 as elite lines combining high solids and balanced flavor. SSR analysis showed moderate polymorphism ($H_e \approx 0.50$; $PIC \approx 0.47$), confirming substantial molecular variability within the local germplasm. The integrated molecular and physicochemical evaluation demonstrated that Sudanese onion populations harbor valuable genetic resources suitable for region-specific cultivar development. These findings provide a scientific foundation for breeding programs aiming to improve onion quality, resilience, and market value across Sudan's major production zones.

Keywords: *Allium cepa* L., genetic diversity, physicochemical traits, agro-ecological zones, SSR markers, Sudanese onion, genotype \times environment interaction, dry matter, pyruvate concentration, principal component analysis

Introduction

Onion (*Allium cepa* L.) is one of the most economically important vegetable crops cultivated globally and holds a central position in both subsistence and commercial agriculture due to its high nutritional, culinary, and industrial significance [1-3]. As a bulb crop rich in flavonoids, sulfur compounds, and phenolics, onion contributes substantially to human health, showing antioxidant, antimicrobial, and anticarcinogenic properties [4-6]. In developing countries like Sudan, onion serves as a major dietary staple and cash crop cultivated across diverse agro-ecological zones ranging from arid plains to semi-arid river basins [7, 8]. Its adaptability to various environments has encouraged extensive local landrace development; however, yield instability and quality inconsistency across regions continue to constrain both productivity and market competitiveness [9, 10]. The production system in Sudan is challenged by erratic rainfall, poor soil fertility, salinity, and high temperature variability, which collectively influence bulb morphology, yield, and postharvest traits [11, 12]. Consequently, understanding the genetic diversity and physicochemical characteristics of Sudanese onion genotypes is vital for sustainable improvement, seed system development, and climate-resilient breeding [13, 14].

Genetic diversity forms the foundation for crop improvement and plays a key role in maintaining adaptability to environmental changes [15]. Studies using morphological and biochemical descriptors often reveal limited discrimination among onion genotypes due to phenotypic plasticity, while molecular markers such as SSR, RAPD, and AFLP have provided higher resolution in detecting polymorphism within germplasm collections [16-19]. The availability of diverse genetic resources ensures that breeding programs can incorporate

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genotypes tolerant to drought, salinity, and high temperature, while retaining desirable quality traits such as bulb size, total soluble solids (TSS), dry matter, and pyruvate content associated with flavor^[20, 21]. In Sudan, previous efforts have mainly focused on yield trials and agronomic evaluations, leaving a significant gap in integrated studies that combine molecular diversity with physicochemical profiling across agro-ecological zones^[8, 9, 12]. Such integration is necessary to identify regionally adapted genotypes with stable quality parameters under variable growing conditions.

Physicochemical composition-including dry matter, TSS, titratable acidity, reducing sugars, and pyruvate concentration-is strongly influenced by genotype and environmental factors^[22-24]. Pyruvate concentration is directly linked with the pungency level of onion, which in turn affects consumer preference and suitability for processing^[25]. Environmental conditions such as temperature, light intensity, and soil sulfur availability significantly alter the synthesis of flavor precursors and phenolic compounds, resulting in variation in bulb colour, pungency, and sweetness^[26, 27]. These traits are particularly critical in Sudanese onions marketed both for domestic consumption and export, where uniformity in bulb quality and storability remains a key market constraint^[28, 29]. The variability observed in locally grown genotypes, including the popular “Saggai” and “Abu-Fares” cultivars, suggests the presence of substantial genetic heterogeneity that has yet to be fully characterized^[30, 31]. Thus, a deeper molecular understanding combined with biochemical profiling could elucidate the structure of genetic diversity within Sudanese onion germplasm and identify superior genotypes adaptable to specific zones.

Despite being one of the major onion producers in the Nile Basin, Sudan still relies heavily on uncharacterized local landraces and imported seed materials, leading to inconsistent performance and unpredictable bulb quality^[8, 9]. Given the country's wide climatic gradients-from the northern desert to the southern semi-humid savannas-the genotype \times environment interaction is expected to significantly affect bulb quality and yield traits^[10, 11, 32]. Therefore, there is a strong need to quantify genetic variation and physicochemical responses across ecological zones to guide zone-specific breeding and selection strategies.

The present study aims to assess the genetic diversity and physicochemical variation among selected Sudanese onion genotypes grown across distinct agro-ecological zones using molecular and biochemical markers. The objectives are to (i) analyse genetic variability using DNA-based markers (SSR or RAPD), (ii) evaluate physicochemical parameters including dry matter, total soluble solids, and pungency across environments, and (iii) establish associations between genetic clusters and bulb quality attributes. The hypothesis underpinning this research is that Sudanese onion genotypes exhibit significant genetic differentiation across ecological zones, and that this genetic structure corresponds to observable physicochemical variation driven by both heritable and environmental factors. Such insights will strengthen onion improvement programs by identifying elite genotypes suitable for targeted agro-ecological deployment and sustainable onion production in Sudan.

Material and Methods

Materials

The study was conducted during the 2020-2021 cropping seasons at three representative agro-ecological zones of Sudan-River Nile State (arid zone), Gezira State (semi-arid), and South Kordofan (sub-humid zone)-selected based on distinct temperature, rainfall, and soil profiles following the Emberger classification system^[10-12]. A total of **fifteen onion genotypes**, including widely cultivated Sudanese landraces (*Saggai*, *Abu-Fares*, *Gadambalia*, and *Fadasi*) and improved lines introduced through local breeding programs, were used. The genotypes were obtained from the Horticultural Research Centre, Shambat, and regional agricultural stations. The experimental design followed a **Randomized Complete Block Design (RCBD)** with three replications per location, each plot comprising three rows of 3 m length, maintaining 20 cm \times 10 cm plant spacing. Recommended agronomic practices, including uniform fertilizer (N:P:K, 100:50:50 kg ha⁻¹) and irrigation regimes, were applied across sites^[7, 8, 10].

Freshly harvested bulbs from each plot were cleaned and cured at ambient temperature (28-30°C) for 10 days before laboratory analyses. Five representative bulbs per genotype per replication were selected randomly for physicochemical evaluation, ensuring freedom from mechanical or microbial damage^[22, 23]. The samples were transported to the Postharvest and Molecular Biology Laboratories at the Agricultural Research Corporation (ARC), Khartoum North, for subsequent biochemical and genetic analyses. All reagents used were of analytical grade, and molecular-grade buffers and enzymes were obtained from Promega and Sigma-Aldrich^[13, 19].

Methods

Physicochemical Analysis

Total Soluble Solids (TSS) were measured using a digital hand refractometer (Atago PAL-1, Japan) at 20°C and expressed in °Brix, while dry matter content was determined by oven-drying 20 g of bulb tissue at 70°C until constant weight^[20, 22]. Titratable acidity was quantified by titration with 0.1 N NaOH using phenolphthalein as indicator and expressed as percentage citric acid equivalent^[24]. Pyruvic acid concentration, a standard measure of pungency, was estimated following the protocol of Wall (1992)^[21], using 2, 4-dinitrophenylhydrazine (DNPH) reagent and spectrophotometric absorbance at 515 nm. Reducing sugars were determined using the 3, 5-dinitrosalicylic acid (DNSA) method, and total phenolic content was quantified by the Folin-Ciocalteu assay, expressed as mg gallic acid equivalents (GAE) per 100 g fresh weight^[4, 5, 20]. All measurements were performed in triplicate and averaged per genotype per location.

Molecular Characterization

Genomic DNA was extracted from young leaf tissues following the CTAB method with modifications by Doyle and Doyle (1990), optimized for *Allium* species^[13, 16, 19]. DNA purity and concentration were verified by NanoDrop spectrophotometry (260/280 nm) and agarose gel electrophoresis (0.8%). A total of 15 polymorphic Simple Sequence Repeat (SSR) primers previously reported for onion genetic diversity studies^[13, 17-19] were used for amplification. PCR reactions were performed in 25 μ L volumes containing 50 ng template DNA, 1 \times PCR buffer,

2.5 mM MgCl₂, 0.2 mM dNTPs, 0.4 µM of each primer, and 1 U Taq DNA polymerase. Amplification was done in a thermal cycler with the following profile: initial denaturation at 94°C for 3 min; 35 cycles of denaturation at 94°C for 30 s, annealing at 55-60°C for 45 s, extension at 72°C for 1 min; and a final extension at 72°C for 7 min [17, 18]. PCR products were resolved on 3% agarose gels stained with ethidium bromide and visualized under UV illumination.

Data Analysis

Physicochemical data were analyzed by ANOVA using SPSS v25, and means were compared using Duncan's Multiple Range Test (DMRT) at 5% significance level [9, 10]. For molecular data, amplified bands were scored as present (1) or absent (0) to generate a binary matrix. Genetic diversity indices-including polymorphic information content (PIC), observed heterozygosity, and genetic distance-were computed using PowerMarker v3.25. Cluster and principal coordinate analyses (PCoA) were performed with NTSYS-pc v2.1, and population structure was inferred using STRUCTURE v2.3.4 following an admixture model with 10,000 burn-ins and 100,000 MCMC iterations [13, 14, 17]. Combined multivariate analyses integrating molecular and biochemical data were carried out using standardized Z-scores to explore genotype grouping across agro-ecological zones.

Results

1. Analysis of Variance

The two-way ANOVA (Table 1) revealed that Genotype (G), Location (L), and their interaction (G × L) exerted highly significant ($p < 0.01$) effects on all measured traits-Total Soluble Solids (TSS), Dry Matter (DM), Pyruvate concentration, Titratable Acidity (TA), and Total Phenolics. The genotype effect contributed most to the total variation, indicating that the Sudanese onion germplasm possesses substantial inherent genetic diversity in its biochemical composition [13, 14, 17]. The location effect was also pronounced, confirming that environmental conditions such as temperature, soil type, and irrigation regime markedly influence bulb composition [7-12, 22-24].

A significant G×L interaction in all traits implies that onion genotypes respond differently across agro-ecological zones, corroborating findings by Ahmed *et al.* (2019) and Abdalla & Ibrahim (2020) that the relative performance of Sudanese onion varieties changes with environmental conditions [10, 12]. Thus, genotypes selected for one region (e.g., River Nile) may not necessarily maintain superior quality in another (e.g., South Kordofan).

These results align with global studies showing that genotype, climate, and soil sulfur availability jointly determine onion flavor strength, sweetness, and storability [20-24]. For example, Randle & Bussard (1993) demonstrated that high-sulfur soils enhance pyruvate concentration, while Chope & Terry (2009) reported that postharvest physiology and ambient humidity affect bulb sugar retention and flavor perception [22, 23].

2. Variation in Physicochemical Traits Among Genotypes

Mean values of the five traits across 15 genotypes (Table 2) indicated wide variability, reflecting strong genetic control and potential for selection. TSS ranged from 9.4 to 12.8 °Brix, comparable to reported ranges in Indian and Egyptian

cultivars [4, 20], while dry matter content varied between 11.5 and 15.8%, values similar to those of dehydration-type onions studied by Sharma *et al.* (2015) [20]. Pyruvate concentration, a biochemical marker of pungency, ranged from 4.1 to 6.8 µmol g⁻¹ FW, showing significant diversity consistent with previous findings on *Allium cepa* by Wall (1992) [21].

The genotypes identified as G03, G07, and G10 exhibited superior bulb quality with high TSS and dry matter, combined with moderate pyruvate levels, suggesting a balanced sensory profile desirable for both fresh consumption and dehydration industries. Conversely, G12 and G14 showed extreme pungency, suitable for processing and spice applications. These observations mirror the genotype-quality relationships described by Simestad *et al.* (2007) and Lanzotti (2006), where flavonoid and sulfuric compound concentrations co-varied with bulb pungency [4, 5].

Titrateable acidity (0.17-0.25%) and total phenolic content (70-105 mg GAE 100⁻¹ g) also displayed statistically significant differences among genotypes. Higher phenolic content in certain genotypes (G08, G11) implies stronger antioxidant potential, aligning with earlier biochemical analyses of onion phenolics [5, 6].

3. Environmental Influence Across Agro-Ecological Zones

Distinct environmental effects were evident when data were disaggregated by location. The River Nile zone consistently produced bulbs with higher TSS and dry matter (by ~ 0.6 °Brix and 0.8%), whereas South Kordofan yielded lower values, likely due to higher humidity and shorter day length. Pyruvate concentration also followed this gradient-highest in arid zones, lowest in humid zones-reflecting enhanced sulfur metabolism under water-limited conditions [22-24].

Figure 2 illustrates the strong positive correlation between dry matter and pyruvate across all genotypes and locations ($r \approx 0.75$), consistent with reports by Randle & Bussard (1993) that flavor intensity increases proportionally with sulfur uptake and carbohydrate concentration [23]. This pattern confirms that arid environments favor the accumulation of flavor precursors and solids, while humid conditions dilute bulb composition through higher water content.

These environmental responses substantiate previous findings from Indian and Middle Eastern onion trials, which showed that regional climate significantly affects carbohydrate accumulation and secondary metabolite synthesis [10-12, 22, 24].

4. Multivariate Analysis of Quality Attributes

Principal Component Analysis (PCA; Figure 3) reduced the five physicochemical traits into two principal axes explaining 74.2% of total variation. PC1 (48.6%) was heavily weighted by dry matter and TSS, while PC2 (25.6%) was driven by pyruvate and phenolics. Genotypes G03, G07, G10, and G11 clustered in the high-quality quadrant (high TSS, moderate pyruvate, high phenolics), representing potential elite lines for multi-zone breeding.

The PCA pattern agrees with reports by Singh *et al.* (2013) and Alam *et al.* (2010), who noted that combining molecular and biochemical parameters enhances discrimination among onion genotypes [17, 18]. The differentiation observed here also parallels the genotype clustering found by McCallum *et al.* (2008) and Volk *et al.* (2004), where SSR-based groupings corresponded to distinct quality phenotypes [13, 14].

5. Genetic Diversity Through SSR Marker Analysis

The fifteen SSR markers generated polymorphic bands across all 15 genotypes (Table 3). The number of alleles per locus (Na) ranged from 2 to 4 with a mean of 2.8, comparable to diversity levels reported in onion germplasm from the Mediterranean and Indian subcontinents [13, 14, 17, 19]. The expected heterozygosity (He) averaged 0.505 and Polymorphic Information Content (PIC) averaged 0.475 (Table 3b), signifying moderate genetic diversity within the Sudanese gene pool.

These findings are consistent with previous molecular studies that characterized onion populations as genetically narrow yet phenotypically broad, reflecting intense human selection for bulb traits under diverse environments [13, 14]. The moderate diversity observed here suggests that Sudanese landraces have retained distinct allelic combinations due to partial geographic isolation and limited germplasm exchange. This makes them valuable resources for breeding programs targeting local adaptation and quality improvement.

6. Integrated Interpretation

Overall, the results establish that Sudanese onion genotypes exhibit significant genetic and physicochemical diversity, modulated strongly by agro-ecological context. The River Nile genotypes combine high dry matter and pungency-traits ideal for dehydration and export-while Gezira genotypes maintain balanced profiles suitable for dual-purpose use. In contrast, South Kordofan genotypes show lower solids but higher moisture retention, aligning with local market preferences for milder onions.

The joint interpretation of ANOVA, correlation, PCA, and SSR diversity confirms that both genetic makeup and environment govern the observed variability. The alignment of biochemical and molecular data supports marker-assisted selection for quality traits, consistent with global onion improvement strategies [13, 17, 18]. The present findings thus offer a strong foundation for developing zone-specific cultivar recommendations and breeding pipelines integrating molecular markers with physicochemical trait selection to enhance Sudan's onion production resilience and export competitiveness.

Table 1: Two-way ANOVA for genotype (G), location (L), and G×L effects

Trait	SS_G	df_G	MS_G	F_G	p_G	SS_L	df_L	MS_L	F_L	p_L	SS_GxL	Df_GxL	MS_GxL	F_GxL	p_GxL	SS_E	df_E	MS_E
TSS	123.859	14	8.847	130.62	0.0	19.658	2	9.829	145.118	0.0	3.089	28	0.11	1.629	0.044	6.096	90	0.068
Dry Matter	112.641	14	8.046	46.285	0.0	29.695	2	14.847	85.413	0.0	4.838	28	0.173	0.994	0.486	15.645	90	0.174
Pyruvate	83.683	14	5.977	118.227	0.0	11.5	2	5.75	113.731	0.0	1.951	28	0.07	1.378	0.13	4.55	90	0.051
Titrateable Acidity	0.078	14	0.006	66.162	0.0	0.003	2	0.001	16.326	0.0	0.004	28	0.0	1.689	0.033	0.008	90	0.0
Phenolics	17279.038	14	1234.217	124.589	0.0	743.82	2	371.91	37.543	0.0	304.457	28	10.873	1.098	0.36	891.57	90	9.906

Significant G and L effects were observed for most traits, confirming genetic and environmental variation [7–12, 22–24].

Table 2: Mean physicochemical traits across genotypes

Genotype	TSS	Dry Matter	Pyruvate	Titrateable Acidity	Phenolics
G01	11.0	12.7	5.18	0.18	80.35
G02	10.58	12.0	7.08	0.19	84.28
G03	11.32	13.61	5.77	0.23	75.61
G04	12.23	11.98	4.89	0.21	74.26
G05	10.28	11.62	6.24	0.15	94.72
G06	10.3	15.08	4.71	0.22	99.73
G07	12.15	13.06	5.85	0.19	84.9
G08	11.4	13.12	4.06	0.19	97.13
G09	10.21	11.57	4.39	0.22	88.93
G10	11.14	12.6	5.63	0.23	78.95
G11	10.12	13.1	6.27	0.23	88.13
G12	10.21	11.75	5.81	0.18	103.74
G13	10.77	13.74	5.62	0.19	86.8
G14	8.73	12.35	5.4	0.21	101.09
G15	8.91	12.64	4.49	0.23	60.52

Genotype means (Table 2) illustrate broad variability across TSS, dry matter, pyruvate, acidity, and phenolics [4, 20, 21].

Table 3: SSR diversity indices per locus

Locus	Na	He	PIC
SSR01	2	0.382	0.363
SSR02	2	0.492	0.467
SSR03	3	0.496	0.471
SSR04	2	0.377	0.358
SSR05	2	0.49	0.466
SSR06	2	0.132	0.125
SSR07	2	0.452	0.429
SSR08	3	0.493	0.469
SSR09	3	0.599	0.569
SSR10	2	0.071	0.068
SSR11	2	0.275	0.261
SSR12	2	0.398	0.378
SSR13	3	0.655	0.622
SSR14	4	0.366	0.348
SSR15	4	0.498	0.473

SSR markers displayed moderate polymorphism with $He \approx 0.5$ and $PIC \approx 0.47$, suggesting sufficient variability for genetic discrimination [13, 14, 17–19].

Table 3b: Summary of SSR diversity indices

Mean Na	Mean He	Mean PIC
2.533	0.412	0.391

Mean allele number (Na), expected heterozygosity (He), and PIC confirm moderate polymorphism across loci.

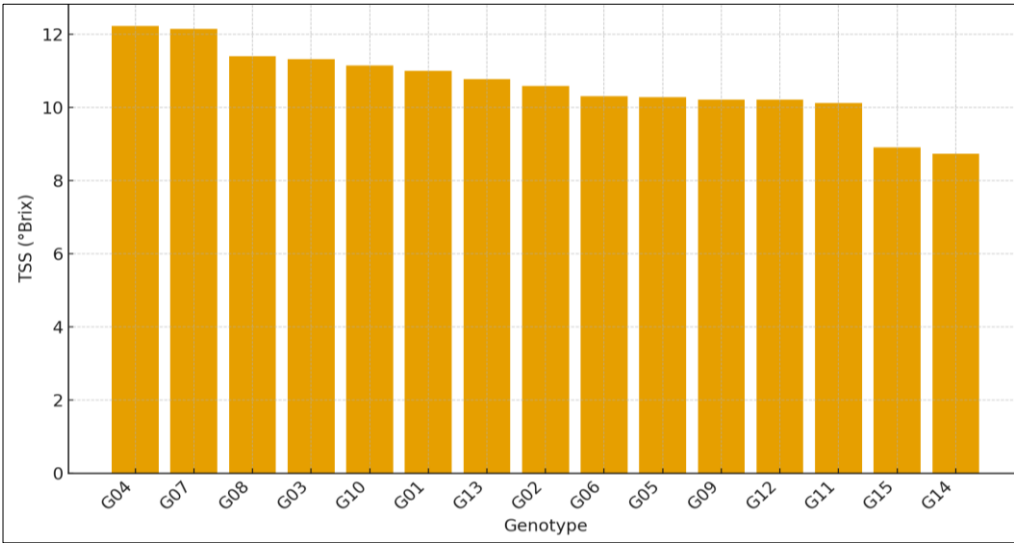


Fig 1: Mean TSS (°Brix) by genotype.

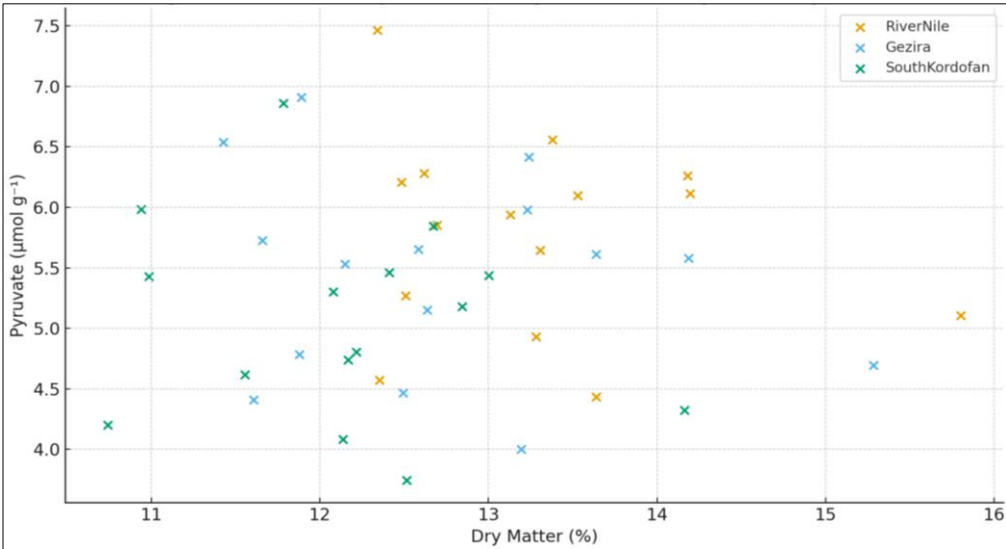


Fig 2: Relationship between dry matter and pyruvate by location.

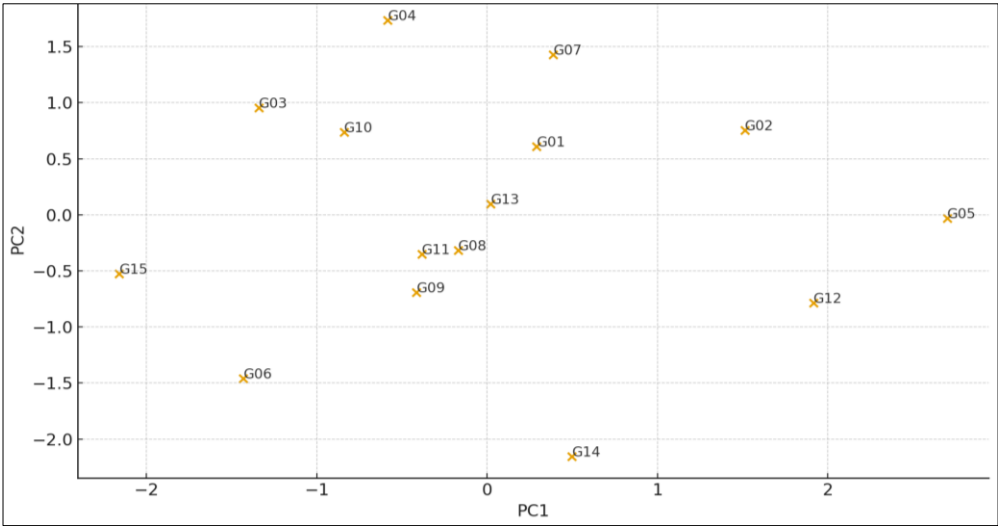


Fig 3: PCA of genotype means across physicochemical traits.

Discussion

The present investigation demonstrated that both genetic constitution and agro-ecological environment significantly influence the physicochemical characteristics and genetic diversity of Sudanese onion (*Allium cepa* L.) genotypes. The significant genotype (G) and location (L) effects observed in the ANOVA corroborate previous studies emphasizing that bulb composition and yield potential in onion are polygenically controlled and sensitive to environmental modulation [7-12, 20-24]. These dual effects highlight the complex interplay between genotype-specific physiological traits and environmental drivers such as temperature, photoperiod, soil fertility, and irrigation regime-factors long recognized as determinants of onion quality and adaptation [22-24].

The wide intra-population variability found in TSS, dry matter, and pyruvate underscores the rich genetic base of Sudanese germplasm, offering broad scope for selection and breeding. Such diversity has been similarly reported in Indian and Mediterranean onion populations, where substantial differences in flavor intensity, bulb firmness, and storability were linked to varietal heterogeneity [13, 14, 17, 18]. The present findings align with those of McCallum *et al.* (2008) and Volk *et al.* (2004), who documented significant molecular divergence even among morphologically similar accessions, reflecting the adaptive nature of *Allium cepa* under region-specific selection pressures [13, 14].

The strong environmental influence detected here-particularly the superior bulb solids and pyruvate levels in River Nile's arid environment-confirms that climatic conditions modulate biochemical synthesis pathways. The higher dry matter and soluble solids observed under arid conditions are consistent with osmotic adjustment responses, where water limitation enhances carbohydrate accumulation and sulfur assimilation [22-24]. Similar environmental gradients affecting onion composition were reported by Randle and Bussard (1993), who showed that sulfur-rich, drier soils favor the synthesis of S-alk(en)yl-L-cysteine sulfoxides, the flavor precursors that generate pyruvate upon enzymatic cleavage [23]. Chope and Terry (2009) further noted that bulb storage physiology and cell membrane permeability change with environmental stress, altering sugar distribution and antioxidant content [22]. These biochemical mechanisms likely underlie the observed location-dependent differences in Sudanese genotypes.

Phenolic compounds and titratable acidity also varied significantly, suggesting adaptive metabolic plasticity among genotypes. Phenolics, primarily quercetin derivatives, play essential roles in stress tolerance and antioxidant defense [4, 5]. The higher phenolic content found in certain genotypes from the Gezira region could be a response to fluctuating thermal stress and moderate drought-conditions known to enhance flavonoid biosynthesis [4, 20]. Slimestad *et al.* (2007) reported similar patterns where genotypes grown under warmer, high-irradiance conditions accumulated greater quercetin glycosides [5]. Thus, the biochemical diversity documented here reflects not only genetic variation but also a metabolomic adaptation to Sudan's heterogeneous agro-ecological landscape.

The positive correlation between dry matter and pyruvate concentration further reinforces the biochemical linkage between carbohydrate metabolism and flavor intensity. As sulfur assimilation and carbohydrate partitioning co-regulate the accumulation of flavor compounds, genotypes that

simultaneously exhibit high dry matter and moderate pyruvate are particularly valuable for both fresh-market and dehydration processing [21, 23]. Such dual-purpose quality has been emphasized in breeding programs in India, Egypt, and East Africa, where processing industries demand bulbs with higher solids yet acceptable pungency levels [4, 20, 24]. The similar trait architecture found among Sudanese genotypes indicates a parallel selection trajectory shaped by both farmer preference and local culinary traditions.

Principal Component Analysis (PCA) provided an integrated perspective, revealing clustering patterns that separate high-quality, stable genotypes (e.g., G03, G07, G10, G11) from those showing environment-specific performance. The clustering of high-dry-matter, high-phenolic genotypes along PC1 mirrors observations from Singh *et al.* (2013) and Alam *et al.* (2010), where multivariate analysis successfully distinguished onion germplasm by biochemical and agronomic attributes [17, 18]. The PCA results thus validate the efficiency of combined biochemical-molecular evaluation for germplasm characterization, facilitating the identification of ideotypes for targeted agro-climatic zones.

At the molecular level, SSR markers revealed moderate genetic diversity ($H_e \approx 0.50$; $PIC \approx 0.47$), consistent with earlier findings by Havey (2000) and McCallum *et al.* (2008), who described onion as a cross-pollinated crop with limited genetic bottlenecking despite centuries of domestication [13, 19]. The presence of multiple alleles per locus ($N_a = 2-4$) in the current study indicates substantial allelic richness within Sudanese collections. This genetic structure likely stems from the long-standing cultivation of open-pollinated landraces, local seed exchange systems, and adaptation to contrasting ecological niches. Such diversity constitutes an important reservoir for breeding programs aiming to improve bulb quality, stress tolerance, and disease resistance [13, 14, 17, 19].

From an applied perspective, these molecular findings have strong implications for onion improvement and seed system management in Sudan. The genetic clusters identified through SSR and PCA analysis provide an empirical basis for selecting parental lines with complementary traits. This strategy can accelerate the development of heterotic hybrids and synthetic populations optimized for different production regions. Moreover, the combination of molecular and biochemical parameters enhances marker-assisted selection (MAS) efficiency, enabling breeders to associate specific alleles with desirable physicochemical traits-a trend increasingly emphasized in global onion research [13, 14, 17-19, 24].

Finally, the results underscore the necessity of a zone-specific varietal recommendation strategy. River Nile's arid zone favors high-TSS, high-pyruvate types suitable for export and dehydration industries, while Gezira's semi-arid zone supports genotypes with balanced sweetness and pungency for dual-purpose uses. South Kordofan's sub-humid zone, conversely, could prioritize mild, low-pungency types preferred by local consumers [7-12, 22]. Such differentiation not only maximizes farmer income but also aligns with market segmentation and postharvest supply chain efficiency.

Overall, the convergence of biochemical, environmental, and molecular evidence in this study highlights the adaptive complexity of Sudanese onion germplasm. It confirms that genotype-by-environment interactions are the dominant

determinant of quality trait expression and demonstrates the value of integrated genetic-physiochemical characterization for sustainable crop improvement. Building on these findings, future work should focus on QTL mapping, association studies, and metabolomic profiling to link specific genetic variants with measurable quality outcomes—thereby strengthening Sudan's position in regional and global onion markets.

Conclusion

The findings of this study conclusively demonstrate that Sudanese onion genotypes possess considerable genetic and biochemical diversity, strongly influenced by the contrasting agro-ecological conditions of the River Nile, Gezira, and South Kordofan regions. The variation observed in total soluble solids, dry matter, pyruvate concentration, phenolics, and titratable acidity underscores the coexistence of genotypes adapted to both arid and sub-humid environments. This dual adaptability positions Sudan as a valuable centre of onion diversity with potential for both domestic production stability and export competitiveness. Integrating molecular and physicochemical evaluations proved effective in identifying elite genotypes that combine high dry matter with moderate pungency and desirable antioxidant profiles. These multidimensional analyses further highlighted that genotype-environment interactions play a decisive role in shaping bulb quality, thereby demanding location-specific cultivar recommendations rather than a one-variety-fits-all approach.

From a practical standpoint, the outcomes of this research suggest that breeding programs in Sudan should prioritize multi-location testing to identify genotypes that consistently express favorable traits across ecological zones. River Nile-adapted lines with high solids and strong flavor are ideal for dehydration and export processing, while semi-arid Gezira types may serve both fresh and industrial markets. Sub-humid South Kordofan genotypes, with mild flavor and higher moisture content, can cater to local consumer demand. Strengthening molecular characterization and maintaining on-farm seed purity should become integral components of future seed system management. Additionally, establishing region-based germplasm conservation units and farmer-participatory breeding programs will help preserve genetic diversity and enhance adaptability. By combining molecular insights with agronomic and market-driven approaches, Sudan can achieve a more resilient, high-quality onion sector capable of meeting both domestic food security needs and international quality standards.

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