Exploring the genetic diversity of Lebanon's underexploited grapevine resources

Joe Merheb, Lamis Chalak, Catherine Roux, Valérie Laucou, Naim Ouaini, Marc Beyrouthy, Joe-Assad Touma, Thierry Lacombe, Patrice This

To cite this version:

Joe Merheb, Lamis Chalak, Catherine Roux, Valérie Laucou, Naim Ouaini, et al.. Exploring the genetic diversity of Lebanon's underexploited grapevine resources. Genetic Resources and Crop Evolution, In press, 10.1007/s10722-024-02203-z . hal-04775179

HAL Id: hal-04775179

https://hal.inrae.fr/hal-04775179v1

Submitted on 9 Nov 2024

Genet Resour Crop Evol
https://doi.org/10.1007/s10722-024-02203-z

RESEARCH ARTICLE

Exploring the genetic diversity of Lebanon's underexploited grapevine resources

Joe Merheb · Lamis Chalak · Catherine Roux · Valérie Laucou · Naim Ouaini · Marc Beyrouthy · Joe-Assad Touma · Thierry Lacombe · Patrice This

Received: 15 August 2024 / Accepted: 28 September 2024

Abstract Lebanon's well-documented history in grape cultivation and winemaking dates back millennia, intertwining with its cultural heritage and landscape. However, until recent years, Lebanon's grapevine genetic resources have received limited attention. This study presents a comprehensive exploration and characterization of Lebanese local underexploited resources, beginning with the collection of 276 accessions throughout the country, with an emphasis on old/abandoned vines and vineyards. Molecular analyses were conducted on these accessions; 22 nuclear simple sequence repeat (SSR) markers and 3 chloroplastic SSR markers were used to assess their genetic diversity. A total of 102 distinct genotypes were identified, 63 of which exhibited original genetic signatures previously undocumented in international databases, highlighting the unique genetic richness of Lebanon's grapevine germplasm. Subsequent morphological characterization using a set of descriptors developed by International Organization of Grapevine and Wine (OIV) provided valuable insights into the phenotypic traits of these newly found grape cultivars. Parentage analysis facilitated the elucidation of genetic relationships among the accessions and the construction of genetic pedigrees. Comparative analysis with a set of cultivars of very diverse geographical origin positioned Lebanese accessions within the Eastern Mediterranean group, suggesting shared genetic affinities with regional counterparts. Lebanon's grapevine genetic resources are key for conservation, breeding, and future viticulture research. Preserving these resources protects the nation's heritage while fostering innovation and resilience in winemaking amid environmental changes.

Keywords *Vitis vinifera* L. · Germplasm · SSR · OIV descriptors · Chlorotype · Cultivar identification

---

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10722-024-02203-z.

J. Merheb (✉) · L. Chalak
Department of Plant Production, Faculty of Agronomy, The Lebanese University, Dekwaneh, Lebanon
e-mail: joe.c.merheb@gmail.com

J. Merheb · C. Roux · V. Laucou · T. Lacombe · P. This
UMR AGAP Institute, University of Montpellier, CIRAD, INRAE, Institut Agro Montpellier, Montpellier, France

C. Roux · V. Laucou · T. Lacombe · P. This
UMT Geno-Vigne®, IFV, INRAE, Institut Agro Montpellier, Montpellier, France

N. Ouaini
Faculty of Arts and Sciences, Holy Spirit University of Kaslik, Jounieh, Lebanon

M. Beyrouthy
Department of Agricultural and Food Engineering, School of Engineering, Holy Spirit University of Kaslik, Jounieh, Lebanon

J.-A. Touma
Chateau St. Thomas, Kab Elias, Lebanon

Introduction

The Near East area, which includes Lebanon, is regarded as one of the two main original domestication centers of grapevine (Dong et al. 2023). Indeed, archaeological findings within the Lebanese territory provide substantial evidence of ancient grape and wine production dating back to the Iron Age, with numerous ancient wine presses unearthed (Orsingher et al. 2020). Lebanon's varied geography and climate provide perfect areas for grape production, fostering a diverse array of local grapevine cultivars adapted to local environments. These traditional cultivars thus hold great genetic potential. Hence, precise characterization of Lebanon's grapevine gene pool is essential (Chalak et al. 2016).

Cultivating fewer grape cultivars has increased crop vulnerability to environmental stresses, endangering the rich genetic heritage of grape cultivars. Preserving a wider range of grape cultivars is essential for meeting the demands of consumers and ensuring environmental sustainability; hence, continuous exploration, characterization and conservation efforts in traditional grape-producing areas are necessary (Augusto et al. 2021; Maraš et al. 2020; Žulj Mihaljević et al. 2020). The initial steps in understanding grapevine diversity involve estimating its genetic and phenotypic diversity and establishing genetic relationships among accessions of a germplasm. Knowledge related to the existing diversity of the gene pool is essential for the effective management and use of a species germplasm (Lacombe 2023). Traditionally, grapevine variety characterization and identification rely on ampelography based on morphological descriptions. However, this method has limitations, especially regarding the distinction between closely related cultivars or clones. Moreover, the accuracy and trueness to type assessments can be influenced by environmental factors (De Lorenzis 2023). Genetic methods, including microsatellite or simple sequence repeat (SSR) and other molecular markers, provide a more precise and efficient approach to characterize genetic diversity. These tools enable comprehensive genetic analysis, complementing morphological assessments and enhancing our understanding of grapevine genetics for improved germplasm management and utilization (Villano et al. 2022).

At the Lebanese level, according to the *Vitis* International Variety Catalog (VIVC), Lebanon holds more than 25 native grape cultivars, with a majority of white table grapes. All the listed cultivars have been described in detail by ampelographers and have been referenced in ancient texts since the early 1900s; these include 'Beitamouni' for table grapes and 'Obeidi' for wine and arak production (Branas and Truel 1967; Galet 2000; Viala and Vermorel 1905). Despite the increased diffusion of international cultivars, local populations have continued to grow some of the native cultivars, recognizing their historic value and cultural significance (Merheb et al. 2024a). Hence, significant initiatives to preserve and understand Lebanon's indigenous germplasm have already been undertaken. Establishing the first repository for grapevine genetic resources was a pivotal step taken by the Lebanon Agricultural Research Institute (LARI) in 1998 (Chehade et al. 2022). Subsequent initiatives were launched to survey grapevine-producing areas; however, characterization efforts have primarily relied on morphological assessments (Chalak et al. 2016, 2023; Merheb et al. 2024a). The national collection has undergone molecular characterization using inter-simple sequence repeat (ISSR) markers, revealing high genetic diversity (Chehade et al. 2022). A small-scale study using simple sequence repeat (SSR) markers was conducted on a limited number of accessions conserved in a traditional vineyard in North Lebanon (Merheb et al. 2024a). Additionally, the germplasm of Hadchit, a village in North Lebanon, was characterized using SSR markers, and more than half of the studied cultivars did not match any of the genotypes found in international databases (Merheb et al. 2024b). A study using descriptors developed by the International Organization of Grapevine and Wine (OIV) and ISSR molecular markers also revealed intervarietal diversity among several commonly grown local grapevine cultivars (Khater et al. 2024). Despite variations in methodologies, all these investigations highlighted the remarkable genetic diversity present but Lebanon has yet gathered limited knowledge regarding the extent of its local grape germplasm. Thus there is a pressing need for further investigation, particularly at the molecular level, utilizing a broader and more extensive range of molecular tools tailored for genetic diversity analysis and with material obtained on a broader national scale.

Recognizing the need for a more thorough understanding of Lebanon's grapevine diversity, we thus conducted a comprehensive investigation of the Lebanese grapevine germplasm utilizing molecular and morphological characterization. To this end, the main objectives of this study were to (i) explore the Lebanese grapevine germplasm, (ii) determine grapevine identities, (iii) detect synonyms, homonyms and miasnamings, (iv) assess the level of genetic diversity, (v) characterize the morphology of previously undocumented grapevine profiles in international databases, and (vi) investigate genetic relatedness within the Lebanese and Mediterranean germplasms. Given the limited prior opportunities for such research in Lebanon, this ongoing endeavor holds profound national importance, contributing significantly to the preservation and valorization of the country's grapevine genetic heritage.

Materials and methods

Prospecting and collection of plant material

Prospecting trips were performed during the 2022 growing season with the aim of collecting indigenous, unknown or abandoned grapevine landraces growing in family gardens and in old/traditional vineyards. Eighty-three locations situated at different elevations across the Baalbek-Hermel (BH), Beirut (BEY), Bekaa (B), Mount Lebanon (ML), North Lebanon (NL), and South Lebanon (SL) governorates were visited (Fig. 1), and GPS coordinates were recorded for each sampling site. These sites were located in different agroclimatic areas throughout Lebanon, with altitudes ranging from 20 m in Beirut to 1600 m a.s.l. in Hadchit, North Lebanon; latitudes between 34.261016 and 35.502129; and longitudes from 35.484711 to 36.800328.

A total of 276 cultivated grapevine accessions were collected: 22 from Baalbek-Hermel (BH), 1 from Beirut (BEY), 66 from Bekaa (B), 97 from Mount Lebanon (ML), 83 from North Lebanon (NL), and 7 from South Lebanon (SL). A list of these accessions, including their codes, vernacular names, geographical data on the sampling location, skin color, and cultivation status, is given in Supplementary Table S1. The majority of the sampling sites were located in the Mount Lebanon (97 accessions) and North Lebanon (83 accessions) governorates (Fig. 1), as these areas have not yet been studied extensively.

All of the collected accessions were from areas with ancient grape cultivation. Among the collected vines, 162 accessions were taken from home gardens in various villages across Lebanon. These accessions were grown on pergolas or stone terraces. Additionally, 8 accessions were collected from commercial plantations, either large (1.5 Ha) or small (0.2 and 0.3 Ha). Moreover, 53 accessions were obtained from ancient vineyards aged between 30 and 80 years, and 10 accessions, over 70 years old, were found in an abandoned state and lying on the ground in the villages of Ainata (Baalbek-Hermel), Bekaa Kafra (North Lebanon), and Akoura, Hdeineh, Yanouh (Mount Lebanon), many with unknown vernacular names. Another 3 accessions were found to be growing naturally on the roadside, mainly in North Lebanon. Notably, three vines older than 100 years were found growing near an abandoned house in Nahr el Dehab (Mount Lebanon), a school in the heart of Beirut, and a monastery in Bsarma (North Lebanon). Additionally, 18 accessions were growing on high-altitude (1400 to 1600 m a.s.l.) ancient stone-walled terraces in Hadchit village (North Lebanon), which is located at a UNESCO World Heritage site encompassing the Qadisha Valley.

Young leaves for DNA extraction were collected on site, dried and preserved in silica gel until extraction. In addition, 15 adult leaves were collected and pressed between two sheets of paper for ampelography analysis, and 5 bunches, when available, were harvested for characterization.

DNA extraction and genotyping

Total genomic DNA was extracted from 0.05 g of dried young leaves using DNeasy Plant Mini Kits (Qiagen, Valencia, CA, USA). Genotyping was carried out by amplifying 22 nuclear SSR loci (nSSR): VMC1b11, VMC4f3.1, VVIb01, VVIh54, VVIn16, VVIn73, VVIp31, VVIp60, VVIq52, VVIv37, VVIv67, VVMD21, VVMD24, VVMD25, VVMD27, VVMD28, VVMD32, VVMD5, VVMD7, VVS2, VrZAG62, VrZAG79 (Laucou et al. 2011), and 3 chloroplastic SSR markers (cpSSR): CCMP3, CCMP5, and CCMP10 (Arroyo-Garcia et al. 2006). The last nine nSSR markers of this set were internationally acknowledged for use

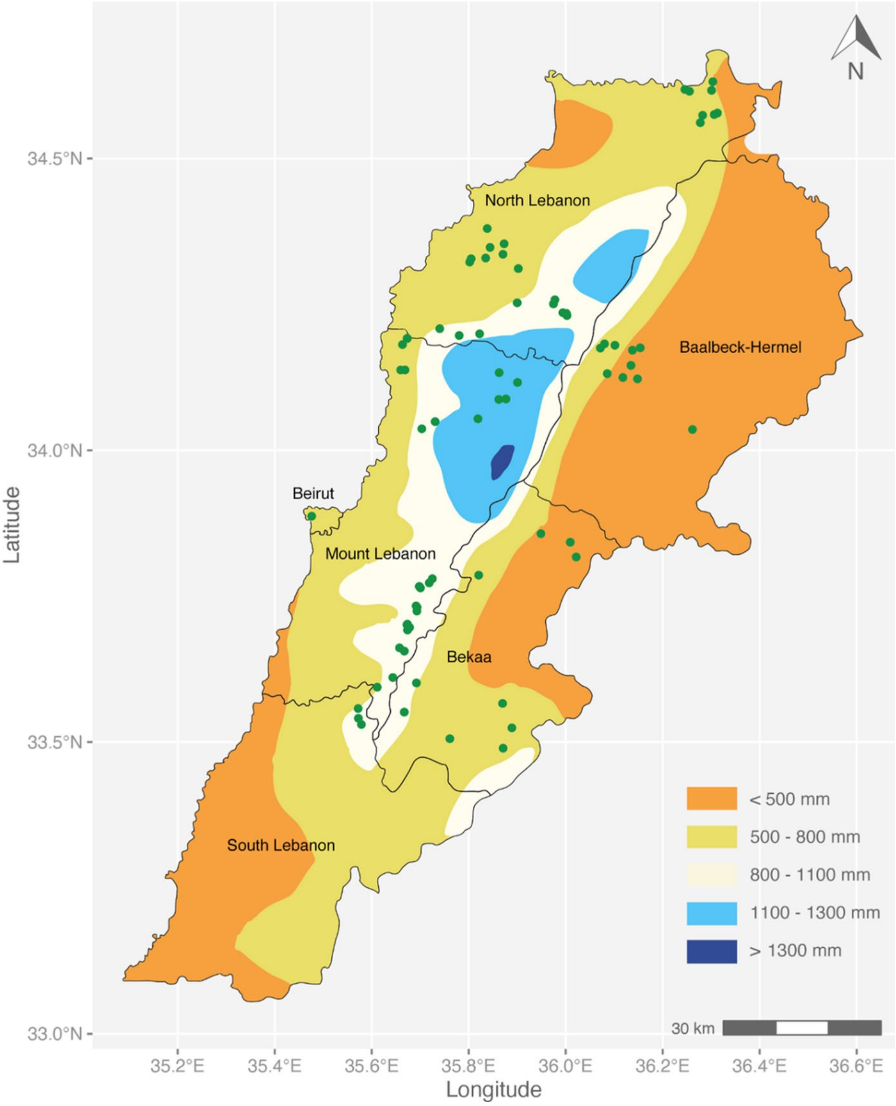


Fig. 1 Map of Lebanon showing the geographic distribution of prospected sampling sites (precipitation data extracted from the Lebanese Central Administration of Statistics 2012). The green dots identify the sites

in grapevine identification as proposed after the GrapeGen06 project (This et al. 2004). The amplifications were performed as previously described by Laucou et al. (2011). The respective loci were detected on an automated ABI PRISM® 310 Genetic Analyzer (Applied Biosystems, Life Technologies, Foster City, CA, USA). The alleles were scored using GeneMapper 6.0 software (Applied Biosystems, Life Technologies), and the results were recorded in base pairs.

Cultivar identification and subset definition

The genetic profiles obtained were compared with those of the Vassal-Montpellier French grapevine collection database (https://vassal.montpellier.hub.inrae.fr/ and https://bioweb.supagro.inra.fr/collections_vigne/) to verify synonyms and homonyms. Genotypes not associated with a known cultivar in the Vassal-Montpellier French grapevine collection database were further compared with the *Vitis* International Variety Catalog database [VIVC; http://www.vivc.de/ (last accessed May 18, 2024)] using ‘Cabernet-Sauvignon’, ‘Chardonnay’, ‘Muscat à petits grains blancs’ and ‘Pinot noir’ as reference cultivars to harmonize nSSR allele sizes and compare the genetic profiles obtained with the published profiles. When accessions exhibited the same SSR profile, they were considered as synonyms and excluded from later analysis. When no match was found in either *Vitis* databases, the profile was considered “unidentified”.

For further analysis, several subsets of SSR data for specific genotypes were defined:

- Subset 1 of nonredundant genotypes was composed of the 102 unique genotypes when synonyms were removed, based on the 22 nSSR and 3 cSSR markers.
- Subset 2, of 78 specific genotypes, includes genotypes of Lebanese origin with no match in international databases and genotypes of foreign origin according to the VIVC when considering data on 22 nSSR markers and morphology. These foreign cultivars were specifically chosen because they were repeatedly found in the country, helping us to better understand the genetic diversity and influence of these cultivars on the local germplasm.
- Finally, subset 3 of large diversity (834 cultivars) was defined, comprising 771 cultivars of international origin from various countries throughout the Mediterranean basin, all of which were classified as traditional (346 from Western Europe, 193 from the Balkan, 127 from the Maghreb, and 105 from the Eastern Mediterranean (Supplementary Table S5)) plus the Lebanese accessions Subset 2. The genetic profiles of the 771 cultivars were obtained from the Vassal-Montpellier French grapevine collection database, which encompasses the same 22 nSSR loci (Laucou et al. 2011).

Genetic diversity analysis

The nuclear SSR genotyping data of all nonredundant genotypes (Subset 1) were used to determine the number of different alleles (Na), the number of effective alleles (Ne), observed heterozygosity (Ho), and expected heterozygosity (He), as well as the Shannon’s information index (I), fixation index (F) and polymorphism information content (PIC), for each nSSR locus using a homemade data analyzer.

The combination of alleles from three chloroplastic SSR loci enabled us to distinguish the main grape chlorotypes, designated A, B, C, D, E and F, according to Arroyo-García et al. (2002).

Ampelographic variation

Morphological characterization of Subset 2 was carried out using a set of descriptors developed by the International Organization of Grapevine and Wine (OIV 2009). Ampelographic characterization was performed in 2022 with 15 leaves, 5 bunches and 15 berries collected from each vine, which were characterized using a set of qualitative traits: leaf form OIV067, teeth form OIV076, upper OIV070 and lower leaf vein pigmentation OIV071; upper OIV088, lower OIV087 and pedicel leaf pilosity OIV090; bunch form OIV208 and consistency OIV204; berry skin color OIV225; and form OIV223. For analysis of the data, PCoA and UPGMA clusters were similarly generated using R software version 4.23.

Parentage analysis

Parentage analysis was performed as described by Lacombe et al. (2013) on Subset 2 using FAMOZ software (Gerber et al. 2003) adapted to grapevine (Di Vecchi-Staraz et al. 2005) and already known as the program of choice for this purpose (Jones et al. 2010).

Structure analysis

Structure analysis was performed using STRUCTURE version 2.3.4 to assess the genetic structure of the Lebanese grapevine germplasm and to position it within the broader context of Mediterranean grapevine diversity (Subset 3). This model aimed to evaluate the number of inferred genetic population clusters (K) and to assign individuals to their likely region of origin utilizing reference information from the Vassal-Montpellier French grapevine collection database. The analysis was conducted under the admixture model with independent allele frequencies following the methodology described previously (Falush et al. 2007). A burn-in period of 20,000 Markov Chain Monte Carlo (MCMC) steps was followed by 100,000 MCMC steps to ensure convergence. Ten replicate runs per K value were performed, with K values ranging from 1 to 10. The online tool STRUCTURE HARVESTER (web version 0.6.94) was used to identify the optimal number of genetic clusters and facilitated the subsequent assignment of individuals to these clusters (Evanno et al. 2005).

Results

Diversity within the Lebanon grape material

The studied accessions had 106 different vernacular names, as initially provided by farmers; the most frequently observed were Merwah (14, potentially indicating an aromatic grape); Sawda (12, meaning black in reference to berry color); Bakhouri (10, suggesting a fragrant grape, musk aroma); Beitamouni (10, meaning growing next to a house); Bayade (8, meaning "white"); and Meksasi (9). Most of these names are directly related to distinctive morphological features, mainly related to berry skin color or shape, taste and use, geographical origin or name of the grapevine cutting provider (possible definitions are provided in Supplementary Table S2). Notably, many of the accessions (37), especially those collected from abandoned vineyards, had no names and were labeled "unknown".

The 276 accessions were genotyped using 22 nuclear SSR markers, which allowed us to identify redundant material efficiently. In total, only 102 individual profiles were identified (Supplementary Table S1). Among them, 61 profiles were found only once, while the five most common genotypes (LBN15, LBN24, LBN11, LBN61 and LBN71) were found 12, 13, 14, 24 and 27 times, respectively, in three to five governorates (Supplementary Table S1). Interestingly, identical profiles, and thus identical cultivars, were observed even from distant locations. These most commonly found genotypes across the sampled old vineyards may reflect their relevance in the past centuries.

At the allelic level, all the markers were polymorphic, and a total of 232 alleles were detected across the 22 loci, with a mean number of alleles (MNA) of 10.55 ± 3.46 (Table 1). Among the loci, VMC4f3.1 had the highest number of observed alleles (19), while VVIn73 had the lowest number of observed alleles (4). The expected number of alleles varied from 1.744 (VVIn73) to 8.667 (VVIv37), with a mean of 2.055. The highest Shannon's information index (I) was observed for the VVIv67.1 locus (1.565), and the lowest was observed for VVIn73 (0.667); moreover, the average value among the SSR loci was 1.08. The observed heterozygosity (Ho) ranged from 0.183 (VVIn73) to 0.882 (VVMD32), while the expected heterozygosity (He) ranged between 0.195 (VVIn73) and 0.879 (VMC4f3.1). The overall mean of He (0.760) was slightly greater than that of Ho (0.736); the fixation index (F) ranged between −0.116 (VVMD32) and 0.282 (VVIv37); and the polymorphism information index ranged between 0.121 (VMC4f3.1) and 0.75 (VVIv37).

Identification of the material of interest

The second objective of this work was to identify the different genotypes corresponding to the 102 unique profiles. For this purpose, the nSSR profiles of these plants were compared to those of the Vassal-Montpellier French grapevine collection and VIVC databases, which harbor genetic profiles of diverse genetic and geographic origins.

A total of 39 profiles corresponding to 163 collected accessions could be assigned to cultivars present in the Vassal-Montpellier French grapevine collection and VIVC databases (Table 2). The most commonly observed profiles corresponded to the cultivars 'Blanc de Dellys' (synonyms 'Marouhé', 'Merwah', 27 times) and 'Dabouki' (24 times) of supposed origins from the Maghreb and Eastern Mediterranean regions, respectively, followed by the cultivars 'Beitamouni' (14), 'Sebai assouad' (12) and 'Inab el Mir' (9) of Lebanese origin. According to the VIVC database, 25 of these 39 cultivars are table grape cultivars, four are wine cultivars, and the rest can be used both for wine or fresh fruits. Ten of them are registered in the VIVC database as Lebanese cultivars; the 29 others are of foreign origin, either from the Eastern Mediterranean (13 cultivars), Eastern Europe (1 cultivar), Maghreb (2 cultivars), Western Europe (4 cultivars), Central Asia or internationally used (1 cultivar); and 8 recent table cultivars from the Americas.

The remaining 63 different genetic profiles (corresponding to 113 accessions) did not match any profile stored in either the Vassal-Montpellier French grapevine collection or the VIVC database. The respective berry skin colors and uses of the vines were reported based on their morphological appearance and information provided by the farmers who cultivated them:

Table 1 Observed and effective number of alleles, information indices, observed and expected heterozygosity, FIS and average estimates of polymorphisms of the 108 unique grapevine genotypes observed in this study at 22 microsatellite loci

Locus	Ra (bp)[a]	Na[b]	Ne[c]	I[d]	Ho[e]	He[f]	F[g]	PIC[h]
VMC1b11	165–188	8	2	0.693	0.7664	0.8113	0.0554	0.5
VMC4f3.1	162–205	19	2.28	1.483	0.8646	0.8791	0.0169	0.121
VVIb01	286–306	8	1.999	1.248	0.3981	0.466	0.145	0.426
VVIh54	139–179	11	2.23	1.438	0.6698	0.8293	0.191	0.152
VVIn16	141–175	8	2.128	0.959	0.7009	0.7108	0.013	0.52
VVIn73	256–257	4	1.744	0.667	0.1827	0.1955	0.067	0.75
VVIp31	172–194	12	2.12	1.544	0.8654	0.8325	−0.038	0.156
VVIp60	303–328	11	2.177	1.315	0.7921	0.7514	−0.051	0.241
VVIq52	71–87	7	2.081	0.953	0.781	0.7226	0.249	0.313
VVIv37	145–177	11	2.33	1.471	0.6238	0.8675	0.282	0.286
VVIv67	315–386	18	2.09	1.565	0.6238	0.7778	0.198	0.282
VVMD21	226–263	8	2.082	0.971	0.8058	0.7225	−0.003	0.384
VVMD24	204–220	7	2.073	0.961	0.7264	0.7772	0.064	0.317
VVMD25	238–266	10	2.053	1.106	0.8113	0.7975	−0.017	0.394
VVMD27	172–191	8	2.082	0.975	0.6731	0.7222	0.069	0.362
VVMD28	216–270	14	2.119	1.248	0.78	0.8057	0.031	0.349
VVMD32	239–273	12	2.068	1.366	0.8824	0.7873	−0.116	0.351
VVMD5	221–263	10	2.189	1.201	0.8384	0.8567	0.022	0.274
VVMD7	233–262	11	2.124	1.333	0.8431	0.8106	0.04	0.184
VVS2	120–153	13	2.209	1.443	0.7404	0.8653	0.145	0.351
VrZAG62	118–204	11	2.132	1.181	0.5962	0.7933	0.247	0.485
VrZAG79	238–264	11	2.092	1.262	0.6869	0.7706	0.107	0.327
Total		232						
Minimum		4	1.744	0.667	0.1827	0.1955	−0.116	0.121
Maximum		19	2.33	1.565	0.8824	0.8791	0.282	0.75
Mean		10.55	2.055	1.077	0.7364	0.7597	0.0644	0.3185

[a]Ra = range of allele size (bp), [b]Na = No. of different alleles, [c]Ne = No. of effective alleles = 1/(Sum pi^2), [d] I = Shannon's Information Index = − 1 * Sum (pi * Ln (pi)), [e]Ho = observed heterozygosity = no. of Hets/N, [f]He = expected heterozygosity = 1 − Sum pi^2, [g]F = Fixation Index = (He − Ho)/He = 1 − (Ho/He), [h]PIC = polymorphism information content

57 of them were table grapes, 4 were wine grapes, 2 were of both use, while the majority were white (55), 6 were red, and 2 were black (Table 3).

The distribution of genetic profiles across different areas of Lebanon was assessed. The lowest diversity was found in the South Lebanon and Beirut districts, each exhibiting 6 and 1 unique genetic profiles for 7 and 1 accessions, respectively (Fig. 2). In contrast, the highest genetic profile diversity was observed in the Chouf district (Mount Lebanon Governorate), which had 30 distinct profiles for 66 accessions, and in the Rachaya–West Bekaa district (Bekaa Governorate), which had 37 different genetic profiles for 55 accessions. Indeed, Chouf harbored the highest number of profiles of Lebanese origin (9 out of 10 observed in total in the country), while Rachaya–West Bekaa (in the Bekaa Governorate) contained the most profiles of Eastern Mediterranean origin (11 profiles). The foreign-origin profiles were predominantly concentrated in the Keserwan-Jbeil districts in Mont Lebanon (6 profiles). The majority of the profiles categorized as unknown were concentrated in three districts (Aakar, Bcharre and Batroun-Koura-Zgharta) of North Lebanon, where almost 65% of the identified profiles lacked identifiable origins (Fig. 2). In further parts of the document, we will refer to each of the genetic profiles as the 'genotype'.

Chlorotype diversity

The chlorotypes of the 102 nonredundant genotypes were determined using three chloroplastic loci. Chlorotype analyses (Table 4, Supplementary Table S3) revealed that a majority of the genotypes were associated with chlorotype D (46 genotypes, 42.6%), followed by chlorotypes C and F (23 genotypes each). The majority of the genotypes in these groups had an unknown region of origin without correspondence in

Table 2 List of 39 profiles matched with the Vassal-Montpellier French grapevine collection and/or VIVC databases, including their region of origin, accession locations, numbers, and observed vernacular names in this study

Profile number	Sample origin (number of accessions per area)[a]	Vernacular names[b]	Cultivar prime name	Variety number VIVC	Country/Region of origin	Berry skin color	Use
LBN1	B(1), ML(1)	Khdoud el banet	Ahmar mawardi	134	Lebanon	Pink	Table
LBN2	B(1)	Sawda	Ahmeur bou ahmeur	140	Maghreb	Red	Table
LBN3	ML(1)	Kerka w sisan	Argentina	4452	Americas	Pink	Both
LBN4	B(3)	Asmi, Franji	Asmi rouge	14,788	Lebanon	Black	Table
LBN5	B(1)	–	Asswad afranji	17,397	Eastern Mediterranean	Black	Table
LBN6	BH(1), ML(1)	Tolki	Asswad karech	12,125	Lebanon	Black	Both
LBN7	B(2), ML(4), NL(2)	Kassoufi, Kassoufi Zahle, Mekaki, Zitani	Assoued kere	724	Eastern Mediterranean	White	Table
LBN8	B(1), BH(2)	Sabbaghi, Ari, Sweideh	Asswad abou khislé	17,396	Eastern Mediterranean	Black	Table
LBN9	B(1), ML(2)	Souri, Ajlouni, Bayadi	Zeini baladi	921	Lebanon	White	Table
LBN10	B(2), ML(3)	Bayade	Bayadi du Liban	24,176	Lebanon	White	Table
LBN11	B(2), BH(1), Ml(6) NL(4) SL(1)	Beitamouni, Bez el anzi, Bez el kalbi, Zeini, Asabih el aarous, Karn el gahzel	Beitamouni	14,790	Lebanon	White	Table
LBN14	B(2), BH(1), ML(3), NL(1)	Tfeifihi, Toffahi	Verico (Verigo)	4752	Eastern Mediterranean	Red	Table
LBN15	BH(3), ML(7), NL(16), SL(1)	Merwah, Baladi, Mekaki, Itani, Zehlawi, Daw el qamar, Ghomri	Blanc de Dellys	5201	Maghreb	White	Both
LBN19	B(1)	Ashlamish ahmar	Blush seedless	1472	Americas	Red	Table
LBN20	B(1)	Cardinal	Cardinal	2091	Americas	Red	Table
LBN21	ML(1)	Ashlamish abyad	Centennial seedless	2380	Americas	White	Table
LBN22	ML(1)	Bez el aanzi	Chami abiad	14,822	Eastern Mediterranean	White	Table
LBN23	ML(2)	Zahre, Chatawi	Crimson seedless	16,019	Americas	Red	Table
LBN24	B(6), BH(2), ML(11), NL(4), SL(1)	Maghdoushi, Hifawi, Solte, Abou loulou, Asabih el aarous	Dabouki	3309	Eastern Mediterranean	White	Both
LBN26	B(1)	–	Darawiski	16,144	Eastern Mediterranean		
LBN27	B(1)	Bez el Kalbi	Einuni (Lattuario nero)	6771	Western Europe		Table
LBN28	B(4), ML(1), NL(4)	Kassoufi, Kassoufi Zahle, Kosseifi	Inab el Mir	5523	Lebanon	White	Both
LBN42	ML(1)	–	Isabella	5560	Americas	Black	Both
LBN43	B(1)	Bakhouri	Italia	5582	Western Europe	White	Table
LBN44	B(1)	–	Jahafi	14,946	Eastern Mediterranean	White	Table

Table 2 (continued)

Profile number	Sample origin (number of accessions per area)[a]	Vernacular names[b]	Cultivar prime name	Variety number VIVC	Country/Region of origin	Berry skin color	Use
LBN57	ML(4), SL(2)	Meksasi	Kassoufi de la Bekaa	21,790	Eastern Mediterranean	White	Wine
LBN58	ML(3)	Kassoufi, Bayadet el hima	Kasoufi	6022	Eastern Mediterranean	White	Wine
LBN59	ML(2), NL(1)	Tkhalite, Mdawar, Kezeze	Kechlibar	6064	Eastern Europe	White	Table
LBN64	B(1)	Maghdoushi mjadad	Marawi	7379	Eastern Mediterranean	White	Both
LBN65	ML(1)	Bakhouri	Muscat de Hambourg	8226	Western Europe	White	Table
LBN66	B(1)	Miski	Muscat seedless Israel	41,959	Eastern Mediterranean	White	Table
LBN67	B(1)	Bayda	Narince	8351	Eastern Mediterranean	White	Both
LBN68	B(1), BH(4), NL(1)	Obeidy	Obeidi	8646	Lebanon	White	Wine
LBN69	ML(1)	Houzeirani	Perlette	9168	Americas	White	Table
LBN70	ML(1)	Bakhouri	Sauvignon blanc	10,790	Western Europe	White	Wine
LBN71	BH(1), ML(10), NL(1)	Sawda, Aswad, Jbaii, Airouni	Sebai assouad	10,851	Lebanon	Black	Table
LBN72	ML(2)	Cherfan	Souri	11,932	Lebanon	White	Both
LBN73	B(1)	Aswadi	Sugraone	12,087	Americas	White	Table
LBN74	B(1), ML(1), NL(1)	Ashlamish abyad, Zeini	Sultanina	12,051	Central Asia	White	Table

[a] Sample origins: Baalbek-Hermel (BH), Bekaa (B), Mount Lebanon (ML), North Lebanon (NL), and South Lebanon (SL) governorates

[b] Unknown vernacular names (-)

Berry skin colors are indicated. The cultivar prime name, code number and use in the VIVC database are also indicated

international databases. Very few genotypes corresponded to chlorotypes A (3), B (5), and E (2).

Genetic variation among a subset of cultivars of Lebanese origin and highly redundant ones

This analysis focused on a subset of 78 genotypes, comprising 63 cultivars of Lebanese origin, genotypes with no correspondence in databases (Table 3), and highly redundant cultivars of foreign origin (‘Blanc de Dellys’, ‘Dabouki’, ‘Verico’, ‘Assoued Kere’, ‘Kasouf’ and ‘Kasoufi de la Bekaa’). Principal coordinate analysis (PCoA) was performed based on the nSSR data for this subset to visualize the distribution of these genotypes (Fig. 3a). The first two PCoA axes explained 17.28% of the total genetic variation. On the resulting scatter plot, genotypes lacking correspondence in databases (red), genotypes of Lebanese origin (green), and the most redundant foreign genotypes in our study (blue) were scattered on the whole plane with no clear grouping, revealing no clear structuration of the genotypes. Additionally, the genotypes were observed in all quadrants of the scatter plot, with some genotypes, notably the red ones (those with no database matches), exhibiting distinct divergence, revealing the high diversity of Lebanese cultivars.

An unweighted pair group method with arithmetic mean (UPGMA) distance tree was constructed to examine the genetic relationships among this subset of 78 nonredundant genotypes. The genotypes exhibited varying levels of similarity, ranging from 20 to 85%. The resulting tree revealed six distinct clusters (G1 to G6), as depicted in Fig. 3b. Cluster G1 contained genotypes that had no database matches, with the exception of ‘Beitamouni’. Clusters G2, G3, G4,

Table 3 List of 63 profiles with no matches in the Vassal-Montpellier French grapevine collection and VIVC databases, including accession locations, numbers, and observed vernacular names in this study

Profile number	Sample origin (number of accessions per area)[a]	Vernacular names[b]	Berry skin color	Use	Profile number	Sample origin (number of accessions per area)[a]	Vernacular names[b]	Berry skin color	Use
LBN12	ML(1)	Loulahalou	White	Table	LBN13	ML(1)	Beitamouni	White	Table
LBN16	NL(1)	Jerdy	White	Table	LBN17	ML(1)	Merwah	White	Table
LBN18	B(2), NL(2)	Bez el kalbi	White	Table	LBN25	ML(1)	Bakhouri	White	Table
LBN29	NL(2)	Halbani	White	Table	LBN30	NL(1)	Bakhouri	White	Table
LBN31	NL(1)	Chatawi abyad	White	Table	LBN32	NL(1)	Alb el tayr	White	Table
LBN33	NL(1)	Bakhouri	White	Table	LBN34	NL(2)	Bakhouri	White	Table
LBN35	NL(1)	Aanabi	White	Table	LBN36	NL(1)	Chatawi	White	Table
LBN37	NL(1)	–	White	Table	LBN38	BH(1)	-	White	Table
LBN39	NL(1)	–	White	Table	LBN40	ML(1)	-	White	Table
LBN41	B(1)	Fokeih	White	Table	LBN45	BH(2), NL(1)	Marine	White	Both
LBN46	B(3), BEY(1), ML(2), SL(1)	Khodre, Kezeze, Aasmi, Kaboushiye	White	Table	LBN47	B(2), ML(1), NL(1)	Aasali, Ghosas, Hourani	White	Table
LBN48	NL(2)	Sabaghi, Sawda	Black	Table	LBN49	NL(4)	Shami, Jerdy, Halabani	White	Table
LBN50	NL(1)	Olhate	White	Wine	LBN51	NL(1)	Zitani	White	Wine
LBN52	NL(1)	Hommosi	White	Wine	LBN53	NL(2)	Kohl el ain, Zeitouni	White	Table
LBN54	B(2)	Aasiri	White	Table	LBN55	B(2)	Fodde	White	Both
LBN56	B(1)	Loulahalou	White	Table					
LBN60	B(2), ML(4), SL(1)	Zawtarani, Chatawi, Sawda, Maryami	Red	Table	LBN61	B(2), BH(2), ML(1), NL(8)	Jouzani, Mokh el baghel, Derbli, Beid el hamem, Baar el jamal, Shquife, Osmane,	White	Table
LBN62	B(3)	Halawani, Chamouti	White	Table	LBN63	ML(1)	Sawda	White	Table
LBN75	NL(3)	Zehlawi, Beid el eejel, Halbouti	White	Table	LBN76	NL(1)	Bez el kalbi	White	Table
LBN77	B(1)	–	White	Table	LBN78	ML(1)	Kerka w sisan	White	Table
LBN79	ML(1)	–	White	Table	LBN80	NL(1)	Sawda	Red	Table
LBN81	NL(1)	Berri	White	Table	LBN82	ML(1)	Sawda	Red	Table
LBN83	NL(1)	Sawda	Red	Table	LBN84	ML(1)	Chatawi	White	Table
LBN85	NL(1)	Aswadi	Red	Table	LBN86	ML(1)	Bakhouri	White	Table
LBN87	ML(1)	Bayadi	White	Table	LBN88	ML(2)	Bakhouri, Ras el maabour	White	Table
LBN89	B(1)	–	White	Table	LBN90	BH(1)	–	White	Table
LBN91	NL(1)	Beid el hamem	White	Table	LBN92	B(1)	–	White	Table

Table 3 (continued)

Profile number	Sample origin (number of accessions per area)[a]	Vernacular names[b]	Berry skin color	Use	Profile number	Sample origin (number of accessions per area)[a]	Vernacular names[b]	Berry skin color	Use
LBN93	ML(1)	–	White	Table	LBN94	B(1), NL(1)	Habb el remen, Asabih el aarous	White	Table
LBN95	B(1), NL(1)	Zitani	White	Wine	LBN96	B(2)	Airouni	Red	Table
LBN97	ML(2)	Karim, Jouzani	White	Table	LBN98	NL(1)	–	White	Table
LBN99	B(1)	–	White	Table	LBN100	B(1)	Bayda	White	Table
LBN101	ML(1)	Meksasi aswad	Black	Table	LBN102	NL(2)	Beid el hamem	White	Table

[a] Sample origins: Baalbek-Hermel (BH), Beirut (BEY), Bekaa (B), Mount Lebanon (ML), North Lebanon (NL), and South Lebanon (SL) governorates

[b] Unknown vernacular name (-)

Berry skin colors and use are indicated

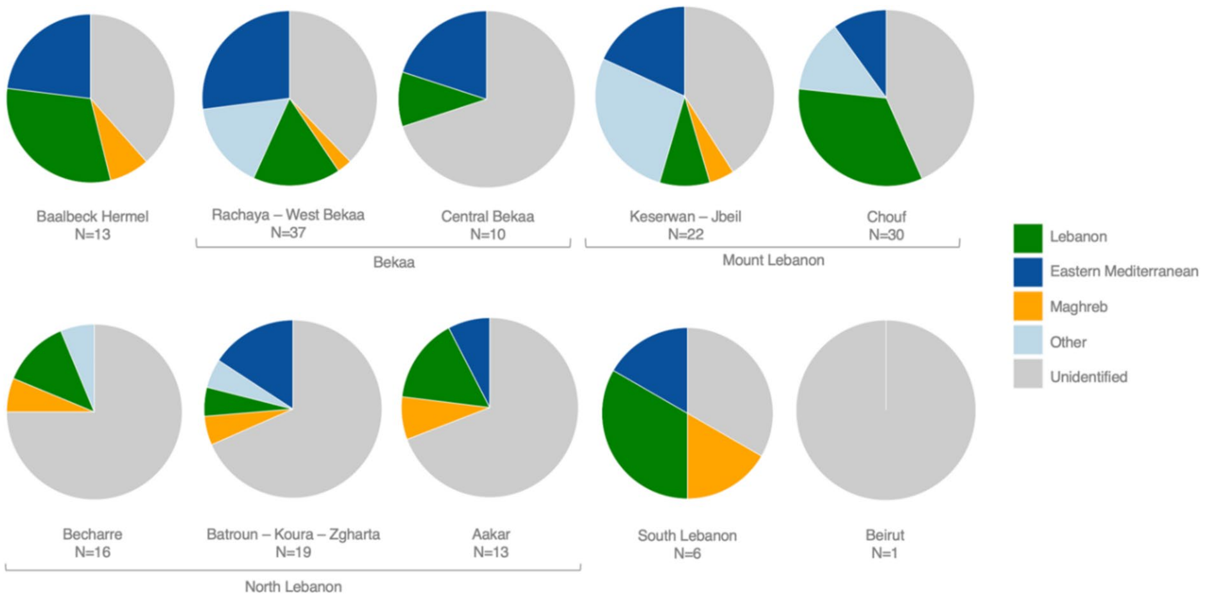


Fig. 2 Distribution of geographical origins of cultivars with identified genetic profiles across the different prospected areas of Lebanon. The numbers (n) indicate how many distinct genetic profiles were observed in each area

and G5 encompassed genotypes primarily of Lebanese and foreign origin alongside those genotypes with no database matches. Interestingly, G6 notably contained 4 genotypes that had no database matches; LBN52, LBN53, LBN80 and LBN81 exhibited considerable divergence from the rest of the other genotypes and were all found growing in the ancient vineyards of the Hadchit village in North Lebanon. The UPGMA distance tree analysis also revealed several pairs of closely related genotypes with similarity scores ranging from 20 to 31%. Among these, 'Beitamouni' was closely related to LBN12 and LBN13,

Table 4 Corresponding chlorotypes of the 102 nonredundant genotypes identified in this study divided according to region of origin according to the *Vitis* International Variety Catalog (VIVC)

Chlorotype	Lebanon	Eastern Mediterranean	Maghreb	Other	Unidentified	Total
A	0	1	0	2	2	3
B	0	1	0	2	2	5
C	1	1	1	3	17	23
D	3	9	0	7	27	46
E	1	1	0	0	0	2
F	5	0	1	0	17	23
Total	10	13	2	14	63	102

‘Blanc de Dellys’ showed similarity with LBN17, ‘Dabouki’ was genetically related to LBN25 and, last, LBN52 was closely related to LBN80.

Ampelographic variation within subset 2

To further characterize the grapevine genotypes without correspondence in the databases, a morphological description was generated using a set of 15 OIV descriptors for leaf, bunch, and berry traits, on subset 2 of 78 genotypes of Lebanese and foreign origin. A large diversity was obtained for the 15 OIV descriptors, as illustrated for the bunch shape in Fig. 4. Among these descriptors, two were consistently similar across all the genotypes; as upper leaf pilosity and pedicel pilosity were absent in all the cases, they were removed from the analysis.

A principal coordinate analysis (PoCA, Fig. 5a) of the morphological traits revealed a scattered distribution throughout the plot (the first two axes explained 27% of the total genetic variation); however, contrary to the genetic analysis, a faint structuration was revealed. Two genotypes (LBN96 and LBN52) clustered in the lower right quadrant of the plot, relatively distant from the others. The PoCA was divided into distinct patterns based on berry color and cluster characteristics. Colored berries in nonuniform, loose clusters were observed on the lower side of the axis. In contrast, denser clusters of green−yellow berries with uniform berry sizes were found on the upper side of the axis (group i). Additionally, as we move higher on the axis, accessions with pilosity on the lower side of the blade become more frequent. Another group included ‘Ahmar Mawardi’, ‘Zeini Baladi’, ‘Kassoufi’, ‘Beitamoni’, and ‘Dabouki’, and 15 genotypes without specific correspondence could be observed (group ii). All these genotypes have narrow ellipsoid green−yellow berries that are mainly used as table grape cultivars.

The UPGMA clustering analysis categorized the genotypes into five distinct groups (M1 to M5), each encompassing a mix of Lebanese, foreign and unidentified genotypes (Fig. 5b). The similarity among these groups ranged from 0 to 64%. Notably, zero similarity was observed for specific pairs, such as ‘Beitamouni’ and LBN25 or LBN17 and LBN16. Additionally, several profiles exhibited similarities below 15%: ‘Blanc de Dellys’, LBN16 and LBN17; LBN80 and LBN102; and ‘Sebai Asouad’ and LBN47. Interestingly, a comparable pattern of grouping based on SSR markers and OIV descriptors was observed, as was the case for the trio ‘Blanc de Dellys’, LBN16 and LBN17; however, LBN52, LBN53, LBN80 and LBN81 (G6 in molecular clustering) were not grouped together at the morphological level.

Parentage analysis

A parentage analysis using 22 SSR markers was conducted to gain deeper insights into the origins of the 63 unmatched genotypes and to underscore the extensive genetic diversity within Lebanese germplasm. The 63 distinct genotypes were integrated with those from the INRAE Vassal-Montpellier French grapevine collection database for an extensive exploration of potential kinship connections employing 22 SSR profiles. The LOD scores for the analyzed parent–offspring trios ranged from 10.59 to 37.5 (Supplementary Table S4). Notably, this pedigree analysis revealed connections to 35 cultivars that lacked matches in databases (Fig. 6), confirming their linkage to those investigated in this study, while 28 unidentified genotypes could not be associated with our dataset. Some pedigrees were also supported by

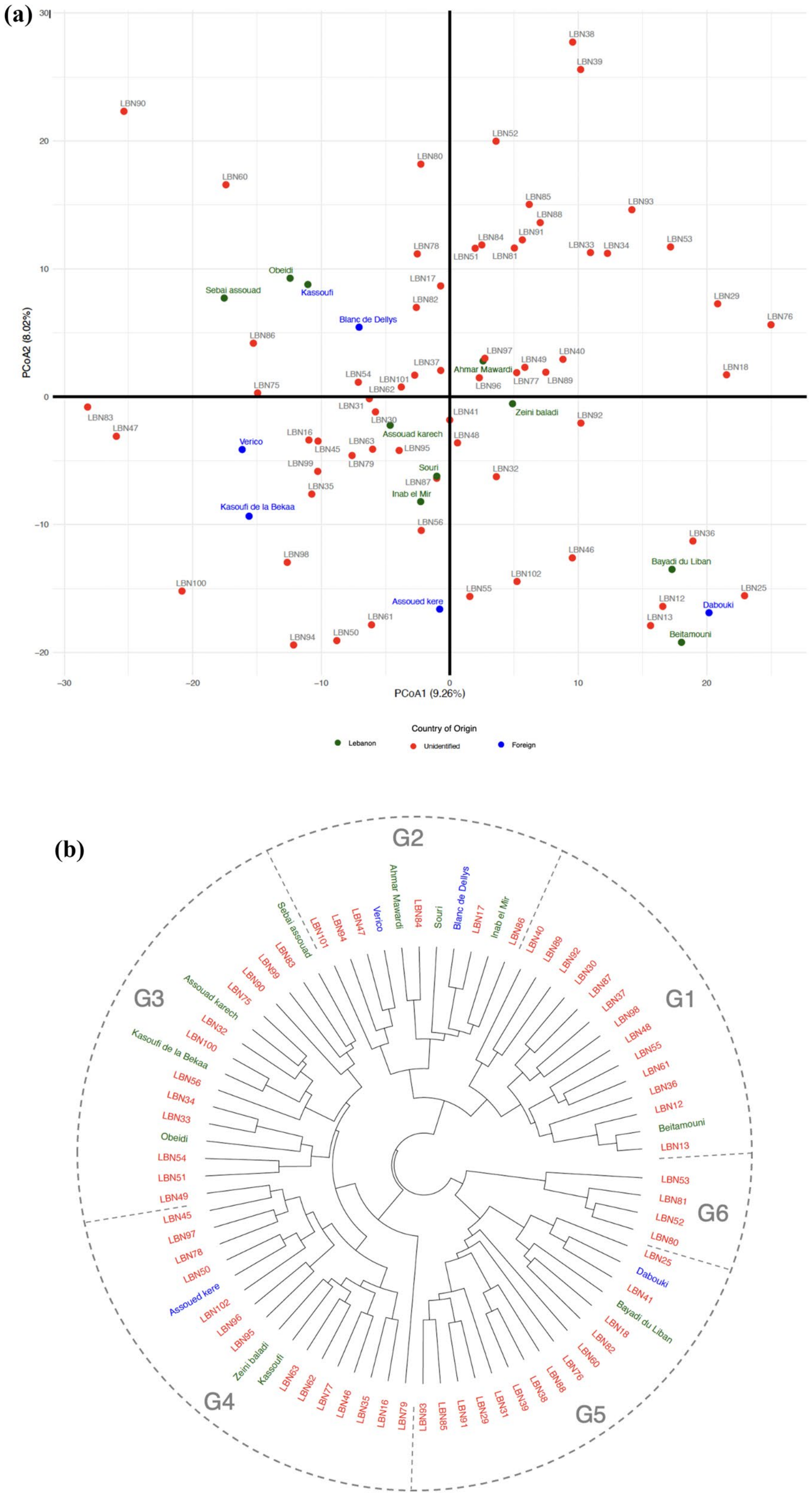


Fig. 3 Principal coordinate analysis (**a**) and unweighted pair group method with arithmetic mean (UPGMA) clustering (**b**) obtained from a dissimilarity matrix using 22 simple sequence repeat (SSR) markers from the set of 78 nonredundant genotypes comprising all identified genotypes of Lebanese origin (in green), genotypes with no correspondence in international databases (in red), and genotypes of foreign origin that were found to be mostly redundant throughout the study (in blue)

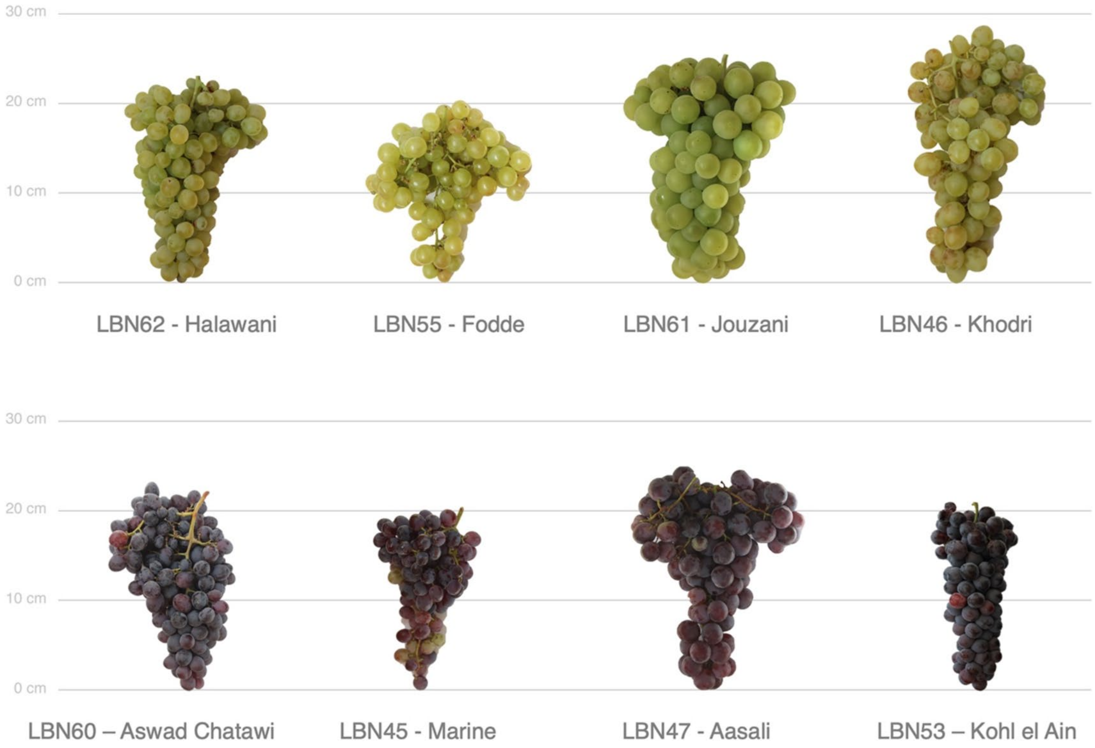


Fig. 4 Clusters of some grape cultivars identified in this study exhibiting unique, previously unrecorded genetic profiles

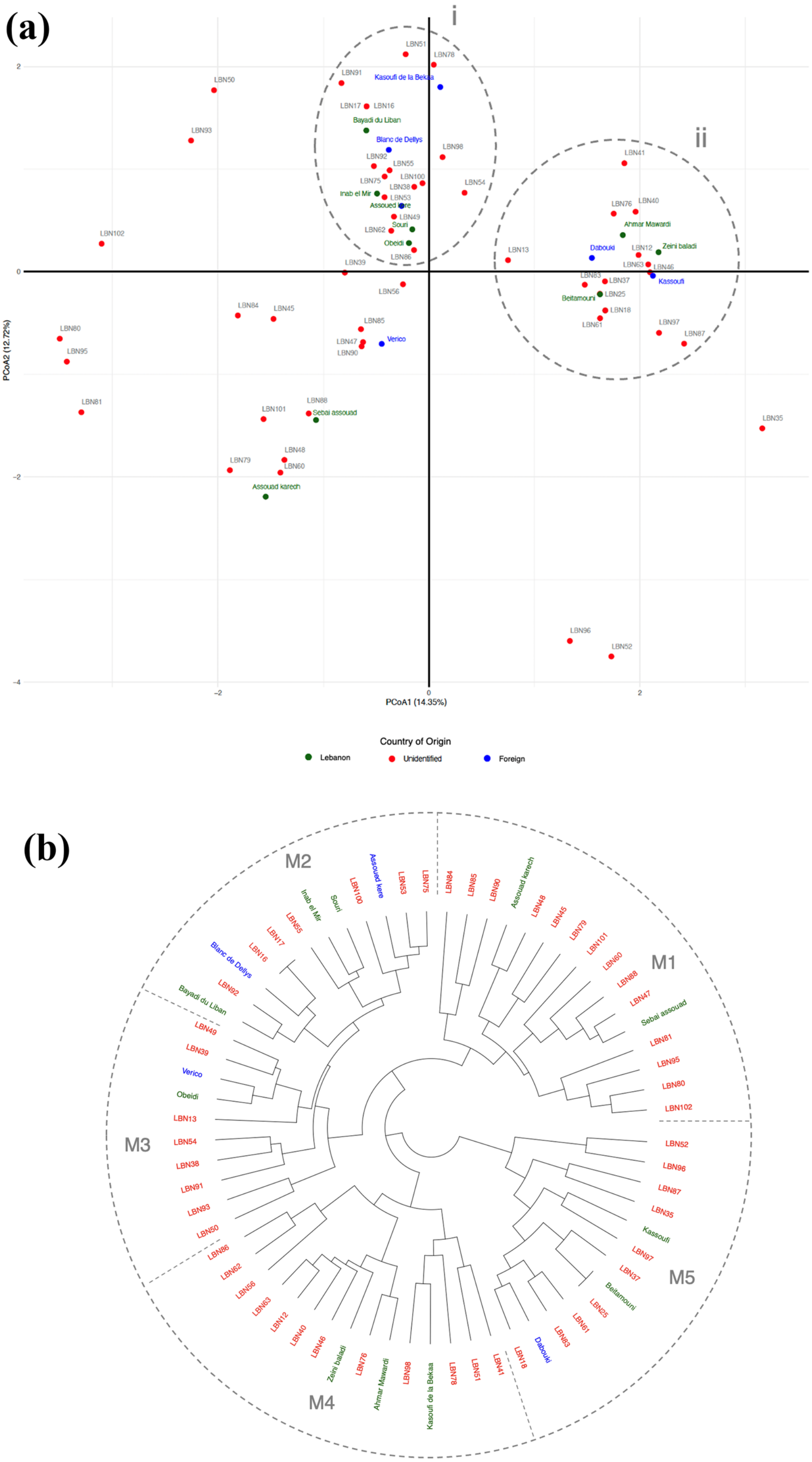
chlorotype analysis, which identified the female progenitor of certain cultivars.

All validated trios (mother, father, and offspring) and duos (parent-offspring) involving at least one of the identified genotypes are listed in Supplementary Table S4, along with their respective LOD scores and mismatching locus counts. Notably, our analyses revealed 7 compatible trios with high LODs (>26.95) and a maximum of 2 mismatching loci. The pedigrees highlight 'Assoued Kere''s role in Lebanese grapevine diversity, as it is involved in 8 pedigrees, 2 trios and 6 duo (Fig. 6). Furthermore, we identified one valid parent–offspring relationship each for 'Beitamouni' and 'Verico', one involving 'Ahmar Mawardi' and 'Kekhlibar' and one involving 'Zeini abiad'. Pedigree analysis also revealed the genetic origin of 'Kassoufi de la Bekaa', known as 'Meksasi' in Lebanon, which was traced back to a hybridization event between two cultivars, LBN62 and LBN100, observed for the first time in this study (LOD score 61.12). In addition, 27 duo relationships were identified. Close relationships were found on the UPGMA tree between 'Beitamouni' and LBN12 and LBN13 and between 'Blanc de Dellys' and LBN17 or 'Dabouki' and LBN25 do correspond to direct relationships.

Lebanese versus Mediterranean germplasms

A structural analysis was performed using STRUCTURE, with 63 unmatched genotypes and 771 cultivars from various countries around the Mediterranean to position Lebanese cultivars relative to others in the region. At $K=4$, four distinct groups were distinguished based on their geographic origin (Fig. 7). The Lebanese cultivars were grouped among the Eastern Mediterranean group. All the genotypes lacking correspondence in international databases in our study were found with the Lebanese cultivars in the Eastern Mediterranean group, along with cultivars from Levant and Turkey.

Fig. 5 Principal coordinate analysis (**a**) and unweighted pair group method with arithmetic mean (UPGMA) clustering (**b**) obtained from a dissimilarity matrix using morphological trait data from the set of 78 nonredundant genotypes comprising all genotypes of Lebanese origin (green), genotypes with no correspondence in international databases (red), and genotypes of foreign origins (blue) that were found to be mostly redundant throughout the study



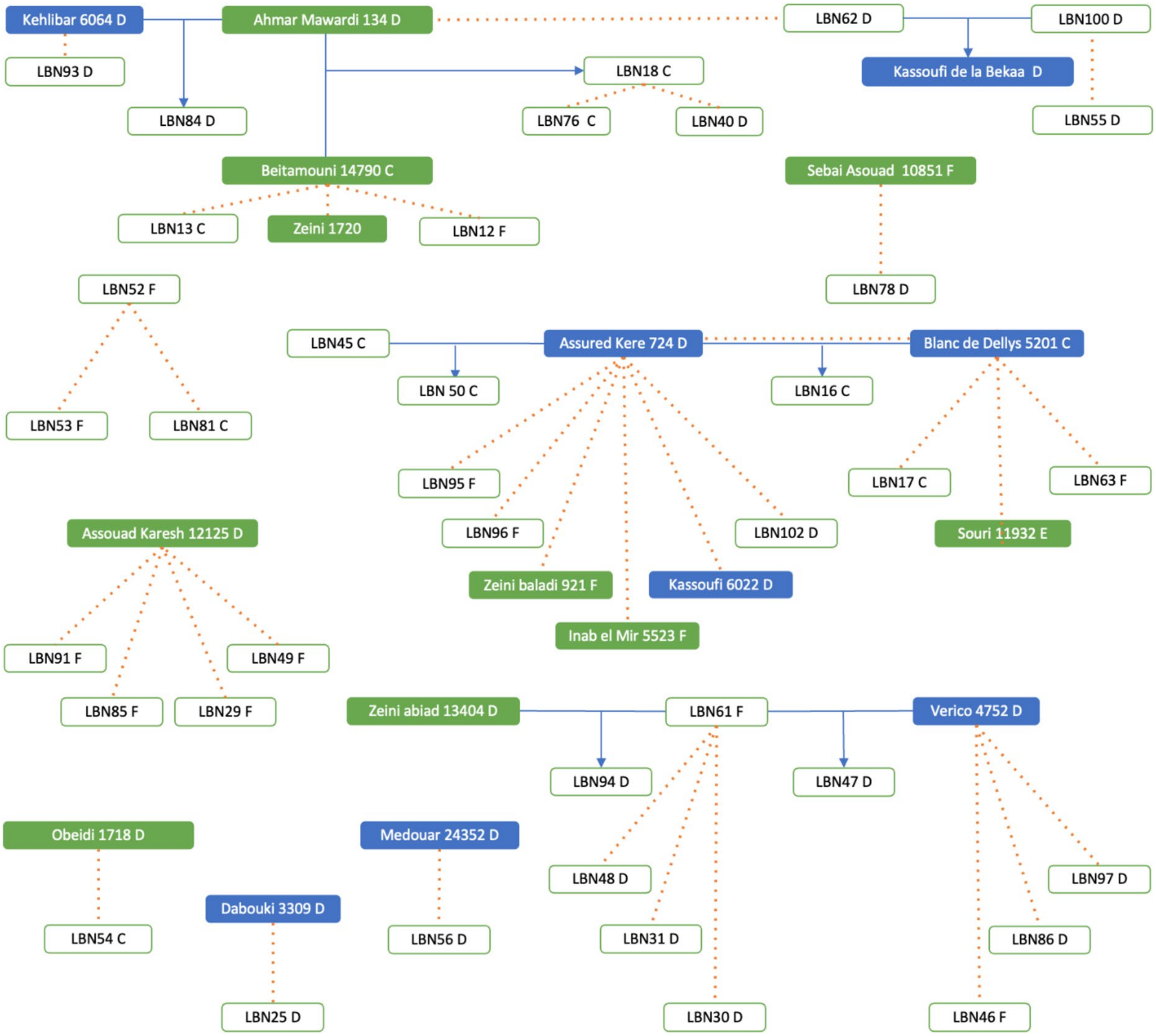


Fig. 6 First-order genetic relationships (trios and duos) detected among the observed grape cultivars sampled in Lebanon. The names include the *Vitis* International Variety Catalog (VIVC) code when known. The origin of the cultivar according to VIVC, if known, is indicated; blue denotes foreign origin, and green denotes Lebanese origin. Unidentified genotypes in international databases are represented in white boxes. Chlorotype information is indicated inside the box. The dashed red lines correspond to the duo relationship, indicating that the direction of the parentage is unknown, while the continuous blue lines represent the trio relationships

Discussion

This study represents a pioneering investigation into the genetic diversity of Lebanese grapevines, a country historically significant for viticulture because of its extensive cultivation heritage, diverse agroclimatic conditions, and Mediterranean presence. Unlike prior research in the country (Chalak et al. 2016, 2023; Chehade et al. 2022), this research used comprehensive molecular techniques to thoroughly characterize the grapevine germplasm, aiming to identify local cultivars and elucidate their genetic relationships within the context of global grapevine diversity. Our analysis revealed significant variations in the distribution of grapevine cultivars across Lebanon. The Chouf district of Mount Lebanon governorate along with the entire North Lebanon governorate hosted the highest number of Lebanese

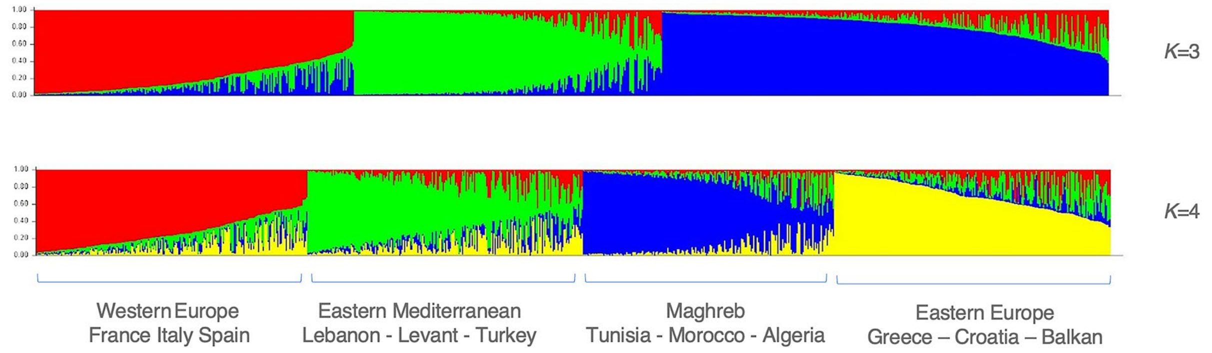


Fig. 7 Population structure of Lebanese accessions relative to Mediterranean populations (total of 834 cultivars) analyzed using the model-based Bayesian approach implemented in the program STRUCTURE and nSSR profiles for the 22 loci extracted from the INRAE Vassal-Montpellier French grapevine collection database

cultivars, indicating a strong historical and cultural connection to viticulture in these areas. Furthermore, the Bekaa Valley stands out as an agricultural hub attracting grapevine cultivars from the eastern Mediterranean due to its historical role as a transportation crossroads.

Almost 2/3 of the prospected accessions corresponded to known cultivars

The sampling survey was conducted in several areas of Lebanon, uncovering grapevine accessions that had not been studied and characterized before. A total of 267 accessions of table grapes, wine or both wine and table grapes were collected from the five governorates. The use of SSR markers and comparison with the very large Vassal-Montpellier French grapevine collection and VIVC databases enabled us to further characterize this material. Many of the accessions corresponded to the same SSR profile (or genotype) since only 102 distinct genotypes out of the 267 studied accessions were found in the sample. Among these, 39 genotypes corresponded to well-known wine, table, or multiple-use grape cultivars, predominantly representing autochthonous cultivars from the Eastern Mediterranean region, including Lebanon. These identified genotypes represented 163 collected accessions, almost 2/3rd of the prospective material. The abundances of ‘Dabouki’, ‘Assoued Kere’ and ‘Verico’, which are also prevalent in neighboring countries and have local names in Lebanon, indicate their significance as emblematic cultivars for the entire region and a shared cultural and historical connections across borders. Our analysis also revealed the notable presence of foreign grape cultivars, supporting historical reports of multiple introduction events into Lebanon from diverse regions. This influx underscores Lebanon’s role as a hub for grapevine exchange and cross-continental breeding activities. However, interestingly, we observed several international grape cultivars, such as ‘Sauvignon blanc’ for wine, ‘Italia’ and ‘Muscat de Hambourg’ for table grape, assigned local names, particularly in Bekaa Valley, likely influenced by nurseries supplying these cultivars or local farmers adopting familiar names. However, the proliferation of these international cultivars poses a potential threat to indigenous grapevine diversity. Nevertheless, prominent cultivars such as ‘Beitamouni’ and ‘Obeidi’, important for table and wine/arak production in Lebanese viticulture, respectively, were widely distributed across the country, as well as ‘Sebai Asouad’ and ‘Inab el Mir’, mainly grown on small family terraces and in gardens, reflecting their historical and economic significance despite the predominance of foreign cultivars in wine and table grape production in Lebanon. Cultivars of putative Lebanese origin, such as Beitamouni, have been reported throughout the Mediterranean basin, including in old vineyards that use other synonyms of this variety, such as ‘Cuerno de Buey’ in Spain, ‘Asba El Arus’ and ‘Safadi’ in the Holy Land, ‘Nychato’ in Greece, and ‘Rich Baba Sam’ in Tunisia (Drori et al. 2017; Ghaffari et al. 2013; Lefort and Roubelakis-Angelakis 2001; Tello et al. 2024). Most of these names are local terms that reference the distinctive horn-shaped berries of this variety. In contrast, despite the prevalence of the cultivar ‘Afuz Ali’, of putative Lebanese origin, which is present in 67 international repositories with 253 synonyms (vivc.de, n.d.), and documentation in various investigations across the Mediterranean (Augusto et al. 2021; Crespan et al. 2021; Ghaffari et al. 2013; Rahali et al. 2019; Maraš et al. 2020; Tello et al. 2024), was not observed in our study.

Vernacular names reflect some cultivar characteristics but may not be used solely for identification

During our study, we discovered and documented new vernacular names for grapevine cultivars not previously observed in the academic literature. Mainly accessions were named based on their geographical origin (‘Sariini’ and ‘Ainati’, villages in the Bekaa), morphological traits like berry shape (‘Hommosi’ meaning “chickpeas”), or distinctive traits (‘Bakhouri’ is related to its distinctive musk aroma). Interestingly, many cultivars carried different vernacular names in multiple collection sites (up to seven names for genotype LBN61). Moreover, a significant number of accessions under the same name, ‘Abyad’ or ‘Bayda’ (white) or ‘Aswad’ or ‘Sawda’ (black), based on berry skin color, exhibited distinct genotypes such as genotypes LBN80, 82 and 83, share the name ‘Sawda’. This highlights the need for genetic characterization to accurately understand and conserve Lebanon’s diverse grapevine germplasm. These results shed light on synonyms, homonyms and misnaming within the dataset, and confirm that vernacular names cannot be used for identification of plant material.

A large number of Lebanese accessions representing minor cultivars were not identified

During our investigation, we identified 63 grapevine genotypes that did not correspond to any entries in the existing databases, and were reported for the first time, such as LBN61, which was observed in various governorates of the country and is known for its different vernacular names reflecting the shape of the berries. Similarly, some profiles were observed in different areas and carry different vernacular names that do not reflect any common characteristics, as observed with profile LBN47 present in 3 regions and holding ‘Aasali’, ‘Ghosas’ and ‘Hourani’ as vernacular names. In contrast, some profiles, such as LBN45, can be found across different governorates and are consistently known by a single vernacular name, ‘Marine’ in this case. Nevertheless most of the profiles were exclusive to specific areas or even villages and found in only one place. For instance, ‘Fodde’ (LBN55) from Kfarmishki in West Bekaa and ‘Halbouti’ (LBN75) from Hadchit in North Lebanon are unique to these well-known grape-producing villages. Additionally, profiles specific to certain governorates include LBN49, specific to North Lebanon, and LBN62, specific to the Bekaa, both of which are known by different vernacular names depending on the location. In general, these unmatched genotypes likely represent minor autochthonous cultivars, but with local importance and valuable traits, such as fruit quality and adaptation to the local environments. These genotypes may originate from vines grown directly from seeds, either intentionally when cuttings are not available or from naturally germinated seeds, or they might be true traditional cultivars that were once historically propagated vegetatively but are now at high risk of disappearing. Maraš et al. (2020) refer to these as “proto-varieties”. And in fact, the parentage analysis revealed notable parent–offspring relationships among those Lebanese cultivars. This analysis also provided valuable clues for tracing the origin of these unidentified cultivars and establishing connections to cultivars of known origin, thus enriching our understanding of Lebanon’s grapevine heritage. Sexual reproduction was recognized as the primary mechanism driving the generation of new grapevine genotypes, with autochthonous cultivars serving as key contributors to local grapevine diversity (This et al. 2006): in the present analysis, ‘Betamouni’, ‘Verico’ and ‘Assoued kere’, involved in many parent–offspring relationships, may have played this role.

Lebanese cultivars revealed significant morphological diversity

Morphological characterization revealed significant diversity, particularly in berry shape and color. This diversity of findings suggests that local farmers have sought variations in berry color and shape and may have selected these cultivars for use as table grapes or for wine/arak production based on specific desirable traits, such as aroma and palatability, as observed in the Muscat-flavored Bakhouri accessions. This selection process was evident in group ii of the PCA, where the majority of table grape cultivars, including Beitamouni and Dabouki, were found. Moreover, the morphological clustering grouped together (group i of the PoCA) a set of accessions with dense clusters and small round berries, including 'Obeidi' and 'Blanc de Dellys' (synonyms 'Marouhé' and 'Merwah'), two cultivars well known in Lebanon for their use in wine production. This finding suggested that, based on their morphological characteristics, these accessions have similar traits to cultivars used for wine production. Therefore, further examination of those genetic profiles could be important for determining whether these accessions can also be used for the production of good wine. Hence, evaluating the fermentation potential of these unidentified grape cultivars is pivotal for the currently booming Lebanese wine market.

While certain genotypes may exhibit divergence between molecular and morphological traits, this underscores the multifaceted nature of genetic diversity within Lebanon's grapevine population. For instance, morphologically similar genotypes, such as 'Beitamouni' and 'Dabouki', which were clustered close to each other based on morphological characteristics, had distinct genetic profiles. This confusion is also evident among producers and even consumers; during our collection process, accessions identified by farmers as 'Beitamouni' were sometimes genetically identified as 'Daboiki', and vice versa.

Lebanese accessions clustered with Eastern Mediterranean cultivars

A previous study (Lacombe et al. 2013) revealed intricate parentage networks linking multiple Lebanese and eastern Mediterranean grapevine cultivars, reflecting a rich history of genetic relationships among these cultivars. The integration of parentage analysis and genetic diversity assessments thus provides greater clarity on the origins and relatedness of grapevine cultivars. However, genotypes with missing parents might still be present in the country but were not sampled yet or might have disappeared over time.

Our comprehensive genetic analysis revealed intriguing insights into the relationships among grapevine cultivars. Both molecular and morphological scatter plots demonstrated close genetic relationships between known and unknown genotypes, suggesting genetic relatedness or even shared ancestry. This characterization highlighted the complementary nature of combining molecular and morphological techniques for distinguishing among cultivars and achieving a broader understanding of grapevine diversity. nSSR markers and ampelography have already been proven useful for determining the identity of collected grapevine accessions (Bacilieri et al. 2013; Margaryan et al. 2021; Vršič et al. 2024; Žulj Mihaljevic et al. 2020). The chlorotype analysis revealed the presence of chlorotypes E and F, which are predominantly associated with wild grapevines rather than cultivated grapevines, according to Arroyo-Garcia et al. (2006). Few cultivars containing chlorotypes E and F have been found in cultivated grapevine plants, particularly in Mediterranean countries, e.g., Croatia and Italy (Rossoni et al. 2003; Salmaso et al. 2008; vivc.de, n.d.), while the presence of the other chlorotypes A, B, C and D has been commonly reported in cultivated grapevine plants (De Mattia et al. 2008; Maraš et al. 2020). The abundance of chlorotype F in our study may be attributed to the exclusion of other areas of the Easter Mediterranean region including Lebanon in the initial 2006 study, which primarily focused on accessions from Turkey. Additionally, Lebanon is recognized as part of the Near East Center of Grapevine domestication (Dong et al. 2023). The presence of these chlorotypes in wild female plants suggested ongoing genetic interactions and hybridization events between cultivated and potentially wild grapevines in the region, enriching the genetic diversity of the population. This underscores the importance of considering the geographic context and historical dynamics of grapevine domestication in elucidating the genetic landscape and evolutionary processes shaping grapevine diversity in the region.

In addition, structural analysis revealed the grouping of Lebanese cultivars within the Eastern Mediterranean cluster, reflecting their genetic affinity and common ancestry within this regional context, similar to the findings of previous research (Nicolas et al. 2016). Structural analysis also revealed differences in the Eastern Mediterranean grapevine germplasm between the Eastern European and Maghreb germplasm groups. This positioning highlights the bridging role of the Eastern Mediterranean as a center of grapevine domestication and diversification, serving as a crucial conduit for genetic exchanges between Eastern Europe, the Maghreb, and adjacent regions.

What is truly autochthonous?

The challenging task of assigning specific origins to grapevine cultivars requires a multifaceted approach in which molecular data are integrated with bibliographic and ampelographic records. An example is the case of 'Merwah', an enigmatic grapevine variety in Lebanon. Despite being the most frequently observed profile in our study and identified in 27 accessions from ancient vineyards with vines older than 80 years, 'Merwah" corresponds to 'Blanc de Dellys', a variety not supposed to be of Lebanese origin. This variety is registered as Tunisian in one database and Algerian in another, with its name referencing Dellys, a city on the Mediterranean coast of Algeria. The discrepancy in database records raises questions about how cultivars are identified and why they are attributed to different countries.

Further analysis through parentage identification revealed a genetic relationship between 'Merwah' (syn. 'Blanc de Dellys') and 'Assoued Kere', which originated from Turkey, and 'Souri', a Lebanese variety. Additionally, structure analysis positioned 'Blanc de Dellys' within the heart of the Eastern Mediterranean group, raising questions about its true origin; is it genuinely from the Maghreb or the Eastern Mediterranean? If it belongs to the Eastern Mediterranean group, does its widespread presence in Lebanon suggest a local origin, possibly transported during the French Mandate era to the Maghreb, where it was first characterized? In contrast, could 'Blanc de Dellys' have been introduced to Lebanon from Algeria by Ottomans or by Christian monks, explaining its abundance near ancient monasteries? Nevertheless, our molecular evidence strongly suggests that 'Blanc de Dellys' could very possibly be of pure Lebanese origin. The similarity we observed with the Eastern Mediterranean gene pool is likely due to the Ottoman rule over Bilad al Sham, which lasted more than 400 years. During this period, the region was subjected to a single administration, facilitating the circulation and exchange of grapevine propagation material. This extensive exchange of genetic material among citizens significantly shaped the current grapevine germplasm across the eastern shores of the Mediterranean, including Lebanon, to present-day Tunisia and Algeria in the western Mediterranean basin.

For instance, the variety 'Assoued Kere', which is of Turkish origin, shows numerous parent–offspring relationships with Lebanese cultivars such as 'Inab el Mir' and 'Zeini Baladi' and several unidentified cultivars found in this study. Interestingly, according to the databases, other synonyms for 'Assoued Kere' are 'Kassoufi' and 'Kassoufi enta', both of which are Lebanese terms commonly found in the Bekaa area, meaning 'involved in eating', reflecting its use as a table grape variety. Additionally, the prime name 'Assoued Kere', meaning 'black circular' in Arabic, does not apply to the variety because it has white and elongated berries. It is probable that this erroneous homnym comes from a mistake in the name of another Lebanese variety with black berries, the 'Assouad Karech'. Additionally, hisotoric ampelogaphic evidence provided by Jean Marie Guillon in 1896, state 'Asoued Kere' of Palestenian origin. All this evidence adds complexity to the origin of this variety and suggests that 'Assoued Kere' might not be of Turkish origin but rather of Lebanese or even Palestenian origin. Nonetheless, this highlights the intricate genetic diversity and lineage within Lebanon's and the eastern Mediterranean grapevine germplasm. Other cases from this period include 'Kassoufi de la Bekaa', where the name reflects a governorate in Lebanon and a variety locally known as 'Meksasi' that is commonly present in the country. The databases used different analyses of such cultivars. For instance, in the Vassal-Montpellier French grapevine collection database, it is registered as Lebanese; however, in the VIVC, it is listed as Syrian. Similarly, 'Kasoufi', which is recorded as Turkish in the Vassal-Montpellier French grapevine collection database and as Syrian in the VIVC. Last, in the case of 'Dabouki', Galet (2000) notes that this variety is cultivated across the Near East, including Palestine, Lebanon, Syria, and Jordan. This widespread cultivation, which was clearly observed in our study, can be interpreted within the historical context of Ottoman rule, raising questions about its country of origin, especially since it was also redundantly identified in Algeria (Rahali et al. 2019).

These inquiries highlight the intricate nature of grapevine origins and historical movements, underscoring the necessity of rigorous genetic and historical investigations to unravel the complex narratives behind grapevine diversity and dissemination across regions. Hence, these cultivars were likely shared across the entire region rather than confined to a single country. This also indicates that these local cultivars were highly valued by local communities over time, leading to their propagation and preservation across various regions.

Conclusion

Our findings highlight the richness and complexity of Lebanon's grapevine germplasm. The discovery of a significant number of previously unidentified genotypes not only enhances our understanding of Lebanon's viticultural landscape but also underlines the resilience and preferences for local cultivars among Lebanese farmers, and underscores the need for concerted conservation efforts to protect and propagate these rare and unique resources, particularly the minor Lebanese autochthonous cultivars. Local farmers, especially in marginal areas such as North Lebanon, play a crucial role in conserving viticultural practices and traditional grapevine cultivars adapted to the area's climate and preferences (Merheb et al. 2024a; b). Nevertheless, the invaluable material and data generated from this study will be added to national and international gene banks. Future research should extend to other parts of the country, particularly South Lebanon, to further enrich the assessed gene pool. Additionally, exploring grapevine wild relatives in Lebanon, which is part of the Near East domestication area, could provide further insights. Finally, assessing local grapevines for their resilience to heat and drought conditions, as well as evaluating their vinification potential, could also be highly useful.

Acknowledgements The authors express their gratitude to all those who assisted in the prospection and collection of plant material in Lebanon. They also extend their thanks to the Lebanese growers of the grapevine accessions who allowed access to their vineyards and family gardens. Special thanks to Cécile Marchal, director of the INRAE Vassal-Montpellier French grapevine collection, and her team for providing access to plant material and documentation. Thanks to Philippe Chatelet, for proof reading of the English language.

Author contributions Study conception and design by P.T. and L.C. Prospections by J.M. Material preparation, data collection and interpretation of genetic diversity and analysis were performed by J.M., C.R. and V.L. The first draft of the manuscript was written by J.M. assisted by P.T., L.C. and T.L. All authors discussed the results, commented on previous versions of the manuscript and read and approved the final manuscript.

Funding This work was supported by the French Lebanese CEDRE project (49320 QJ), the PRIMA 2021 Sustemicrop project (No ANR-22-PRIM-0012-04) and the LU Scientific Research Support Program (DIVAG project).

Data availability Molecular data from the Lebanese accessions are available in Supplementary Table S3.

Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval No approval was required for this study.

Consent for publication Not applicable.

References

Arroyo-García R, Lefort F, Andrés MT, Ibáñez J, Borrego J, Jouve N, Cabello F, Martínez-Zapater JM (2002) Chloroplast microsatellites polymorphisms in *Vitis* species. Genome 45:1142–1149. https://doi.org/10.1139/g02-087

Arroyo-García R, Ruiz-García L, Bolling L, Ocete R, López MA, Arnold C, Ergul A, Söylemezo LuG, Uzun HI, Cabello F, Ibáñez J (2006) Multiple origins of cultivated grapevine (*Vitis vinifera* L. ssp. *sativa*) based on chloroplast DNA polymorphisms. Mol Ecol 15:3707–3714. https://doi.org/10.1111/j.1365-294X.2006.03049.x

Augusto D, Ibáñez J, Pinto-Sintra AL, Falco V, Leal F, Martínez-Zapater JM, Oliveira AA, Castro I (2021) Grapevine diversity and genetic relationships in Northeast Portugal Old Vineyards. Plants 10:2755. https://doi.org/10.3390/plants10122755

Bacilieri R, Lacombe T, Le Cunff L, Di Vecchi-Staraz M, Laucou V, Genna B, Péros JP, This P, Boursiquot JM (2013) Genetic structure in cultivated grapevines is linked to geography and human selection. BMC Plant Biol 13:25. https://doi.org/10.1186/1471-2229-13-25

Branas J, Truel P (1967) Viticulture. Imprimerie Paul Déhan, Montpelier

Chalak L, Rahme S, Azzi R, Guiberteau F, Touma JA, Boursiquot JM (2016) Assessment of the Lebanese grapevine germplasm reveals a substantial diversity and a high potential for selection. BIO Web of Conferences 7:1020. https://doi.org/10.1051/bioconf/20160701020

Chalak L, Merheb J, Massaad M (2023) Phenotyping grapevine landraces diversity in the dry Bekaa region of Lebanon. Acta Hortic 1370:95–102. https://doi.org/10.17660/ActaHortic.2023.1370.13

Chehade A, Chalak L, Merheb J, Elbitar A, Rmeily E, Madi N, Massaad M (2022) Genetic and ampelographic characterization of grapevine accessions maintained in the Lebanese national collection. Adv Hort Sci 36:215–226. https://doi.org/10.36253/ahsc-13045

Crespan M, Migliaro D, Larger S, Pindo M, Palmisano M, Manni, et al (2021) Grapevine (*Vitis vinifera* L.) varietal assortment and evolution in the Marche region (central Italy). Oeno One 55:17–37. https://doi.org/10.20870/oeno-one.2021.55.3.4628

De Mattia F, Imazio S, Grassi F, Baneh HD, Scienza A, Labra M (2008) Study of genetic relationships between wild and domesticated grapevine distributed from Middle East regions to European countries. Rendiconti Lincei-Scienze Fisiche E Naturali 19:223–240. https://doi.org/10.1007/s12210-008-0016-6

Dong Y, Duan S, Xia Q, Liang Z, Dong X, Margaryan K et al (2023) Dual domestications and origin of traits in grapevine evolution. Science 379:892–901. https://doi.org/10.1126/science.abh2166

Drori E, Rahimi O, Marrano A, Henig Y, Brauner H, Salmon-Divon M, Netzer Y, Prazzoli ML, Stanevsky M, Failla O, Weiss E, Grando MS (2017) Collection and characterization of grapevine genetic resources (*Vitis vinifera*) in the holy land, toward the renewal of ancient winemaking practices. Sci Rep 7:44463. https://doi.org/10.1038/srep44463

Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. Mol Ecol 14:2611–2620. https://doi.org/10.1111/j.1365-294X.2005.02553.x

Falush D, Stephens M, Pritchard JK (2007) Inference of population structure using multilocus genotype data: dominant markers and null alleles. Mol Ecol Notes 7:574–578. https://doi.org/10.1111/j.1471-8286.2007.01758.x

Galet P (2000) Dictionnaire encyclopédique des cépages. Hachette, Paris, France

Gerber S, Chabrier P, Kremer A (2003) FAMOZ: a software for parentage analysis using dominant, codominant and uniparentally inherited markers. Mol Ecol Notes 3:479–481. https://doi.org/10.1046/j.1471-8286.2003.00439.x

Ghaffari S, Hasnaoui N, Zinelabidine LH, Ferchichi A, Martínez Zapater JM, Ibáñez J (2013) Genetic identification and origin of grapevine cultivars (*Vitis vinifera* L.) in Tunisia. Am J Enol Vitic 64:538–544. https://doi.org/10.5344/ajev.2013.12135

Guillon JM (1896) Les cépages orientaux. G. Carré

Jones AG, Small CM, Paczolt KA, Ratterman NL (2010) A practical guide to methods of parentage analysis. Mol Ecol Res 10:6–30. https://doi.org/10.1111/j.1755-0998.2009.02778.x

Khater S, Chehade A, Elbitar A, Karam N, Merheb J, Chalak L (2024) Intravarietal genetic diversity in grapevine (*Vitis vinifera* L.) cultivars of Lebanon as revealed by ampelographic descriptors and ISSR markers. Acta Hortic (in press)

Lacombe T (2023) *Vitis* genetic resources: current challenges, achievements and perspectives. Vitis 62:65–75. https://doi.org/10.5073/vitis.2023.62.65-75

Lacombe T, Boursiquot JM, Laucou V, Di Vecchi M, Pedros JM, This P (2013) Large-scale parentage analysis in an extended set of grapevine cultivars (*Vitis vinifera* L.). Theor Appl Genet 126:401–414. https://doi.org/10.1007/s00122-012-1988-2

Laucou V, Lacombe T, Dechesne F, Siret R, Bruno JP, Dessup M, Dessup T, Ortigosa P, Parra P, Roux C, Santoni S, Varès D, Péros JP, Boursiquot JM, This P (2011) High throughput analysis of grape genetic diversity as a tool for germplasm collection management. Theor Appl Genet 122:1233–1245. https://doi.org/10.1007/s00122-010-1522-1

Lebanese Central Administration of Statistics (2012) Morphology, climatology, hydrology, vegetation, and environment. Retrieved May 20, 2024, from http://www.cas.gov.lb

Lefort F, Roubelakis-Angelakis KA (2001) Genetic comparison of Greek cultivars of *Vitis vinifera* L. by nuclear microsatellite profiling. Am J Enol Vitic 52:101–108. https://doi.org/10.5344/ajev.2001.52.2.101

De Lorenzis G (2023) From ancient to modern grapevine cultivars: a lesson from cultivars that made the history of viticulture. In Proceedings of XIII international conference on grapevine breeding, genetics and management, Eds: A Atak and G Costa, Turkey, August 2023. Acta Hortic 1385: 47–58. https://doi.org/10.17660/ActaHortic.2023.1385.5

Maraš V, Tello J, Gazivoda A, Mugoša M, Perišić M, Raičević J, Štajner N, Ocete R, Božović V, Popović T, García-Escudero E, Grbić M, Martínez-Zapater JM, Ibáñez J (2020) Population genetic analysis in old Montenegrin vineyards reveals ancient ways currently active to generate diversity in *Vitis vinifera*. Sci Rep 10:15000. https://doi.org/10.1038/s41598-020-71918-7

Margaryan K, Melyan G, Röckel F, Töpfer R, Maul E (2021) Genetic diversity of Armenian grapevine (Vitis vinifera L.) germplasm: molecular characterization and parentage analysis. Biology 10:1279. https://doi.org/10.3390/biology10121279

Merheb J, Roux C, Laucou V, Ouaini N, Beyrouthy M, Ghorra Chammoun Y, Touma JA, This P, Chalak L (2024a) Genetic diversity of grapevine landraces grown in a traditional vineyard in North Lebanon. In Proceedings of xiii international conference on grapevine breeding, genetics and management, Eds: A Atak and G Costa, Turkey, August 2023. Acta Hortic 1385:73–80. https://doi.org/10.17660/ActaHortic.2024.1385.10

Merheb J, Roux C, Laucou V, Touma JA, Ouaini N, Beyrouthy M, Karam N, Ghorra Chammoun Y, Lacombe T, This P, Chalak L (2024b) Genetic profiling of a hidden grapevine germplasm in the ancient terraces of Hadchit village, North Lebanon. Acta Hortic (in press)

Nicolas SD, Péros JP, Lacombe T, Launay A, Le Paslier MC, Bérard A et al (2016) Genetic diversity, linkage disequilibrium and power of a large grapevine (*Vitis vinifera* L) diversity panel newly designed for association studies. BMC Plant Biol 16:74. https://doi.org/10.1186/s12870-016-0754-z

OIV (2009) OIV descriptor list for grape varieties and *Vitis* species, 2nd edn. Organization Internationale de la Vigne et du Vin, Paris

Orsingher A, Amicone S, Kamlah J, Sader H, Berthold C (2020) Phoenician lime for Phoenician wine: iron age plaster from a wine press at Tell el-Burak Lebanon. Antiquity 94:1224–1244. https://doi.org/10.15184/aqy.2020.165

Rahali M, Migliaro D, Laiadi Z, Bertazzon N, Angelini E, Crespan M (2019) Genetic identification, origin and sanitary status of grapevine cultivars (*Vitis vinifera* L.) grown in Babar. Algeria Vitis 58:153–158. https://doi.org/10.5073/vitis.2019.58.153-158

Rossoni M, Labra M, Imazio S, Grassi F, Scienza A, Sala F (2003) Genetic relationships among grapevine cultivars grown in Oltrepò Pavese (Italy). Vitis 42:31–34

Salmaso M, Malacarne G, Troggio M, Faes G, Stefanini M, Grando MS, Velasco R (2008) A grapevine (*Vitis vinifera* L.) genetic map integrating the position of 139 expressed genes. Theor Appl Genet 116:1129–1143. https://doi.org/10.1007/s00122-008-0723-6

Tello J, Galán A, Rodríguez-Torres I, Martínez-Zapater JM, Rubio Casanova A, Ibáñez J (2024) Genetic fingerprinting reveals how traditional farming practices aided to preserve ancient table grape varieties in Almería (southeastern Spain). Plants, People, Planet. https://doi.org/10.1002/ppp3.10537

This P, Jung A, Boccacci P, Borrego J, Botta R, Costantini L, Crespan M, Dangl GS, Eisenheld C, Ferreira-Monteiro F, Grando S, Ibáñez J, Lacombe T, Laucou V, Magalhães R, Meredith CP, Milani N, Peterlunger E, Regner F, Zulini L, Maul E (2004) Development of a standard set of microsatellite references alleles for identification of grape cultivars. Theor Appl Genet 109:1048–1058. https://doi.org/10.1007/s00122-004-1760-3

This P, Lacombe T, Thomas MR (2006) Historical origins and genetic diversity of wine grapes. Trends Genet 22:511–519. https://doi.org/10.1016/j.tig.2006.07.008

Di Vecchi-Staraz M, Boselli M, Laucou V, Lacombe T, This P, Gerber S, Varès D, du Domaine UE (2005) Famoz A software for large scale parentage analysis in *Vitis vinifera* L. species. In: ISHS (ed) Proceedings of the international workshop on advances in grapevine and wine research. Acta Hortic 754:79–83. https://doi.org/10.17660/ActaHortic.2007.754.9

Viala P, Vermorel V (1905) Traité général de viticulture : Ampélographie (Vol. 1). Masson et Cie

Villano C, Aiese Cigliano R, Esposito S, D'Amelia V, Iovene M, Carputo D, Aversano R (2022) DNA-based technologies for grapevine biodiversity exploitation: state of the art and future perspectives. Agronomy 12:491. https://doi.org/10.3390/agronomy12020491

Vivc.de. (n.d.). *Vitis* international variety catalog. Retrieved May 18, 2024, from https://www.vivc.de

Vršič S, Trapp O, Maul E, Röckel F, Perko A (2024) Monitoring and genetic characterization of historical grapevine varieties (*V. vinifera* ssp.) from Styria in Slovenia. Agriculture 14:640. https://doi.org/10.3390/agriculture14040640

Žulj Mihaljević M, Maletić E, Preiner D, Zdunić G, Bubola M, Zyprian E, Pejić I (2020) Genetic diversity, population structure, and parentage analysis of croatian grapevine germplasm. Genes 11:737. https://doi.org/10.3390/genes11070737