



Phenotypic Differentiation Reveals High Diversity in Moroccan Grapevine (*Vitis vinifera* L.) Germplasm Based on Agro-morphological, Colorimetric, and Physicochemical Traits

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ARTICLE INFO

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ABSTRACT

Article history:

Received: 1 October 2025,

Received in revised form: 13 November 2025,

Accepted: 6 January 2026,

Article type:

Research paper

Keywords:

Agro-morphological traits,
Colorimetric traits,
Germplasm characterization,
Morocco,
Physicochemical composition,
Vitis vinifera L.

This study evaluated the agro-morphological, colorimetric, and physicochemical diversity of 62 grapevine cultivars from the INRA collection in Ain Taoujdate, Morocco, with the aim of supporting germplasm conservation and breeding strategies. Standardized field and laboratory assessments were conducted over two consecutive seasons (2023–2024), and the resulting data were analyzed using ANOVA, MANOVA, principal component analysis (PCA), and cluster analysis. Significant differences ($P < 0.001$) were detected among cultivars for all measured traits. Coefficients of variation ranged from 5.72% for pH to 87.34% for yield per vine, demonstrating substantial phenotypic variability. Berry- and bunch-related traits exhibited the greatest variation, whereas several physicochemical parameters were strongly influenced by seasonal effects. Broad-sense heritability (H^2) estimates ranged from 0.54 to 0.99, with the highest values observed for berry weight, seed number, and hue angle, indicating strong genetic control over these traits. Cluster analysis classified the cultivars into four main groups, while PCA accounted for 50.74% of the total variability. Fruit size, seed characteristics, color indices (L^* , C^* , H^*), and maturity index emerged as the most discriminating variables. The diversity observed, including both seeded and seedless genotypes, as well as a broad spectrum of berry color and sweetness levels, highlights the rich genetic foundation of Moroccan grapevine germplasm. Collectively, these findings offer valuable guidance for the identification and selection of superior cultivars and support targeted breeding programs aimed at improving productivity, fruit quality, and resilience in Mediterranean viticulture.

Introduction

Grapevine (*Vitis vinifera* L.) is a major fruit crop of immense agricultural and economic importance. Its domestication, which occurred approximately 6,000–8,000 years ago in the Near East, represented a pivotal event in human history and marked a turning point in civilization due to its profound cultural and economic impact (McGovern, 2013).

Over millennia, grapevine cultivation spread throughout Europe, North Africa, and Asia along established trade routes, facilitating the diversification of cultivated varieties (Forni, 2012; De Lorenzis et al., 2015; Vignani et al., 2024). During Roman times, viticulture was further

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developed in North African provinces, including the fertile plains and valleys of northern Morocco.

Today, Morocco produces approximately 320,000 t of grapes, ranking as the world's 31st largest producer (FAOSTAT, 2024). The country possesses a rich vine heritage composed of diverse indigenous grape varieties adapted to contrasting agroclimatic conditions. This genetic reservoir, shaped by centuries of natural selection and sustained human management, holds considerable agronomic, economic, and cultural value. However, Moroccan viticulture currently faces multiple challenges, including the homogenization of cultivated material, the widespread introduction of foreign varieties, the abandonment of traditional agricultural practices, and the increasing impact of climate change. In addition, the excessive use of phytosanitary products threatens the sustainability of viticulture by adversely affecting the environment and reducing soil biodiversity (Aoujil et al., 2024; Cobelli et al., 2025). Preserving Morocco's grapevine genetic resources has therefore become both a national and scientific priority.

To address this need, a grapevine germplasm collection was established at the experimental station of Ain Taoujdate in Meknes, which is now considered the primary organized grape genetic resource in Morocco. Recent molecular analyses of this collection revealed substantial genetic diversity and provided a foundation for the effective utilization of local cultivars (Zinelabidine et al., 2024). Complementary studies conducted in other Mediterranean regions, including Lebanon, Galicia, and Tuscany, similarly emphasized the importance of integrating molecular and phenotypic data to improve germplasm management and breeding strategies (Díaz-Fernández et al., 2024; Zombardo et al., 2024; Merheb et al., 2025).

Morphological characterization, cultivar identification, and pathotype differentiation within *Vitis* are essential for cultivar classification, resistance breeding, and marketing. Ampelometry, which enables the quantitative discrimination of leaf shape and size, remains a robust method for cultivar identification and can be effectively combined with genetic data (Atak, 2012; Salimov et al., 2015; Bodor-Pesti et al., 2023). Complementary pomological characterization, based on bunch and berry traits, provides additional phenotypic markers. Qualitative traits—such as fruit shape, size, color, and seed number—are particularly important for distinguishing stable varieties and determining their intended use (Vafaei et al., 2017; Abiri et al., 2020). Furthermore, fruit quality attributes, including pH, titratable acidity, and total soluble solids, serve as critical biochemical markers that reflect the internal characteristics of berries and provide insight into ripeness, flavor development, and overall quality. These traits are especially valuable for classifying

grapes according to their end use (Gaštol, 2015; Kazemi et al., 2024).

Despite advances in molecular characterization, the absence of large-scale agro-morphological and biochemical data for Moroccan grapevine germplasm remains a significant limitation. This gap restricts a comprehensive understanding of phenotypic variability and the agronomic potential of local cultivars. Accordingly, this study aimed to evaluate the phenotypic variability of 62 grapevine cultivars, encompassing both local and introduced genotypes, through the assessment of agro-morphological traits, berry skin color, and physicochemical composition. The objectives were to characterize and describe the cultivars, identify key traits for their differentiation, and assess overall phenotypic diversity in order to support the conservation and effective utilization of Moroccan grapevine germplasm. By integrating phenotypic evaluations with existing genetic knowledge, the findings provide deeper insight into trait variability and contribute to the development of marker-assisted breeding strategies aimed at enhancing agronomic performance and long-term sustainability.

Materials and Methods

Plant materials and experimental design

The study was conducted over two consecutive growing seasons (2023 and 2024). Yield, pomological traits, and fruit quality were evaluated for 62 grape cultivars (*Vitis vinifera* L.; Table 1) at the experimental vineyard collection of the National Agricultural Research Institute of Morocco (INRA), located in Ain Taoujdate, Sais Plain (latitude: 33.65°N, longitude: 6.74°W; altitude: 480 m) (Fig. 1). The region is characterized by a semi-arid climate, with high mean temperatures and mild winters. The soil exhibits a sandy-clay texture (46.59% sand, 42.1% clay, and 10.09% silt) and contains 2.5% organic matter. In the 0–35 cm soil layer, available phosphorus (P_2O_5) and potassium (K_2O) levels were 73.3 and 458.8 ppm, respectively, and electrical conductivity measured 0.10 mS cm^{-1} . The grapevines were ten years old and were grafted onto 1103 Paulsen rootstock. Vines were trained using the Royat cordon system and short-pruned to maintain four to six spurs per vine with two to three buds per spur. A drip irrigation system provided 24 L d^{-1} per vine. The field experiment was arranged in a randomized complete block design (RCBD) with four replicate vines per cultivar; cultivars were randomly assigned to vines to avoid positional bias. Each experimental unit consisted of four vines planted in a single oriented north-south row, with a spacing of 2.5 m within rows and 4 m between rows. Seasonal observations were recorded over the two consecutive growing seasons.

Table 1. Grapevine cultivars with their berry skin color, country of origin, and intended use according to the VIVC database (<https://www.vivc.de/>).

No.	Cultivar name	Berry skin color	Country of origin	Utilization
1	Dattier de Bayrouth	White	Lebanon	Table, wine
2	Ahmer Bouamar	Red	Algeria	Table, wine
3	Esp. N.E	White	Spain	Table, wine
4	ESP.NOA	Black	Spain	Table
5	ESP nobi	White	Spain	Table
6	Muskat Madine	Red	United Kingdom	Table
7	Datal	White	France	Table
8	Danane	White	France	Table
9	Enselia	White	Spain	Table, wine
10	Perlina	White	United Kingdom	Table, wine
11	Tripoli	Rose	Italy	Table
12	sabat kanstantini	Red	Portugal	Table
13	Doukalia	Black	Tunisia	Table
14	Rezouki	Black	Morocco	Table, wine, raisin
15	Diamant noir	Black	Italy	Table
16	Tapperial	Black	Morocco	Table, wine, raisin
17	Oubouhou	Black	Morocco	Table
18	Lual	Black	France	Table
19	Oliviette noir	Black	Hungary	Table, wine
20	Cardinal	Red	United States of America	Table, wine
21	Sultanine Rosée	Rose	Azerbaijan	Table, raisin
22	Sultanine	White	United Kingdom	Table, wine
23	Muskat de Hambourg	Black	United Kingdom	Table, wine
24	Muskat d'Italie	White	Italy	Table, wine
25	Delcia Divapine	White	Italy	Table, wine
26	Maria Prevane	Black	United States of America	Table, wine
27	Teresa de Prevane	Rose	Italy	Table
28	Pause precoce	White	France	Table, wine
29	Ergilluie	White	Greece	Table, wine, raisin
30	Alphonse Lavallée	Black	France	Table, wine, raisin
31	FMH	Black	United States of America	Table
32	Danlas	White	France	Wine
33	FAL	Black	Greece	Table, wine, raisin
34	Alval	Red	-	-
35	DF2	Black	-	-
36	Flame seedles	Red	United States of America	Table
37	Dattier st vallier	White	France	Table, wine
38	Ardona	Black	France	Table, wine
39	Early lardinal	Red	United States of America	Table, wine

40	Christmas	Red	United States of America	Table
41	Glaciere	Red	France	Table
42	Rival	Red	United States of America	Table, wine
43	Gros grain	Black	France	Table, wine, raisin
44	Carrière	White	Italy	Table, wine
45	Red glob	Red	United States of America	Table
46	1S Early supérieur	White	Argentina	Table
47	Chelva	Black	United States of America	Table
48	Danan	White	France	Table
49	Muscat douille	White	Lebanon	Table, wine
50	Ribol	Red	France	Table, wine
51	Chenasan	Black	France	Table, wine
52	Muskat d'Italie A	White	Italy	Table, wine
53	Muskat d'Italie B	White	-	-
54	Thomson	White	Turkey	Table, wine, raisin
55	Rutra	White	Argentina	Table
56	Early supérieur	White	-	-
57	2B Jaamen	White	United States of America	Table
58	2S Aarabia lybie	White	Asia Minor	Table, wine
59	Jaamen	Black	France	Table
60	Reine vigne	White	Hungary	Table, wine
61	Flem des Valliers	Red	Argentina	Table
62	Dabouki	White	Israel	Table, wine

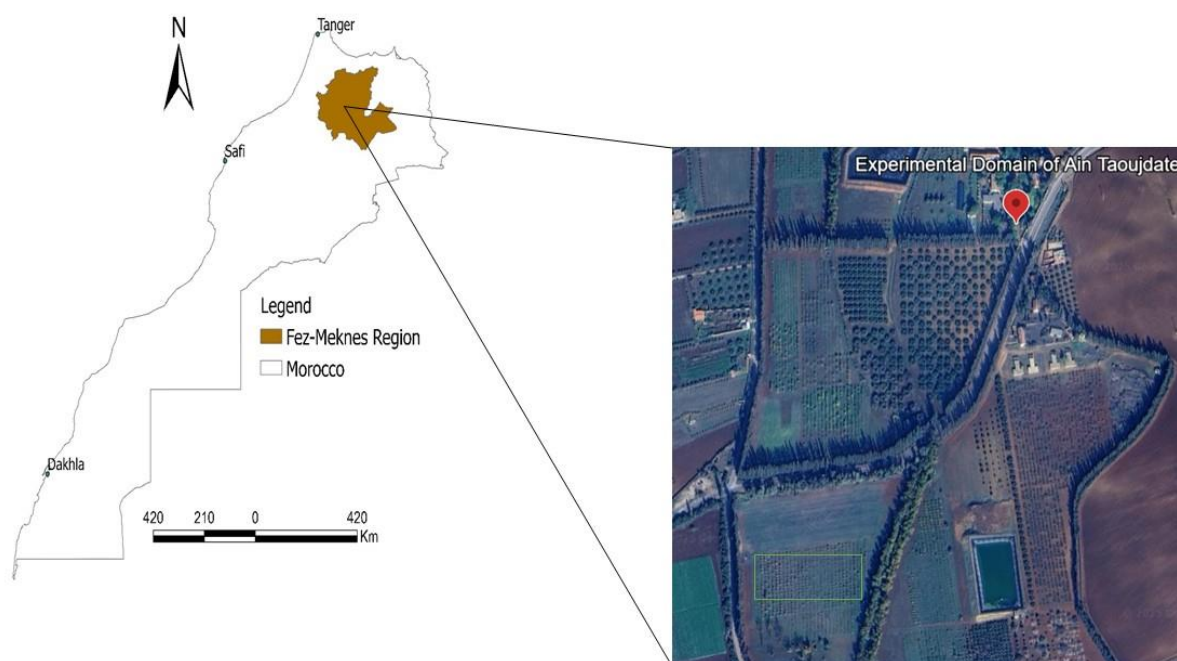


Fig. 1. Geographical location of the experiment site.

Climate data

Meteorological data were obtained from the National Agricultural Research Institute (INRA) weather station, approximately 1 km from the study site. Meteorological parameters, including maximum, minimum, and mean temperatures, as well as precipitation values, were collected for the 2023 and 2024 growing seasons through the official FieldClimate platform, which provides climate data for INRA domains (Table S1).

Agro-morphological and colorimetric evaluations

All measurements were taken on four vines for each cultivar. At harvest, the yield per vine (kg) was determined by measuring the total weight and counting the number of grape clusters per vine. Representative bunches were sampled from each vine (10 bunches per cultivar in total) to measure bunch weight, bunch length, bunch width, peduncle length, and the number of berries. The average berry weight was obtained by weighing a sample of 100 berries per cultivar. Berry dimensions, including length and width, were measured using a digital caliper (DIGITALCALIPER 300 mm; Insize Co. Ltd., China). The number of seeds per berry was counted, and their total weight (g) was recorded. Berry skin color was assessed using a Minolta CR-300 colorimeter (Konica Minolta Sensing Americas Inc., Ramsey, NJ), positioned on the central surface of each berry. Color attributes were recorded using the CIELAB color space parameters: L^* (lightness), a^* (red-green), and b^* (yellow-blue). From these values, the chroma (C^*) and hue angle (H°) were calculated. Ten measurements were taken for each color parameter per cultivar. Additionally, six qualitative traits were evaluated, i.e., cluster compactness, pedicel detachment, berry shape, anthocyanin coloration of the flesh, seed formation, and pulp succulence, using a rating and coding system based on the descriptors provided by IPGRI (1997).

Physicochemical composition

The total soluble solids content (TSS), pH, titratable acidity (TA, g L⁻¹), and maturity index (MI = TSS/TA) were calculated as key indicators of fruit quality. The TSS was measured using a digital refractometer equipped with automatic temperature compensation (Model DR301-95, Krüss Optronic, Germany). Titratable acidity was determined by titrating grape juice with a 0.1 N NaOH solution using a semi-automatic titrator, with the endpoint set at pH 8.2, following the protocol described by IAL (2008). Samples for physicochemical analyses were obtained from berries harvested from each cultivar's four replicate vines.

Statistical analysis

Statistical analyses were performed using R software (version 4.4.2) with appropriate packages for univariate and multivariate analyses. Data from four replicate vines per cultivar were first checked for normality (Shapiro–Wilk test) and for outliers (based on 1.5×IQR rule and Grubb's test) before analysis. Non-normal traits were log- or square-root-transformed to meet the assumptions of parametric tests.

Two-way ANOVA was conducted to evaluate the effects of cultivar (C), season (S), and their interaction ($C \times S$) on each trait, followed by Tukey's HSD test ($P < 0.05$) for mean comparison. Broad-sense heritability (H^2) was estimated from ANOVA variance components to quantify the proportion of phenotypic variation attributable to genetic factors. Additionally, a multivariate analysis of variance (MANOVA) was performed to assess the combined effects of factors across all traits.

Pearson correlation coefficients (r) were calculated to examine pairwise associations among traits, and only significant correlations ($P < 0.05$) were highlighted. Principal component analysis (PCA) was then conducted on standardized data to summarize the overall variability and identify the traits contributing most to cultivar differentiation. The suitability of the dataset for PCA was assessed using Bartlett's test of sphericity and the Kaiser-Meyer-Olkin (KMO) measure of sampling adequacy. Principal components with eigenvalues > 1 were retained, representing over 70% of the total variance.

Hierarchical clustering analysis (HCA) using Ward's method on Euclidean distances was applied to visualize cultivar groupings based on similarity in trait performance. Cluster validation was performed using silhouette coefficients and cophenetic correlation to ensure robustness of the grouping.

Results

Agro-morphological, colorimetric, and physicochemical descriptions

Descriptive statistics for all quantitative traits are presented in Supplementary Table S2. The coefficient of variation (CV) ranged from 5.72% for pH to 87.34% for yield per vine, revealing substantial variability among cultivars. Overall, berry- and bunch-related traits exhibited greater variability than colorimetric or physicochemical traits, reflecting broad phenotypic diversity among genotypes across the two growing seasons.

The univariate ANOVA results (Table 2) further confirmed highly significant differences ($P < 0.001$) among cultivars for all evaluated traits, highlighting a pronounced level of genotypic variability within the collection. Seasonal effects were also significant for most traits, particularly those related to fruit

composition (total soluble solids, pH, and titratable acidity), color parameters (L^* , C^* , and H°), and berry dimensions, indicating a strong influence of environmental conditions on fruit development. In contrast, peduncle length, number of berries per bunch, and seed weight were not significantly affected by season ($P > 0.05$), suggesting greater environmental stability for these traits.

Significant cultivar $\times$ season ($C \times S$) interactions ($P < 0.001$) were detected for all traits, demonstrating differential genotypic responses to environmental variation. Broad-sense heritability (H^2) estimates ranged from 0.54 for bunch width and peduncle length to 0.99 for hue angle (H°). The highest H^2 values were recorded for berry weight (0.936), seed

number (0.929), seed weight (0.898), and hue angle (0.99), indicating strong genetic control and stability across environments. Conversely, lower H^2 values were observed for peduncle length (0.548) and maturity index (0.596), reflecting a greater influence of environmental factors.

The multivariate analysis of variance (MANOVA) revealed highly significant effects ($P < 0.001$) of cultivar, season, and their interaction ($C \times S$) on the overall set of quantitative traits (Table 2). These results indicate marked genetic differentiation among cultivars, while also confirming that seasonal conditions and genotype $\times$ environment interactions contributed substantially to the observed phenotypic variability.

Table 2. Summary of ANOVA and MANOVA (Pillai's trace) results for cultivar, season, and their interaction effects on quantitative traits, with broad-sense heritability (H^2) estimates.

Trait	Cultivar (C)	Season (S)	Interaction C $\times$ S	H^2
Yield per vine	< 0.001	< 0.001	< 0.001	0.669
Bunch weight	< 0.001	0.004	< 0.001	0.685
Bunch length	< 0.001	< 0.001	< 0.001	0.767
Bunch width	< 0.001	< 0.001	< 0.001	0.537
Length of peduncle	< 0.001	0.697	< 0.001	0.548
Number of berries per bunch	< 0.001	0.386	< 0.001	0.79
Berry weight	< 0.001	< 0.001	< 0.001	0.936
Berry length	< 0.001	< 0.001	< 0.001	0.826
Berry width	< 0.001	< 0.001	< 0.001	0.817
Seed count	< 0.001	< 0.001	< 0.001	0.929
Seed weight	< 0.001	0.685	< 0.001	0.898
Lightness (L^*)	< 0.001	< 0.001	< 0.001	0.838
Chroma (C^*)	< 0.001	< 0.001	< 0.001	0.646
Hue angle (H°)	< 0.001	< 0.001	< 0.001	0.99
Total soluble solids	< 0.001	< 0.001	< 0.001	0.777
pH	< 0.001	< 0.001	< 0.001	0.659
Titratable acidity	< 0.001	< 0.001	< 0.001	0.717
Maturity index	< 0.001	< 0.001	< 0.001	0.596
MANOVA	Pillai's trace	11.0961	1.00	5.8382
	P-value	< 0.001	< 0.001	< 0.001

The five most discriminant traits identified by the principal component analysis were bunch weight, berry width, seed weight, lightness (L^*), and maturity index. They exhibited marked variability among the sixteen grapevine cultivars (Table 3). The complete

dataset, including Tukey's groupings for all cultivars and traits, is provided in Table S3 and S4 (Supplementary Material).

Table 3. Average values ($\pm$ SD) of the five most discriminant traits across sixteen grape cultivars.

Cultivar	Bunch weight (g)	Berry width (mm)	Seed weight (g)	Lightness (L*)	Maturity index
Perlina	299.75 $\pm$ 95.43	20.91 $\pm$ 2.39	0.15 $\pm$ 0.05	47.73 $\pm$ 3.7	11.13 $\pm$ 4.45
Rezouki	251.5 $\pm$ 111.36	20.69 $\pm$ 1.79	0.19 $\pm$ 0.07	39.33 $\pm$ 2.6	11.83 $\pm$ 3.36
Diamant noir	244 $\pm$ 78.1	18.64 $\pm$ 0.9	0.14 $\pm$ 0.05	23.3 $\pm$ 8.16	12.11 $\pm$ 3.48
Cardinal	177.79 $\pm$ 37.65	21.92 $\pm$ 1.26	0.13 $\pm$ 0.06	29.35 $\pm$ 2.28	16.14 $\pm$ 5.99
Muskat de Hambourg	227.5 $\pm$ 77.49	14.52 $\pm$ 3.56	0.11 $\pm$ 0.04	30.89 $\pm$ 7.04	13.87 $\pm$ 1.25
Alphonse Lavallée	248.5 $\pm$ 92.3	23.35 $\pm$ 1.68	0.17 $\pm$ 0.04	27.99 $\pm$ 1.54	12.67 $\pm$ 2.14
DF2	98.53 $\pm$ 47.74	10.47 $\pm$ 1.03	0.11 $\pm$ 0.14	29.15 $\pm$ 2.69	10.53 $\pm$ 1.44
Dattier st vallier	295 $\pm$ 125.39	20.53 $\pm$ 3.34	0.2 $\pm$ 0.06	47.53 $\pm$ 7.34	10.05 $\pm$ 2.03
Christmas	417.5 $\pm$ 238.02	22.2 $\pm$ 2.86	0.15 $\pm$ 0.05	35.1 $\pm$ 9.09	11.06 $\pm$ 5.24
1S Early supérieur	181.65 $\pm$ 97.24	17.64 $\pm$ 1.41	0 $\pm$ 0	41.52 $\pm$ 4.68	5.83 $\pm$ 2.97
Danan	530.75 $\pm$ 250.18	21.71 $\pm$ 1.49	0.16 $\pm$ 0.06	42.25 $\pm$ 3.16	7.35 $\pm$ 3.44
Chenasan	293.95 $\pm$ 130.67	14.47 $\pm$ 1.01	0.13 $\pm$ 0.05	36.7 $\pm$ 8.58	8.91 $\pm$ 2.86
Rutra	268 $\pm$ 147.97	18.98 $\pm$ 1.42	0 $\pm$ 0	41.51 $\pm$ 2.31	5.47 $\pm$ 3.69
2B Jaamen	225.79 $\pm$ 83.19	19.02 $\pm$ 0.84	0 $\pm$ 0	47.83 $\pm$ 3.26	12.8 $\pm$ 4.22
Jaamen	130.32 $\pm$ 71.81	16.46 $\pm$ 1.18	0.1 $\pm$ 0.04	34.42 $\pm$ 7.73	9.34 $\pm$ 1.94
Reine vigne	385.5 $\pm$ 133.53	18.95 $\pm$ 1.94	0 $\pm$ 0	41.92 $\pm$ 2.4	6.77 $\pm$ 2.3

Bunch weight exhibited wide variation, ranging from 98.53 $\pm$ 47.74 g in 'DF2' to 530.75 $\pm$ 250.18 g in 'Danan', reflecting marked differences in bunch compactness and productivity potential among cultivars. Berry width also varied substantially, from small-berried cultivars such as 'DF2' (10.47 $\pm$ 1.03 mm) to large-berried cultivars such as 'Alphonse Lavallée' (23.35 $\pm$ 1.68 mm), demonstrating broad morphological diversity within the collection.

Seed weight showed considerable variation. It was null in several seedless cultivars ('1S Early supérieur', 'Rutra', '2B Jaamen', and 'Reine vigne') and reached up to 0.2 g in seeded cultivars such as 'Dattier St vallier'. Color lightness (L*) ranged from 23.3 $\pm$ 8.16 in 'Diamant noir' to 47.83 $\pm$ 3.26 in '2B Jaamen', highlighting clear differences in berry skin pigmentation and anthocyanin accumulation, and distinguishing dark-skinned cultivars from lighter ones.

The maturity index (MI), which reflects the sugar–acid balance, exhibited wide variation, from 5.47 $\pm$ 3.69 in 'Rutra' to 16.14 $\pm$ 5.99 in 'Cardinal'. Higher MI values were generally associated with cultivars

characterized by higher total soluble solids and lower titratable acidity, such as 'Cardinal' and 'Muskat de Hambourg', whereas lower MI values corresponded to cultivars with higher acidity levels, including 'Rutra' and 'Reine vigne'.

Bunch compactness was classified as medium in 30 cultivars, compact in eight, and very compact in one (Table 4). Pedicel detachment was generally easy in most cultivars, favoring table grape handling and postharvest quality. Seven berry shapes were identified: flattened spherical (3 cultivars), spherical (13), narrow ellipsoid (18), broad ellipsoid (20), cylindrical (6), ovoid (1), and arched (1). Flesh anthocyanin coloration was medium in more than 50% of the cultivars, with strong pigmentation observed in 'Muskat de Hambourg', 'FAL', and 'DF2', and very strong pigmentation in 'FMH'. Seed formation was rudimentary in 'Cardinal', 'Pause precoce', and 'Ribol', whereas 48 cultivars produced well-developed seeds and eleven cultivars were seedless. Most cultivars (44) were characterized by juicy pulp, while a few were described as slightly or very slightly juicy.

Table 4. Distribution of cultivars according to qualitative fruit traits.

Trait	Cultivars count (n)						
Compactness	Very loose (6)	Loose (17)	Medium (30)	Compact (8)	Very compact (1)		
Detachment of the pedicel	Difficult (19)	Easy enough (32)	Very easy (11)				
Berry shape	Flattened spherical (3)	Spherical (13)	Narrow ellip psoid (18)	Broad ellip soid (20)	Cylindrical (6)	Ovoid (1)	Arched (1)
Anthocyanin coloration of flesh	Absent or very weak (3)	Weak (21)	Medium (34)	Strong (3)	Very strong (1)		
Formation of seeds	Seedless (11)	Rudimentary (3)	Well-devel oped (48)				
Succulence of the pulp	Very little juicy (2)	A little juicy (16)	Juicy (44)				

Correlations among the studied characteristics

Pearson's correlation heatmap revealed significant associations among agro-morphological,

colorimetric, and physicochemical traits, with particularly strong correlations observed within berry and seed characteristics and among acidity-related parameters (Fig. 2).

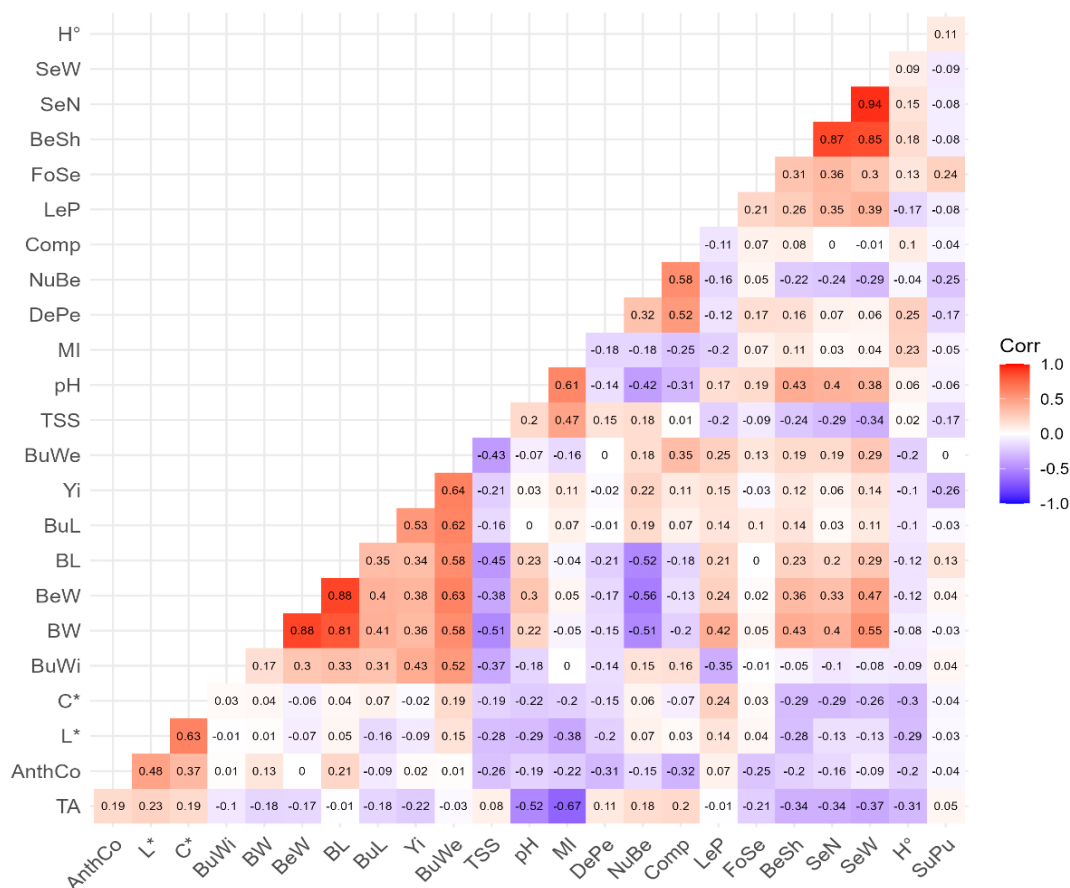


Fig. 2. Pearson's correlation matrix among agro-morphological, colorimetric, and physicochemical traits of grape cultivars. Trait abbreviations: Yi = Yield per vine, BuWe = Bunch weight, BuL = Bunch length, BuWi = Bunch width, LeP = Length of peduncle, NuBe = Number of berries per bunch, BeW = Berry weight, BL = Berry length, BW = Berry width, SeN = Seed number, SeW = Seed weight, Comp = Compactness, DePe = Detachment of the pedicel, BeSh = Berry shape, AnthCo = Anthocyanin coloration of flesh, FoSe = Formation of seeds, SuPu = Succulence of the pulp, TSS = Total soluble solids, TA = Titratable acidity, MI = Maturity index, L* = Lightness, C* = Chroma, H° = Hue angle.

Yield per vine exhibited strong positive correlations with bunch weight ($r = 0.64$), bunch length ($r = 0.53$), and bunch width ($r = 0.43$), indicating that larger and heavier bunches were primary contributors to overall yield. Moderate positive correlations were also observed with berry weight and berry dimensions ($r = 0.34$ – 0.38).

Bunch weight was positively associated with bunch size traits, length and width ($r = 0.52$ – 0.62), and showed moderate correlations with berry-related traits ($r = 0.58$ – 0.63), confirming the interdependence of size- and weight-related parameters in determining productivity. The number of berries per bunch was positively correlated with bunch compactness ($r = 0.58$) but negatively correlated with berry weight and berry size ($r = -0.51$ to -0.56), indicating that cultivars producing a

higher number of berries tended to develop smaller individual berries.

Berry length, width, and weight were strongly interrelated ($r = 0.81$ – 0.88). Seed weight showed a very strong positive correlation with seed number ($r = 0.94$) and a strong correlation with seed formation ($r = 0.85$).

Regarding color parameters, L* was positively correlated with C* ($r = 0.63$) and negatively correlated with hue angle ($r = -0.29$). Among physicochemical traits, pH was strongly and positively associated with maturity index ($r = 0.61$), while titratable acidity was negatively correlated with pH ($r = -0.52$), reflecting the typical decline in acidity during the ripening process.

Principal component analysis

Principal Component Analysis (PCA) was performed based on the correlation matrix to investigate fruit differentiation among cultivars and identify the traits that most strongly contributed to

the observed variability. The contributions of individual traits to the first two principal components (Dim1 and Dim2) are shown in Figure 3. Traits with higher contributions were considered key drivers of variation among cultivars.

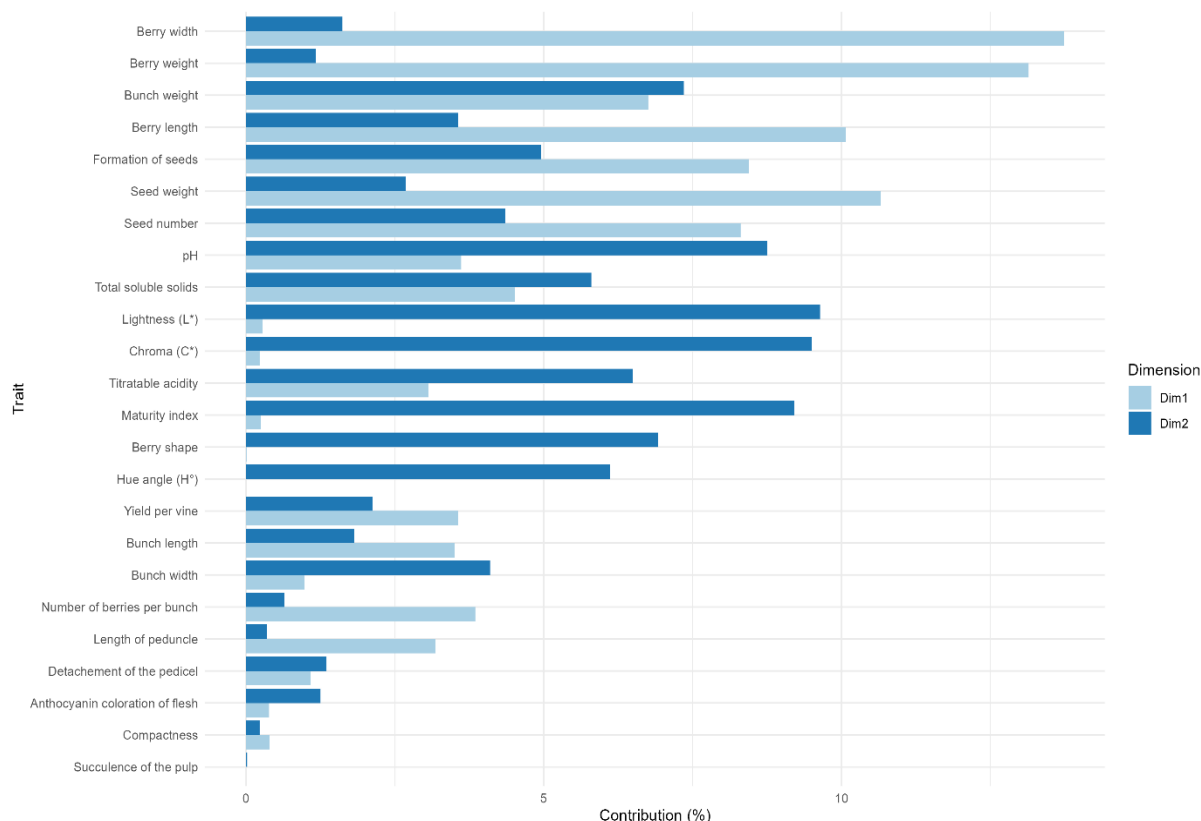


Fig. 3. Contribution of studied traits to the first two principal component axes (Dim1/Dim2).

The first three principal components together explained 50.74% of the total variability, with the first principal component (Dim1) accounting for 23.13% of the variance. This dimension captured the largest share of variation and was primarily associated with size-related traits, including berry and seed morphology (berry length, berry width, berry weight, bunch weight, seed number, seed weight, and seed formation). The second principal component (Dim2) explained 15.77% of the total variance and mainly reflected variability in colorimetric and chemical traits, including L*, C*, maturity index, titrateable acidity, hue angle, and berry shape. In contrast, traits such as pulp succulence, bunch compactness, and flesh anthocyanin coloration contributed minimally to this dimension. Overall, fruit size, color, and maturity-related parameters emerged as the principal drivers

of cultivar differentiation. The scatter plot constructed from the first two principal component axes discriminated the 62 grapevine cultivars according to their agro-morphological, colorimetric, and physicochemical characteristics (Fig. 4). Along the Dim1 axis, cultivars with larger berries, higher sugar content, greater seed presence, and higher pH values, mainly those belonging to the red and yellow groups, were contrasted with cultivars characterized by smaller, seedless, and more acidic berries, which were predominantly grouped within the first cluster. The Dim2 axis was more closely related to characteristics of colorimetric and maturity attributes, distinguishing cultivars with more intense pigmentation and advanced ripening stages, such as those in the yellow group, from lighter-colored cultivars represented in the grey and blue groups.

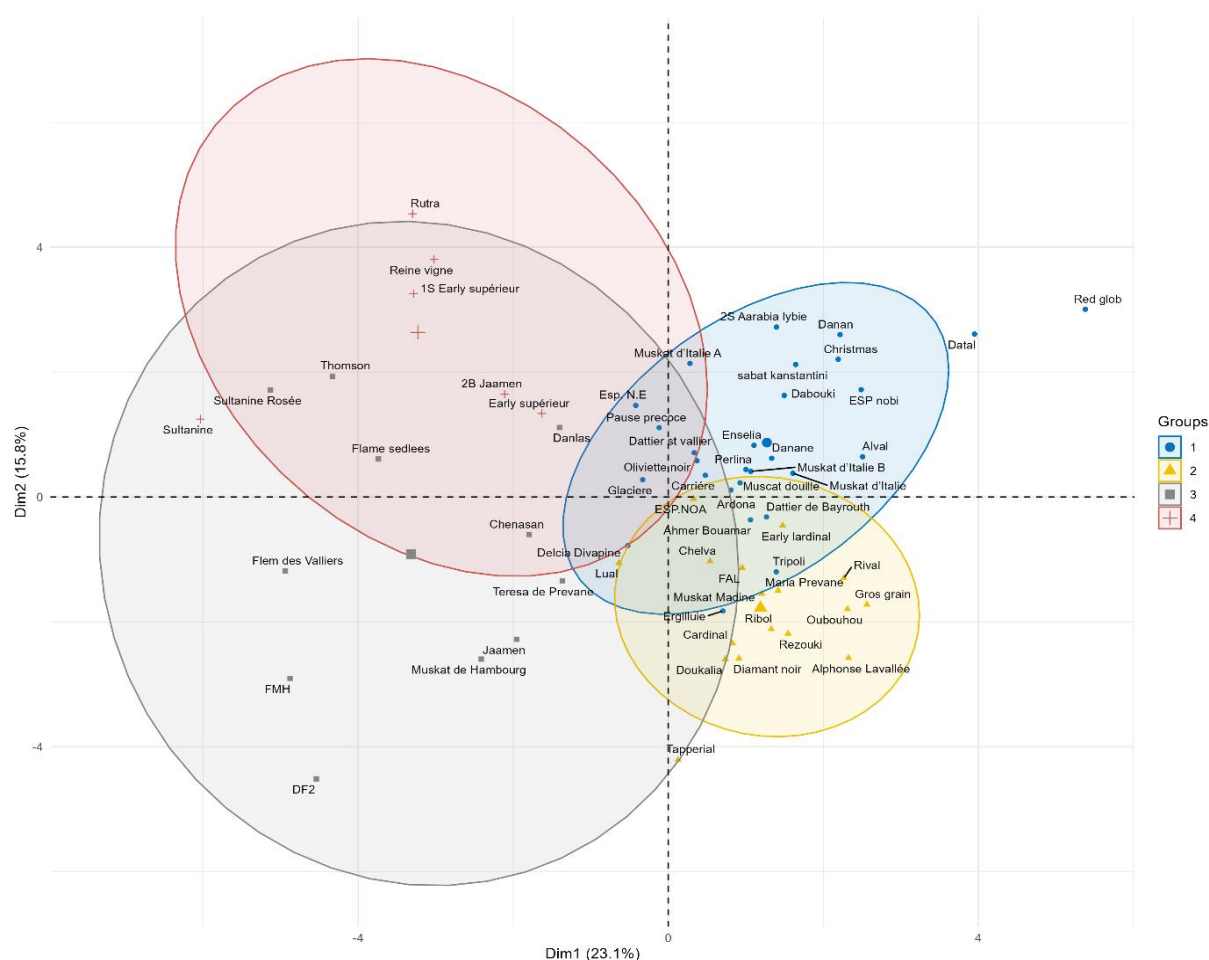


Fig. 4. Scatter-plot for the studied grape collection based on the first two principal components axes (Dim1/Dim2).

Cluster analysis

The hierarchical cluster analysis (UPGMA based on Euclidean distances) grouped the studied grapevine cultivars into four main clusters (Fig. 5), highlighting the diversity and phenotypic relationships among the genotypes based on agro-morphological, colorimetric, and physicochemical traits.

The first included cultivars such as ‘Diamant noir’, ‘Ahmer Bouamar’, ‘sabat kanstantini’, and ‘Tapperial’. These cultivars were characterized by similar profiles in traits, including the number of berries and compactness. The second cluster included 28 cultivars such as ‘Cardinal’, ‘Muskat d’Italie’, ‘Christmas’, ‘Pause précoce’, ‘Danlas’, ‘Teresa de Prevane’, ‘Sultanine Rosée’, and ‘Sultanine’, characterized by their lighter fruit skin coloration and moderate lightness (L^*) and chroma (C^*) values and anthocyanin coloration of flesh.

The third cluster included 6 cultivars such as ‘Chenasan’, ‘Danan’, and ‘Muscat douille’. These genotypes were characterized by similar profiles in yield and pomological traits, including bunch weight, length, and width, berry weight, and berry

length. Finally, the fourth cluster comprised 11 cultivars such as ‘Thomson’, ‘Rutra’, and ‘Reine vigne’, which shared similarities in seed-related traits, berry shape, hue value (H°), pH, total soluble solids, and maturity index.

Discussion

The evaluation of the Moroccan grapevine germplasm revealed substantial variability in agro-morphological, colorimetric, and physicochemical traits, reflecting the broad genetic and phenotypic diversity preserved within the collection. The significant differences observed among traits indicate the combined influence of genetic background and environmental conditions. Although variations in temperature and precipitation were recorded between the two seasons (Table S1), these differences were relatively modest. Precipitation during the April–June period—corresponding to vegetative growth and bunch development—was moderately higher in 2023 than in 2024, whereas 2024 was slightly cooler; however, temperature differences were not statistically significant.

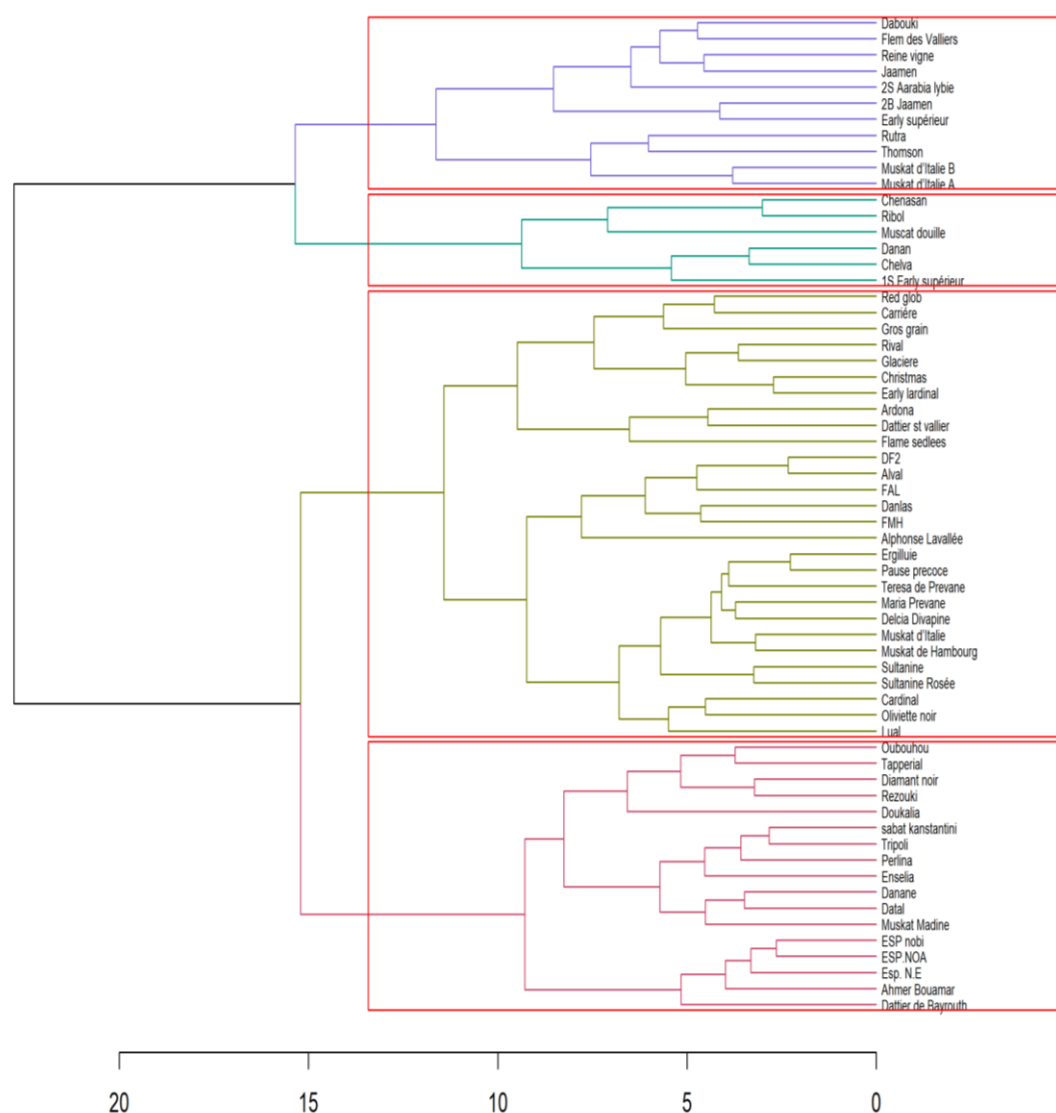


Fig. 5. Cluster analysis of the studied grapevine genotypes based on the agro-morphological, colorimetric, and physicochemical traits using Euclidean distances.

This limited climatic variation likely contributed to the generally high broad-sense heritability (H^2) estimates obtained for most traits, confirming that genetic factors were the primary determinants of grape quality and morphology in the studied germplasm. In contrast, the lower H^2 values observed for peduncle length and maturity index indicate that approximately 45% and 40% of their phenotypic variation, respectively, were attributable to environmental influences, suggesting greater responsiveness to year-to-year climatic fluctuations. Similar trends have been reported in previous studies, which documented high heritability for most agronomic and morphological characteristics in grapevine, alongside a notable environmental influence on physicochemical parameters such as total soluble solids, pH, and titratable acidity (Gonçalves et al., 2020; Gisbert et al., 2022; Leão

and Oliveira, 2023; Pou et al., 2023; Brault et al., 2024).

Overall, these findings underscore the importance of multi-season evaluations for accurately assessing trait stability and guiding genotypic selection aimed at improving yield and fruit quality under variable environmental conditions. The performance of the studied cultivars varied markedly. Varieties such as 'Red glob' (12.43 kg vine⁻¹), 'Flame seedles' (10.79 kg vine⁻¹), and 'Datal' (9.46 kg vine⁻¹) exhibited the highest yields, producing large and well-formed bunches, whereas cultivars such as 'Sultanine' (0.25 kg vine⁻¹) and '2B Jaamen' (1.13 kg vine⁻¹) showed low productivity. Bunch dimensions and peduncle length also varied considerably, reflecting differences in genotype and adaptation (Table S3). Yield variation among cultivars was influenced by both genetic and environmental factors, in addition

to vineyard management practices and disease pressure (Alabi et al., 2016; McClymont et al., 2012). Genes encoding MADS-box transcription factors regulate reproductive development and fruit set, which may explain part of the variability observed in yield components (Zinelabidine et al., 2021). The present results for bunch length, bunch width, and peduncle length confirm the genotype-dependent nature of these traits while also highlighting environmental modulation (Abiri et al., 2020; Vafae et al., 2017). Furthermore, the observed variation in berry number and berry weight suggests a trade-off in resource allocation, consistent with previous reports (Khadivi-Khub et al., 2014; Martin et al., 2022).

Seed traits exhibited strong intraspecific diversity, ranging from seedless types to cultivars bearing multiple seeds, with most genotypes producing two seeds per berry, as previously reported in other germplasm studies (Vafae et al., 2017; Abiri et al., 2020; Boz et al., 2011; Khadivi-Khub et al., 2014). The slightly higher seed weights observed in the present study may reflect specific cultivar characteristics or local environmental influences.

Skin color diversity reflects the combined effects of genetic regulation and biochemical pigmentation pathways. Mutations and transposable element insertions in *MYBA1* and *MYBA2* genes explain the occurrence of white phenotypes, whereas variation in anthocyanin composition and color reversions contributes to phenotypic plasticity (Tsantili et al., 2010; Fournier-Level et al., 2010; Röckel et al., 2020). These mechanisms are consistent with the broad variation revealed by the colorimetric analyses.

With respect to fruit composition, the studied cultivars displayed wide variation in total soluble solids (TSS) and maturity index (MI), reflecting diverse sweetness levels and ripening profiles. Some cultivars, such as ‘Muscat de Hambourg’ (TSS = 24.5%, MI = 13.87) and ‘Tapperial’ (TSS = 23.12%, MI = 13.87), combined high sugar content with high MI values, whereas others, including Esp. N.E (TSS = 11.78%, MI = 6.36) and ‘2S Aarabia lybie’ (TSS = 12.77%, MI = 6.41), exhibited both low TSS and low MI. Notably, certain cultivars showed relatively high TSS but comparatively lower MI—for example, ‘Muscat Madine’ (TSS = 19.85%, MI = 13.03)—indicating that sugar accumulation alone does not fully determine maturity status.

This pattern can be explained physiologically. While some cultivars efficiently accumulated sugars during ripening, they retained higher acidity due to delayed organic acid degradation or differential regulation of sugar transport and metabolic pathways, as well as pigment and secondary metabolite biosynthesis (Conde et al., 2024; Lu et al., 2024). Recent studies further demonstrated that cultivar-dependent differences in enzyme activity, transporter function,

and gene regulation involved in sugar–acid metabolism contribute to these compositional patterns (Li et al., 2024; Lu et al., 2024). Cultivars with high MI values are particularly suitable for table grape consumption, whereas those with lower MI are better adapted for processing.

These findings emphasize that fruit quality results from the interaction of genetic, biochemical, and environmental factors, highlighting the physiological basis underlying the observed variation in TSS and MI (Khadivi-Khub et al., 2014; Vafae et al., 2017; Razi et al., 2023; Plantevin et al., 2024; Li et al., 2024).

Bunch compactness, an agronomically important trait, influences air circulation within clusters, susceptibility to disease, and overall fruit quality. In this study, cultivars such as ‘FMH’ (very compact), ‘Red glob’ (compact), and ‘Thomson’ (compact) exhibited the most compact cluster architecture, whereas cultivars such as ‘Sultanine’ (very loose), ‘Muscat Madine’ (very loose), and ‘Maria Prevane’ (very loose) produced loose clusters. Regarding seed formation, ‘Sultanine Rosée’, ‘Sultanine’, ‘Danlas’, ‘Thomson’, ‘Rutra’, ‘Early supérieur’, ‘Reine vigne’, and ‘Flem des Valliers’ were seedless, representing particularly desirable genotypes for table grape production, while the majority of the remaining cultivars produced well-developed seeds. The observed diversity in cluster compactness and seedlessness further underscores the genetic richness of the Moroccan germplasm. Seedlessness is primarily regulated by *VvAGL11* and modulated by multiple loci distributed across the genome, whereas rachis architecture—an important determinant of bunch density—is associated with *VviUCC1* (Tello et al., 2024). In addition to these genetic determinants, environmental conditions may also influence the expression of both traits. Seasonal fluctuations in temperature and precipitation can affect rachis elongation and berry set, thereby altering cluster compactness and the degree of seed development, as reported in other grapevine populations exposed to variable climatic conditions (Gisbert et al., 2022; Pou et al., 2023).

The significant correlations identified among agromorphological, colorimetric, and physicochemical traits further illustrate the interdependence of yield and quality components. Yield was mainly driven by bunch weight and dimensions, whereas the negative association between berry count and berry size confirmed a trade-off in resource allocation. Likewise, correlations between colorimetric indices (L^* , H°) and physicochemical parameters highlighted the close relationship between pigmentation and fruit composition (Abiri et al., 2020; Khadivi-Khub et al., 2014; Leão et al., 2011; Migicovsky et al., 2017; Vafae et al., 2017).

Multivariate analyses supported these trait interrelationships. UPGMA cluster analysis grouped

cultivars according to size, acidity, and color, while principal component analysis (PCA) identified berry and seed dimensions, coloration, and acidity-related variables as the main discriminating factors. Although the first two principal components explained 38.9% of the total variance, Dim1 primarily captured variation associated with size and seed traits, whereas colorimetric and ripening-related parameters structured much of the remaining variability. These results are consistent with previous studies (Abiri et al., 2020; Ekhvaia and Akhalkatsi, 2010; Leão et al., 2011; Vafaei et al., 2017) and confirm the importance of pomological and biochemical traits for grapevine characterization and conservation.

Overall, both genetic background and environmental conditions contribute to the final expression of these key agronomic traits, underscoring the importance of multi-season evaluations to identify stable and desirable phenotypes. Nevertheless, it should be acknowledged that the present study did not include direct metabolic or molecular analyses. Future research integrating transcriptomic, metabolomic, or gene expression approaches would be valuable for elucidating the molecular mechanisms underlying the observed phenotypic variation and for strengthening the scientific basis of grapevine selection and breeding strategies.

Conclusion

This study provided a comprehensive assessment of phenotypic diversity within the Moroccan grapevine germplasm, revealing substantial variation in agromorphological, colorimetric, and physicochemical traits. Principal component and cluster analyses demonstrated that berry dimensions, seed and bunch weight, color indices (L^* , C^* , H°), and maturity index were the most discriminating variables driving cultivar differentiation. High broad-sense heritability values for berry weight, seed number, and hue angle confirmed the strong genetic control of these traits, whereas moderate heritability estimates for maturity index and peduncle length reflected a greater environmental influence. The integration of multivariate analyses further confirmed the effectiveness of combining phenotypic descriptors to distinguish cultivars and identify unique genotypes of agronomic interest. This multidimensional characterization underscores the genetic richness of Moroccan germplasm, including the presence of seedless types and extensive color variability, both of which are valuable for table and wine grape breeding.

Beyond providing an updated phenotypic inventory, these findings carry direct implications for germplasm conservation, cultivar selection, and breeding strategies. The identification of stable and highly heritable traits offers practical guidance for

selecting elite genotypes with improved productivity, fruit quality, and adaptation to semi-arid conditions. Consequently, this research strengthens the foundation for the sustainable management and valorization of Morocco's grapevine genetic resources and supports their integration into future breeding programs and climate-resilient viticultural systems.

Acknowledgments

The authors gratefully acknowledge the scientific and technical staff of the Regional Center for Agronomic Research in Meknes, as well as the teams at the Ain Taoujdate experimental station, for their valuable field support and technical assistance.

Author Contributions

Conceptualization and methodology, JC and LO; Software and formal analysis, KE, HB, AB, and ME; Writing and original draft preparation, LO; Writing, review, editing, and visualization, JC, AH, and HZ; Supervision, JC; All authors reviewed and approved the final version of the manuscript.

Funding

This research received no external funding.

Conflict of Interest

The authors indicate no conflict of interest in this work.

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Supplementary Materials

Table S1. Monthly average air temperature, minimum air temperature, maximum air temperature, and precipitation for Ain Taoujdate weather station during the 2023 and 2024 growing season.

	2023				2024			
	Average Air Tem perature (°C)	Maximum Air Te mperature (°C)	Minimum Air Te mperature (°C)	Precipitation (m m)	Average Air Tem perature (°C)	Maximum Air Te mperature (°C)	Minimum Air Te mperature (°C)	Precipitation (m m)
April	20.18	40.58	6.04	0.4	17.1	32.1	7.11	30
May	19.43	36.27	8.94	30.4	20.16	38.95	6.17	0.8
June	24.93	44.7	12.61	12.6	22.41	39.42	11.28	1.8
July	27.15	44.95	15.43	0	27.25	44.6	13.68	0.6
August	29.43	45.43	11.78	0	27.08	42.71	15.78	1
September	24.55	36.32	14.93	0.8	23.3	37.35	11.93	12.4
October	19.01	31.77	12.48	2.2	19.06	35	8.08	45

Table S2. Correlation between utilized variables among studies cultivars.

	Yi	BuWe	BuL	BuWi	LeP	NuBe	BeW	BL	BW	SeN	SeW	Comp
Yi	1											
BuWe	.752**	1										
BuL	.538**	.623**	1									
BuWi	.510**	.517**	.303*	1								
LeP	0.068	0.249	0.137	-.351**	1							
NuBe	.307*	0.177	0.192	0.148	-0.160	1						
BeW	.394**	.630**	.394**	.296*	0.234	-.559**	1					
BL	.348**	.577**	.406**	0.167	.419**	-.508**	.883**	1				
BW	.331**	.578**	.346**	.331**	0.204	-.523**	.876**	.809**	1			
SeN	0.104	0.192	0.038	-0.099	.350**	-0.240	.335**	.404**	0.199	1		
SeW	0.170	.284*	0.106	-0.082	.395**	-.288*	.459**	.548**	.282*	.939**	1	

Comp	.259*	.350**	0.061	0.159	-0.110	.582**	-0.134	-0.204	-0.182	0.006	-0.012	1
DePe	0.055	0.129	0.108	-0.012	0.207	0.045	0.022	0.053	-0.005	.357**	.307*	0.069
BeSh	-0.062	0.012	-0.086	0.007	0.069	-0.155	-0.003	0.132	0.209	-0.157	-0.099	-.315*
AnthCo	0.055	0.003	-0.011	-0.135	-0.120	.320*	-0.167	-0.149	-0.213	0.067	0.067	.520**
FoSe	0.140	0.221	0.090	-0.065	.318*	-0.245	.349**	.418**	0.177	.893**	.887**	0.032
SuPu	-0.157	0.028	-0.025	0.063	-0.042	-0.209	0.015	-0.043	0.102	-0.085	-0.089	-0.015
TSS	-.277*	-.431**	-0.161	-.361**	-0.203	0.184	-.379**	-.506**	-.448**	-.293*	-.338**	0.012
pH	-0.069	-0.069	0.000	-0.178	0.163	-.416**	.302*	0.215	0.225	.404**	.374**	-.310*
TA	-0.141	-0.034	-0.173	-0.149	0.024	.325*	-.289*	-0.235	-0.151	-.293*	-.321*	.285*
MI	-0.022	-0.160	0.070	0.008	-0.205	-0.186	0.062	-0.048	-0.028	0.013	0.006	-.260*
L*	-0.048	0.150	-0.155	-0.016	0.142	0.068	-0.075	0.010	0.047	-0.134	-0.138	0.034
a*	-0.109	-0.224	-0.018	-0.089	-0.095	-0.023	-0.084	-0.155	-.262*	0.018	0.082	-0.099
b*	0.116	.330**	0.100	0.088	0.148	0.042	0.124	0.151	.269*	-0.223	-0.225	0.001
C*	-0.014	0.193	0.073	0.024	0.244	0.062	-0.059	0.037	0.044	-.294*	-.269*	-0.074
H°	-0.047	-0.197	-0.096	-0.096	-0.167	-0.038	-0.121	-0.081	-0.115	0.150	0.090	0.097

Table S2. (Continued).

	DePe	BeSh	AnthCo	FoSe	SuPu	TSS	pH	TA	MI	L*	a*	b*	C*	H°
Yi														
BuWe														
BuL														
BuWi														
LeP														
NuBe														
BeW														
BL														
BW														
SeN														

SeW														
Comp														
DePe	1													
BeSh	-0.246	1												
AnthCo	0.169	-.313*	1											
FoSe	.391**	-0.182	0.149	1										
SuPu	.276*	-0.049	-0.144	-0.018	1									
TSS	-0.091	-.262*	0.149	-.280*	-0.204	1								
pH	0.195	-0.195	-0.140	.398**	-0.097	0.201	1							
TA	-0.122	0.138	0.224	-.314*	0.012	0.054	-.595**	1						
MI	0.044	-0.207	-0.188	0.034	-0.088	.492**	.605**	-.745**	1					
L*	0.041	.476**	-0.197	-0.184	0.007	-.278*	-.289*	.252*	-.376**	1				
a*	-.328**	-0.172	-0.063	0.026	-0.011	.251*	0.017	-0.079	0.170	-.518**	1			
b*	0.152	.353**	-0.113	-0.227	0.007	-0.233	-0.136	0.227	-.271*	.796**	-.655**	1		
C*	0.027	.374**	-0.152	-0.220	-0.004	-0.192	-0.219	0.173	-0.187	.634**	-0.220	.656**	1	
H°	0.131	-0.196	.252*	0.167	0.078	0.020	0.061	-.255*	0.215	-.286*	-0.135	-.467**	-.301*	1

Note: *, ** = Significant at 0.05 and 0.01 probability levels, respectively. Abbreviations: Yi = Yield per vine, BuWe = Bunch weight, BuL = Bunch length, BuWi = Bunch width, LeP = Length of peduncle, NuBe = Number of berries per grape, BeW = Berry weight, BL = Berry length, BW = Berry width, SeN = Seed number per berry, SeW = Seed weight per berry, Comp = Compactness, DePe = Detachment of the pedicel, BeSh = Berry shape, AnthCo = Anthocyanin coloration of flesh, FoSe = Formation of seeds, SuPu = Succulence of the pulp, TSS = Total soluble solids, TA = Titratable acidity, MI = Maturity index, L* = Lightness, a* = Redness/greenness, b* = Yellowness/blueness, C* = Chroma, H° = Hue angle.

Table S3. Eigenvalues of principal component axes from the PCA of pomological, colorimetric and physicochemical parameters utilized for the studied grape cultivars.

Trait	Component							
	1	2	3	4	5	6	7	8
Yi	0.460	0.264	0.547**	-0.362	0.085	0.154	-0.082	-0.139
BuWe	0.654**	0.468	0.452	-0.213	0.056	0.099	0.093	-0.003
BuL	0.442	0.189	0.355	-0.397	0.120	0.218	0.272	0.017
BuWi	0.258	0.304	0.328	-0.558**	0.002	-0.300	-0.098	-0.319
LeP	0.425	0.111	-0.147	0.454	-0.019	0.407	0.311	0.081

NuBe	-0.454	0.230	0.701	-0.002	0.184	0.250	0.008	-0.240
BeW	0.864**	0.087	-0.085	-0.262	-0.142	-0.019	-0.004	0.296
BL	0.882**	0.145	-0.122	-0.065	-0.180	0.044	-0.050	0.217
BW	0.770**	0.272	-0.184	-0.261	-0.123	-0.152	-0.055	0.326
SeN	0.655**	-0.407	0.128	0.495	-0.037	0.063	-0.102	-0.221
SeW	0.739**	-0.363	0.116	0.428	-0.118	0.113	-0.082	-0.190
Comp	-0.138	0.151	0.785**	0.146	0.039	-0.033	-0.058	0.121
DePe	0.263	-0.082	0.194	0.413	0.550**	-0.259	0.355	-0.043
BeSh	0.016	0.484	-0.476	0.036	-0.175	0.032	-0.319	-0.252
AnthCo	-0.158	-0.132	0.606**	0.301	0.038	-0.016	-0.186	0.428
FoSe	0.658**	-0.404	0.174	0.462	0.002	0.027	-0.043	-0.196
SuPu	0.023	0.050	-0.094	0.036	-0.024	-0.679**	0.625	-0.044
TSS	-0.543**	-0.417	-0.035	-0.167	0.272	0.367	0.083	0.315
pH	0.403	-0.550**	-0.318	-0.053	0.406	0.176	-0.011	0.116
TA	-0.422	0.485	0.192	0.336	-0.413	0.058	0.114	0.292
MI	0.058	-0.575**	-0.223	-0.483	0.524	0.104	-0.044	-0.051
L*	-0.045	0.742**	-0.261	0.341	0.242	0.002	-0.170	-0.155
a*	-0.164	-0.477	0.015	-0.248	-0.524**	0.308	0.316	-0.253
b*	0.096	0.809**	-0.206	0.140	0.410	0.068	-0.020	0.118
C*	-0.050	0.664**	-0.260	0.114	0.256	0.193	0.118	-0.136
H°	-0.031	-0.444	0.191	0.074	0.132	-0.493	-0.345	0.076

Extraction method: Principal component analysis. Variables with an eigenvalue greater than |0.45| for any of the components were highlighted in bold. Abbreviations: Yi = Yield per vine, BuWe = Bunch weight, BuL = Bunch length, BuWi = Bunch width, LeP = Length of peduncle, NuBe = Number of berries per grape, BeW = Berry weight, BL = Berry length, BW = Berry width, SeN = Seed number per berry, SeW = Seed weight per berry, Comp = Compactness, DePe = Detachment of the pedicel, BeSh = Berry shape, AnthCo = Anthocyanin coloration of flesh, FoSe = Formation of seeds, SuPu = Succulence of the pulp, TSS = Total soluble solids, TA = Titratable acidity, MI = Maturity index, L* = Lightness, a* = Redness/greenness, b* = Yellowness/blueness, C* = Chroma, H° = Hue angle.