

Research Article

The Genetic Characterization of Grapevine Genetic Resources in Peru Identifies Novel Criolla Varietal Genotypes

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Received 23 June 2025; Revised 26 August 2025; Accepted 30 August 2025

Academic Editor: Jicheng Zhan

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Today's wine and Pisco grape production in Peru is largely dominated by a reduced number of grapevine (*Vitis vinifera* L.) varieties. However, Peru is home to a high number of lesser-known local varieties that are still present in traditional vineyards and/or preserved in national or regional grapevine collections, of interest to diversify the local industry. Here, we analyzed 121 grapevine accessions preserved in the ampelographic collection of the Instituto Nacional de Innovación Agraria (INIA-EEA) at Chincha (Ica, Peru), using a combined SNP and SSR genetic profiling strategy for their molecular characterization and identification. This approach led to the differentiation of 45 different grapevine genetic profiles, 40 of them corresponding to already catalogued table and wine grape varieties of diverse geographic origin. Interestingly, we found five grapevines with genetic profiles not registered before. Some of them were found to be descendants of Listán Prieto and/or Muscat of Alexandria, increasing the known role of these two varieties as founders of the Criolla varieties, the autochthonous South American grapevine germplasm. A predominance of the varieties Listán Prieto and Quebranta was also observed, as they were found to be preserved multiple times in the INIA-EEA Grapevine Collection under different local synonyms. Strikingly, the phenotypic description of different accessions matching the genotypes of these two relevant varieties showed a high degree of phenotypic diversity, including the identification of novel berry-color and Muscat-flavored somatic variants that might have a direct impact toward local grape industry diversification. These findings underline the importance of the local genetic resources preserved at the INIA-EEA Grapevine Collection for grapevine improvement. Registering the newly identified varieties and somatic variants with novel traits of interest would represent a crucial first step toward making this plant material available to local grape growers, ultimately promoting the diversification of the Peruvian grape, wine, and Pisco industries.

Keywords: genetic diversity; molecular ampelography; pisco; simple sequence repeat (SSR); single nucleotide polymorphism (SNP); *Vitis vinifera* L.

1. Introduction

The grapevine (*Vitis vinifera* L.) has been fundamental for the development of civilizations due to its versatility and adaptability, consolidating itself as one of the oldest and most globally extended fruit crops. Today's grapevine genetic and phenotypic diversity stems from centuries of human selection aimed at enhancing specific traits of interest, especially those that are important to ensure fruit production and improve grape quality [1, 2]. Due to the high heterozygosity of grapevines, each individual resulting from the sexual crossing of two varieties has a unique genetic makeup, which translates into a distinct assortment of phenotypic characteristics. When a particular phenotype of interest is identified, it is maintained by vegetative propagation (cuttings), and it can be multiplied to satisfy the need of plant material for planting new vineyards [1]. Although this process of vegetative (clonal) propagation should ensure that all plants have the same genotype, the eventual occurrence of somatic mutations might result in a plant having a slightly different genotype. This intravarietal variation might be of interest for cultivar innovation, as well as for improvement strategies focused on cultivar adaptation to climate challenges, new regulations, and consumer expectations [3].

Viticulture in America began at the end of the 15th century after the introduction of a few European grapevines to ensure the need of wine for Catholic celebrations [4]. This initial viticulture system was mostly based on the cultivation of the black-berried Spanish cultivar Listán Prieto, which steadily spread all over the continent, where it is known today under many synonyms, like Criolla Chica, Mission, Negra Corriente, Negra Criolla, and País [5]. Later on, the white-berried cultivar Muscat of Alexandria was introduced in South America too [6]. Today, Listán Prieto and Muscat of Alexandria are recognized, by far, as the two most relevant founders of local varieties of South America, which are commonly known as Criollas. Different works have identified numerous American-born varieties as offspring of Listán Prieto and Muscat of Alexandria, including the varieties Blanca Oval, Canelón, Cereza, Criolla Grande Sanjuanina, Moscatel Amarillo, Pedro Giménez, Torrontés Sanjuanino, or Uva Anís, to cite some [7–10]. Other Criolla varieties resulted from the offspring of one of these two major founders with other grapevine varieties introduced from Europe. This is the case of the Peruvian variety Quebranta (Listán Prieto × Mollar Cano) [9], or the Argentinian Canela (Listán Prieto × Muscat of a Petits Grains) [7]. Criollas have been also identified as parents of other local varieties (like Prieta Mollar (Listán Prieto × Quebranta), or Moscatel Rosada de Cañete (Moscatel Rosado × Muscat of Alexandria) [11]), denoting their impact on the South American grapevine germplasm.

During the 16th century, Peru became one of the most important centers for grapevine cultivation in South America [12]. Historical records indicate that local viticulture started in the Rimac River Valley (Lima), from where it expanded to the Peruvian Andes region (Cuzco, Ayacucho) and then to the southern coast, to regions such as Ica,

Arequipa, Moquegua, and Tacna [4, 13–15]. Today, grape cultivation is present in almost all regions of the Peruvian coast, with the Ica region (south of Lima) concentrating the highest production levels. In 2023, the total national vineyard area exceeded 40,000 ha, with wine production reaching 19.1 million liters (<https://www.oiv.int>). The favorable agroclimatic conditions in the Peruvian regions of Ica and Piura also enable the cultivation of high-quality table grapes, positioning Peru as one of the world's leading producers [16] and the second-largest exporter of this fruit, after Chile (<https://www.oiv.int>). In addition, the Peruvian viticulture sector is globally known for the production of Pisco, a distinctive spirit distilled from recently fermented grapes of selected varieties [15]. In contrast to other South American countries where extensive works cataloguing local varieties are available [7, 10, 17], the genetic diversity of the Peruvian grapevine germplasm has been poorly explored. Some notable exceptions are the studies of Martínez et al. [12], which explored the genetic relatedness of some of the most relevant Peruvian Criolla varieties, as well as the works of Almanza Cano et al. [18] and Mendoza et al. [11], which characterized some genetic resources preserved in regional grapevine collections and some collected in traditional vineyards of regions of historical relevance. The detection of new Peruvian Criolla varieties in these two works denotes the existence of unexplored local varieties that can be useful for unveiling the evolution of the unique viticultural heritage of the country, which is an essential part of the Peruvian culture and national identity. In addition, these novel local varieties can aid in diversifying current national grape, wine, and Pisco markets and can be useful as an adaptive strategy to face current viticulture challenges. Criolla varieties are grown in Peru for different purposes, including the production of Pisco [19]. The production of Pisco in Peru is regulated by the Pisco Designation of Origin, which limits its production to coastal regions located in the regions of Lima, Ica, Moquegua, Arequipa, and Tacna [19]. Likewise, Pisco production is limited to the spirit obtained by the distillation of wines from eight grapevine varieties: Quebranta, Negra Criolla (syn. Listán Prieto), Mollar Cano, Uvina (syn. Jacques), Albilla (syn. Palomino Fino), Moscatel Negro de Perú, Torontel Peruano, and Italia (syn. Muscat of Alexandria) [19]. Considering this varietal limitation, the identification of beneficial intravarietal diversity within these eight varieties might be of high interest for the Peruvian Pisco sector.

The existence of synonyms (different names for the same variety), homonyms (different varieties with the same name), and cultivars without precise genetic information in grapevine collections complicates the traceability and appropriate use of the grapevine germplasm, ultimately limiting the potential for innovation and optimization in processes of the Peruvian wine and Pisco production chains [19]. Grapevine varietal identification in different genetic pools has been efficiently accomplished by genotyping standard sets of molecular markers like simple sequence repeats (SSRs, microsatellites) or single nucleotide polymorphisms (SNPs) and comparing the resulting genetic profiles with available references [20–22], with the exception of the varieties originated by somatic variation. The

combination of this molecular genetic data with morphological and agronomic information can lead to the detection of beneficial intravarietal diversity for traits of interest in grapevine cultivars of economic and/or historical relevance [23]. In this context, this work focused on the genetic characterization of the grapevine genetic resources preserved in the ampelographic collection of the Instituto Nacional de Innovación Agraria (INIA-EEA-Chincha) at Chincha (Ica, Peru), the largest grapevine collection in the country. This collection not only preserves grapevine accessions from the no longer available local collections of the Peruvian regions of Moquegua, Arequipa, and Ica, but also grapevines collected from private farms of different wine-growing regions where they are preserved by local grape growers. SSR and SNP genetic profiling enabled us to identify the majority of these genetic resources, as well as to uncover novel Criolla varieties among the nonidentified grapevine accessions. Further phenotypic characterization revealed a high degree of morphological diversity in several traits of interest for cultivar improvement, including novel white-berried and Muscat-flavored somatic variants, which offer strong potential of innovation for the Peruvian grape, wine, and Pisco industries.

2. Materials and Methods

2.1. Plant Material. One hundred and twenty-one grapevine accessions preserved at the ampelographic collection of the Instituto Nacional de Innovación Agraria at Chincha (Ica, Peru) (INIA-EEA-Chincha) have been analyzed (13°27'32"S, 76°09'46"W) (Supporting File 1). From each accession, young leaves were collected from one plant for whole genomic DNA extraction. Leaf samples were transported to the laboratory in individual envelopes containing absorbent paper and silica gel to prevent fungal growth.

2.2. DNA Extraction and Quantification. Leaf samples were individually ground into fine powder in liquid nitrogen. Duplicates were performed per sample to ensure the reproducibility of the results. DNA extractions were carried out using the CTAB method [24] and modified with NaCl for polysaccharide removal and with PVP to minimize polyphenol interference, following the optimized protocol of Lodhi et al. [25]. DNA concentration and purity were determined by spectrophotometry by means of a NanoPhotometer (Implen, Germany), while its integrity was verified by minigel electrophoresis, as described previously [26].

2.3. Genetic Characterization, Varietal Identification, and Pedigree Analyses. Each sample was characterized using 13 highly discriminating SSR markers, grouped in two multiplex polymerase chain reactions (PCRs), as described previously [21]. One multiplex PCR included seven SSR markers (VVMD27, VVMD32, VVMD5, VVMD7, VVS2, VrZAG62, and VrZAG79), whilst the other multiplexed the remaining six SSR markers (VVMD25, VVMD28, VrZAG112, VrZAG29, VrZAG67, and VrZAG83). This set of

markers includes the nine SSRs agreed upon for the efficient genetic discrimination and identification of grapevine genetic resources, as recommended by the International Organization of Vine and Wine (OIV) [27]. SSR primers were used as described elsewhere [28–31], and PCR amplification conditions can be found in Tello et al. [21]. The amplified products were analyzed by capillary electrophoresis in an ABI PRISM 3100 Genetic Analyzer (Applied Biosystems, Germany). The sizes of the amplified fragments were determined using GeneMapper V.4.0 software (Applied Biosystems, Germany). All the different genetic profiles identified were genotyped at 240 SNPs, which include a set of 48 SNPs for cultivar identification [32] and 192 for extended pedigree analyses [33]. This set also contains five chloroplast SNPs for the differentiation of the four most common grapevine chloroplast haplotypes (chlorotypes) [34].

The SSR and SNP genetic profiles obtained were pairwise compared with those stored in the databases of the Instituto de Ciencias de la Vid y del Vino (ICVV, <https://www.icvv.es>, 3574 genetic profiles) and the *Vitis* International Variety Catalogue (VIVC, <https://www.vivc.de>, 6354 genetic profiles). Profiles without a matching coincidence in these two databases were considered as new. SNP genetic profiles were used for a wide search of compatible trios (mother–father–offspring) and duos (parent–offspring), using the genetic profiles stored at the ICVV database and the methodology previously described [21]. The robustness of each detected relationship was evaluated considering the overall likelihood ratio (LOD) score of each test. For trios, the maximum number of mismatching SNPs was set to five to allow for possible mutations or genotyping errors. Given the low diversity existing among Criolla founders, delta values (difference between the LOD value of the selected trio and of the second more probable pair of parents) were considered too. For duos, only two mismatching SNPs were allowed, and only those pairs with a LOD value over 25 have been considered. SSR profiles were used to confirm the pedigree relationships indicated by SNP data. Chlorotype information was used to determine the female progenitor in each trio, considering the maternal inheritance of chloroplasts in grapevine [34].

The overall similarity between the genetic profiles identified in this work was evaluated by an unweighted neighbor-joining phylogenetic tree based on a Euclidean dissimilarity matrix derived from molecular data using DARwin 6.0 [35], as detailed before [20].

2.4. Morphological Characterization. Morphological evaluations were carried out following the descriptors of the OIV [36], focusing on the accessions identified at the molecular level as new genotypes and on some accessions genetically identified as Listán Prieto or Quebranta but with evident phenotypic differences. Five plants per accession were selected for evaluation. For each plant, one representative bunch of the accession was selected. Berry trait evaluations were based on the analysis of five seeded berries per bunch (so, 25 berries per accession). We focused on nine traits related to bunch and berry morphology, namely bunch length (OIV descriptor N° 202), bunch width (OIV 203), bunch compactness (OIV 204), berry length (OIV 220),

berry width (OIV 221), berry shape (OIV 223), and berry color (OIV 225). The particular berry flavor (OIV 236) was also evaluated. Phenotypic evaluations were carried out on berries and bunches at full maturity (modified E–L stage 38 [37]) to guarantee a comparative result between accessions. An analysis of variance (ANOVA) followed by a Tukey HSD post hoc test was performed to detect phenotypic differences in bunch length, bunch width, berry length, and berry width within the variants of Listán Prieto or Quebranta. Tests were conducted with the R functions *aov* and *TukeyHD*, as detailed before [23], and differences were considered significant at $p < 0.05$.

3. Results and Discussion

3.1. The Genetic Characterization of the Grapevine Accessions Preserved at the Ampelographic Collection of the Instituto Nacional de Innovación Agraria (INIA-EEA-Chincha) Identified a Wide Number of Varieties of Different Use and Origin. There is a growing interest in studying the grapevine genetic resources generated in regions with variable pedoclimatic conditions, as they might be valuable in addressing current and future viticulture challenges, including those related to climate change conditions [38]. Moreover, analyzing these local grapevines contributes to a better understanding of how national and regional viticulture systems developed, adding value to winemaking regions of historic tradition [21, 22]. Such studies are typically conducted through the characterization of grapevines found in old vineyards [21, 22] or through the study of the grapevine accessions available in national or regional repositories that usually preserve varieties of local relevance [20, 33, 39]. Here, we performed the genetic characterization of 121 grapevine accessions preserved at the INIA-EEA-Chincha ampelographic collection (Ica, Peru) (Supporting File 1), which is one of the largest grapevine collections in the country. Their genotyping at 13 SSR and 240 SNP markers identified 45 different genetic profiles, which are listed in Table 1 and fully provided in the Supporting File 2. Within them, we were able to identify 40 genetic profiles (found in 110 accessions) as widely known grape cultivars (Table 1).

Due to the purpose of the INIA-EEA-Chincha Collection to preserve all types of grapevine genetic resources, we identified both varieties intended for fresh consumption as table grapes and varieties mainly used for winemaking or Pisco elaboration. Within the genetic profiles identified as table grapes, we found a wide number of varieties obtained in breeding programs of the 20th century (like Emerald Seedless, Red Globe, or Flame Seedless, Table 1). In addition to these improved varieties, we found other table grape varieties that have been traditionally cultivated for centuries in different regions, like Ahmeur Bou Ahmeur (from Algeria), Dodrelyabi (Georgia), Opsimos Edessis (Greece), and Krivalja Bijela (Yugoslavia) (Table 1). Some of them are progenitors of cultivars used for table grape production (like Exotic (Ahmeur Bou Ahmeur × Alphonse Lavallee), Crvena Krivaja (Parmak

Cerven × Krivalja Bijela), or Princeps (Muscat Hamburg × Dodrelyabi) [22, 40, 41]), so they might store traits of interest to foster new local breeding programs. Indeed, Peru has emerged as one of the world's leading exporters of fresh grapes in the last decades [16], with national production largely centered around bred varieties such as Red Globe, Crimson Seedless, Flame Seedless, and Sugraone (<https://www.provid.org.pe>). This success is due in part to the country's favorable climatic conditions for grape production, which allow for multiple fruit harvests per year and enable the grapes to reach optimal color and sugar levels that are highly valued in international markets [16].

On the other hand, we identified 29 genetic profiles as wine grape varieties (Table 1). Listán Prieto was the most commonly identified variety within the accessions of the INIA-EEA Collection, being found up to 20 times. We found that this variety was preserved under different names, including its acknowledged Peruvian synonym, Negra Criolla. We also identified this variety in accessions named Uva Común and Uva Prieta, which could be considered new local synonyms of Listán Prieto. The Peruvian Criolla variety Quebranta was the second most abundantly found in the collection (14 times). One of the accessions genetically identified as Quebranta was mislabeled in the INIA-EEA-Chincha Collection as Mollar Cano, the father of Quebranta [7], probably due to the phenotypic resemblance between both varieties, at least for grape cluster features [18, 19]. The abundance of Listán Prieto and Quebranta in the INIA-EEA-Chincha Collection likely mirrors the relevance of both varieties for the Peruvian wine and Pisco sector. In fact, these two varieties are widely cultivated in the country for the elaboration of Pisco [19], together with other varieties that were preserved in the collection like Palomino Fino (locally known as Albilla), Torontel Peruano, and Muscat of Alexandria (locally known as Italia) (Table 1). We also identified some Criolla varieties that have been documented in other neighboring countries, like Torrontés Riojano and Pedro Giménez [7, 17]. The latter has been recently identified after the genetic analysis of some relict plants collected from old vineyards of Peru, as well as the lesser-known variety Moscatel Rosada de Cañete [11], which was identified three times in our work (Table 1). Moscatel Rosada de Cañete is an alleged autochthonous variety from Peru that might have been used for winemaking and distilling since the beginning of the 20th century [11]. Thus, the presence of this variety in the INIA-EEA-Chincha Collection supports its suggested relevance for the traditional elaboration of wines and Pisco in Peru and reinforces the interest for its further agronomic and oenological characterization. Lastly, we identified some European varieties like Carignan, Garnacha, Semillon, or Cabernet Franc in the INIA-EEA-Chincha Collection. The finding of these varieties likely reflects the recent replacement of traditional varieties by some internationally renowned varieties from Central Europe to adapt local markets to international wine trends [10, 42].

TABLE 1: List of 45 molecular profiles identified in the ampelographic collection of the Instituto Nacional de Innovación Agraria (INIA-EEA-Chincha) (Ica, Peru, in 121 accessions using 13 SSR and 240 SNP markers).

Name	N	ICVV genotype code	VIVC variety number	Country or region of origin ¹	Use ¹
Ahmeur Bou Ahmeur	2	GEN_DNA_0473	140	Algeria	Table
Danugue	3	GEN_DNA_1454	3425	France	Table
Flame Seedless	1	GEN_DNA_2053	4141	United States	Table
Krivalja Bijela	4	GEN_DNA_3293	10,050	Yugoslavia	Table
Nevado	2	GEN_DNA_4823	16,877	Argentina	Table
Patricia INTA	1	GEN_DNA_3772	4440	Argentina	Table
Princess	2	GEN_DNA_4808	19,941	United States	Table
Red Globe	4	GEN_DNA_2157	9972	United States	Table
Emperatriz	2	GEN_DNA_1237	15,452	Argentina	Table, raisin
Pasiga	2	GEN_DNA_0925	8964	Argentina	Table, raisin
Perlon	1	GEN_DNA_2170	9170	Argentina	Table, raisin
Cabernet Franc	3	GEN_DNA_0796	1927	France	Wine
Carignan	1	GEN_DNA_0540	2098	France	Wine
Chenin Blanc	1	GEN_DNA_0537	2527	France	Wine
Emerald Riesling	1	GEN_DNA_1151	3894	United States	Wine
Garnacha	1	GEN_DNA_1456	4461	Spain	Wine
Moscatel Rosada de Cañete	3	GEN_DNA_3023	27,437	Peru	Wine
Pedro Gimenez	3	GEN_DNA_2459	24,977	Argentina	Wine
Riesling Weiss	1	GEN_DNA_2105	10,077	Germany	Wine
Semillon	2	GEN_DNA_2185	11,480	France	Wine
Torontel Peruano	5	GEN_DNA_2554	27,440	Peru	Wine
Torrantes Riojano	1	GEN_DNA_2592	15,162	—	Wine
Viognier	1	GEN_DNA_0990	13,106	France	Wine
Argentina	1	GEN_DNA_2586	4452	Argentina	Wine, table
Black Rose	1	GEN_DNA_0130	1407	United States	Wine, table
Cereza	2	GEN_DNA_0985	2390	Argentina	Wine, table
Dabouki Arub	2	GEN_DNA_2558	24,600	Asia Minor	Wine, table
Dodrelyabi	1	GEN_DNA_0984	3616	Georgia	Wine, table
Isabella	3	GEN_DNA_7007	5560	United States	Wine, table
Italia	2	GEN_DNA_0264	5582	Italia	Wine, table
Listán Prieto	20	GEN_DNA_1274	6860	Spain	Wine, table
Muscat Hamburg	3	GEN_DNA_2047	8226	United Kingdom	Wine, table
Niagara	2	GEN_DNA_4810	8537	United States	Wine, table
Opsimos Edessis	1	GEN_DNA_2593	8789	Greece	Wine, table
Palomino Fino	2	GEN_DNA_1063	8888	Spain	Wine, table
Quebranta	14	GEN_DNA_2500	9840	Peru	Wine, table
Tempranillo	1	GEN_DNA_1316	12,350	Spain	Wine, table
Alphonse Lavallee	1	GEN_DNA_1032	349	France	Wine, table, raisin
Moscatel Rosado	4	GEN_DNA_2466	8040	—	Wine, table, raisin
Muscat of Alexandria	3	GEN_DNA_2153	8241	Greece	Wine, table, raisin
<i>Rosada Limeña</i>	1	GEN_DNA_4822	—	—	—
<i>Uva Blanca de Pacarán</i>	2	GEN_DNA_4805	—	—	—
<i>Uva Negra de Ocucaje</i>	2	GEN_DNA_4833	—	—	—
<i>Uva Verde de Caraveli</i>	4	GEN_DNA_4807	—	—	—
<i>Uva Violeta de Moquegua</i>	2	GEN_DNA_4806	—	—	—

Note: Unidentified varieties are indicated in italics.

¹According to VIVC information.

3.2. Genetic Profiling and Pedigree Analyses Identified Some Novel Criolla Varieties From Peru. We identified five genetic profiles not reported before in international databases, which were found in 11 accessions (Table 1 and Supporting File 1). In the absence of a local name, these new varietal genotypes have been provisionally designated according to grape characteristics and the place where they were originally found [11, 21]. The most abundant genotype was found four times in the INIA-EEA-Chincha Collection, which

corresponded to an unidentified wine grape variety of dense clusters of globose and green-yellow berries with neutral flavor (Figure 1, Table 2). This variety was preserved twice in the collection as Uva Verde, a name that merely describes its berry color (verde means green in Spanish). These two accessions originated from Caraveli and Lunahuaná (Supporting File 1), two Peruvian towns located approximately 600 km apart, in the coastal regions of Arequipa and Lima, respectively. Another accession with this genotype was

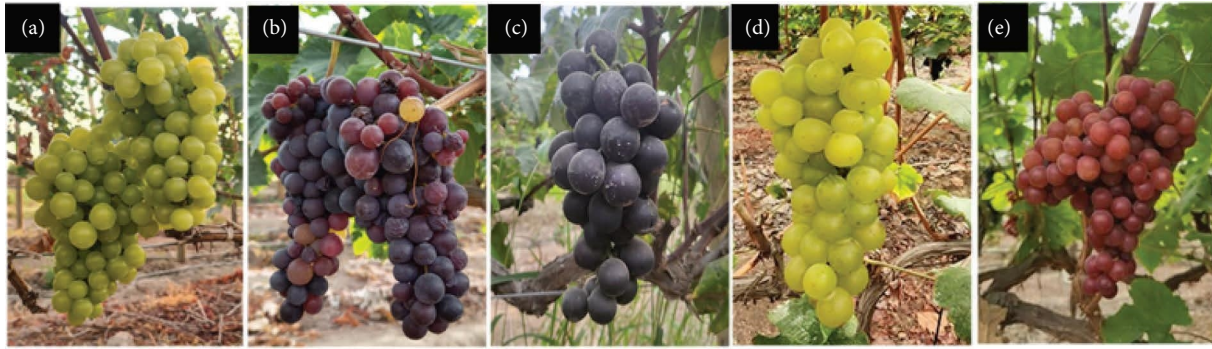


FIGURE 1: Grapevine clusters of the five nonidentified varieties found in the ampelographic collection of the Instituto Nacional de Innovación Agraria (INIA-EEA-Chincha), Ica, Peru: (a) Uva Verde de Caravelí, (b) Uva Violeta de Moquegua, (c) Uva Negra de Ocucaje, (d) Uva Blanca de Pacarán, and (e) Rosada Limeña.

misnamed as the green-berried cultivar Viognier, probably due to their phenotypic resemblance. Given that this variety lacks a specific varietal name, we propose naming it Uva Verde de Caravelí to indicate its berry characteristics and one of the places where it was originally found (Caravelí, Arequipa, Peru). The finding of isolated grapevines within a given area with the same genotype suggests that this variety might have had some viticultural relevance in the past [21]. Uva Verde de Caravelí was originally found in old vineyards for wine production, so it may have been an important wine grape variety for growers of the coastal region of Peru, now supplanted by other varieties. Given the global interest in discovering and evaluating minor wine grape varieties for their potential use, it would be valuable to conduct an in-depth agronomic and oenological characterization of this variety, as well as to promote its preservation. Interestingly, pedigree analyses revealed that Uva Verde de Caravelí is the offspring of Listán Prieto and Muscat of Alexandria (Table 3). So, Uva Verde de Caravelí can be catalogued as a novel Criolla variety of Peruvian origin, and it can be added to the long list of grapevine cultivars originating in South America arising from natural crossings between Listán Prieto and Muscat of Alexandria [7, 10, 11, 17].

Similarly, we found other three unidentified genetic profiles preserved twice in the INIA-EEA-Chincha Collection (Table 1). One of them corresponded to a wine grape variety with dense clusters of dark-red-violet berries with a neutral taste (Figure 1, Table 2). This variety was preserved in the collection as Burdeos, possibly because of the dark color of its burgundy berries. To avoid any misunderstanding that could link this unidentified variety with the Bordeaux region of France, we propose renaming it as Uva Violeta de Moquegua to indicate its berry color and the Peruvian region where it was originally found (Supporting File 1). As for Uva Verde de Caravelí, pedigree analyses suggested that Uva Violeta de Moquegua is another compatible offspring of Listán Prieto and Muscat of Alexandria (Table 3), supported by a high LOD value (59.57). However, as noted in Table 3, we found four mismatching SNPs (but no mismatching SSRs) for this pedigree (Table 3). The dominant role of the two main foundational varieties (Listán Prieto and Muscat of Alexandria) and some of their known

descendants (like Moscatel Rosado, Cereza, or Canela) in the origin of local Criolla varieties causes an overall reduced allelic diversity, which, in parentage analyses, translates into alternative compatible pedigrees for the same variety [10, 17]. Genotyping errors (and mutations) introduce noise in the analysis and increase the complexity of discriminating between compatible pedigrees and the actual parentage, even though the Cervus software considers mismatching markers for the calculation of LOD values. In complex cases, it is useful to consider the Delta value, which evaluates the difference between the LOD values obtained for the first and the second pairs of more probable parents. In the case of Uva Violeta de Moquegua, the Delta value is very high (25.52, Table 3), supporting Listán Prieto and Muscat of Alexandria as their most likely parents. The observed mismatching SNP alleles could derive from technical genotyping errors or be true allele differences due to spontaneous mutations [10].

Another unidentified genetic profile, found twice in the collection, corresponded to a table grape variety with loose and elongated clusters of big and dark-red-violet berries, with no distinctive flavor (Figure 1, Table 2). This unidentified variety was preserved in the collection as Portuguesa Azul, meaning blue (grape) from Portugal. To avoid any equivocation with the European variety Portugieser Blau, we propose Uva Negra de Ocucaje to name this variety, which reflects the place where this variety was discovered (Ocucaje, Peru) and its berry color (Supporting File 1). Pedigree analyses revealed that this variety is compatible with being the offspring of Muscat of Alexandria and Huevo de Gato. Huevo de Gato is registered as a cultivar with functionally female flowers (<https://www.vivc.de>). However, detailed morphological descriptions indicated that it has hermaphrodite flowers [43], which agrees with its role as father in the origin of Uva Negra de Ocucaje, following chlorotype data (Table 3). The region where Uva Negra de Ocucaje originated remains unknown. Nevertheless, whilst the ancient variety Muscat of Alexandria is widely present in multiple European and South American regions [44], Huevo de Gato is an alleged minor Spanish table grape variety whose geographical origin is supported by the eventual finding of old plants of this variety in Central Spain [45] and by the fact that all the reported pedigrees in which Huevo de

TABLE 2: Main cluster and grape characteristics of the five unidentified genotypes preserved at the ampelographic collection of the Instituto Nacional de Innovación Agraria (INIA-EEA-Chincha), Ica, Peru.

Variety	Bunch length (mm)	Bunch width (mm)	Berry length (mm)	Berry width (mm)	Berry width (mm)	Bunch density	Berry shape	Berry skin color	Berry flavor
Rosada Limeña	198.34 ± 6.27	162.80 ± 17.45	17.47 ± 0.40	17.81 ± 0.85	17.81 ± 0.85	Compact	Globose	Rose	Muscat
Uva Blanca de Pacarán	141.16 ± 3.70	85.75 ± 2.53	15.36 ± 0.70	14.20 ± 0.35	14.20 ± 0.35	Medium	Obovoid	Green-yellow	Muscat
Uva Negra de Ocucaje	181.41 ± 20.66	106.81 ± 15.47	25.78 ± 1.92	22.35 ± 0.73	22.35 ± 0.73	Loose	Narrow-ellipsoid	Dark-red-violet	None
Uva Verde de Caraveli	164.81 ± 22.78	107.72 ± 12.46	16.60 ± 1.50	16.41 ± 1.38	16.41 ± 1.38	Dense	Globose	Green-yellow	None
Uva Violeta de Moquegua	129.58 ± 19.86	95.87 ± 15.39	17.74 ± 0.54	15.88 ± 0.59	15.88 ± 0.59	Dense	Broad-ellipsoid	Dark-red-violet	None

TABLE 3: Full pedigrees (mother–father–offspring) found for the grapevine varieties from the varieties identified in the ampelographic collection of the Instituto Nacional de Innovación Agraria (INIA-EEA-Chincha), Ica, Peru.

No genotype	Offspring (chlorotype)	Parent 1 (chlorotype)	Parent 2 (chlorotype)	SNP compared/mismatched	LOD	Delta	SSR compared/mismatched	Reference
GEN_DNA_2470	Autumn Black (C)	Black Rose (C)	Calmeria (C)	212/3	77.84	30.64	9/0	[9]
GEN_DNA_1237	Emperatriz (D)	Emperor (D)	Sultanina (C)	217/2	80.57	33.46	9/0	[39]
GEN_DNA_3023	Moscatel Rosada de Cañete (D)	Listán Prieto (D)	Moscatel Rosado (A)	234/0	84.33	11.66	13/0	[11]
GEN_DNA_4823	Nevado (A)	Beba (A)	Sultanina (C)	215/2	78.92	5.53	12/0	This work
GEN_DNA_3772	Patricia INTA (A)	Moscatel Rosado (A)	Garguilo 530 (A)	223/3	75.58	26.43	0/0	This work
GEN_DNA_2459	Pedro Gimenez (B)	Muscatel of Alexandria (B)	Listán Prieto (D)	224/2	64.50	27.04	13/0	[9]
GEN_DNA_2170	Perlon (D)	Emperor (D)	Perlette (A)	226/2	81.15	22.76	13/0	[39]
GEN_DNA_2500	Quebranta (D)	Listán Prieto (D)	Mollar Cano (A)	221/1	75.66	30.89	13/0	[1]
GEN_DNA_2554	Torontel Peruano (D)	Listán Prieto (D)	Muscatel of Alexandria (B)	238/1	69.01	27.76	13/0	[11]
GEN_DNA_4833	<i>Uva Negra de Ocucaje</i> (B)	Muscatel of Alexandria (B)	Huevo de Gato (C)	218/1	68.13	30.37	9/0	This work
GEN_DNA_4807	<i>Uva Verde de Caraveli</i> (nd)	Listán Prieto (D)	Muscatel of Alexandria (B)	218/1	63.19	11.48	13/0	This work
GEN_DNA_4806	<i>Uva Violeta de Moquegua</i> (nd)	Listán Prieto (D)	Muscatel of Alexandria (B)	216/4	59.50	25.52	13/0	This work

Note: Unidentified varieties are indicated in italics.

Abbreviation: nd, not determined.

Gato is involved are of table grape varieties of Spanish origin: Fondo de Orza (Huevo de Gato × Muscat a Petits Grains) [9], Albilla Real (Huevo de Gato × Palomino), and Uva Chinche de Tíjola (Huevo de Gato × Muscat of Alexandria) [21]. In fact, we could not find any information reporting the past cultivation of Huevo de Gato in South America, and the first mention of this variety in the available literature traced back its use to the mid-20th century, when it was used in Argentina for a series of experimental crosses aimed at obtaining new table grape varieties [46]. Huevo de Gato could have been transferred as cuttings from Spain to South America during the colonial period, as reported for other European varieties with relevance in the South American germplasm [47]. Given the presence of Muscat of Alexandria in South America since the 17th century [10], this introduction would have allowed the spontaneous pollination of Muscat of Alexandria by airborne pollen of Huevo de Gato. In this regard, further prospections in old vineyards of the Ocucaje district of the Ica region might be useful for the eventual identification of ancient plants of Huevo de Gato, which will add some evidence to support a Criolla status for Uva Negra de Ocucaje. Another option is that Uva Negra de Ocucaje could have been brought into Peru as a seed, where it could have germinated and then been selected and propagated to become a new variety. In this regard, it is thought that Spanish missionaries first introduced grapevines in South America as seeds, as they were easier to transport than cuttings [1, 5, 8]. Thus, Uva Negra de Ocucaje might represent one of those old cultivars that originated from the early introduction of grapevines from Europe via seed propagation. Another hypothesis is that Uva Negra de Ocucaje could have originated in Spain and later been introduced to Peru through cuttings. However, despite being a variety that disappeared in Europe after being brought to Peru, Uva Negra de Ocucaje has never been identified in Spain or elsewhere in Europe, which weakens the plausibility of this hypothesis.

The third genotype that was found twice in the collection corresponded to a wine grape variety with obovoid and green-yellow berries with a Muscat flavor (Figure 1, Table 2). Although parentage analyses did not reveal its full pedigree, we found a compatible duo (LOD: 25.55) between this variety and Muscat a Petits Grains (syn. Moscatel de Grano Menudo), from which it could have inherited its Muscat flavor. This variety was preserved under the generic name Uva Blanca, meaning white grape. Therefore, we suggest naming it as Uva Blanca de Pacarán, to indicate its berry color and the place where it was originally prospected (Pacarán, Cañete Valley, Peru) (Supporting File 1). Lastly, we found an unidentified genotype of a table grape variety of long and compact clusters of rose- and Muscat-flavored berries (Figure 1, Table 2). This variety was preserved once in the collection under the generic accession named Rosada, which reflected its berry color. Originally discovered in a private garden in the Puente Piedra district of Lima (Peru) (Supporting File 1), grown by owners for fresh grape consumption, we propose naming it Rosada Limeña. In contrast to the previous varieties, Rosada Limeña was found only once in the INIA-EEA-Chincha Collection (Table 1),

indicating that it is a variety at greater risk of extinction, or it could be a vine directly grown from a seed [10, 21]. In this regard, a proposed way for the origin of local Criolla varieties was the traditional practice of using grape marcs as vineyard fertilizer, an approach that inadvertently sowed seeds that eventually germinated and generated new varietal genotypes [47]. Unfortunately, pedigree analyses did not reveal any confident result for Rosada Limeña, and phylogenetic results suggested a different origin to the other novel varieties identified in this work and to other Criolla varieties (Supporting File 3). Parentage analyses commonly do not reveal the full pedigree of a variety, as the true parents may have disappeared due to genetic loss through viticulture history [9]. However, given the relatively short history of grapevine cultivation in South America and the dominating role of a few founder cultivars, the identification of partial pedigrees or the absence of pedigree results for local varieties has been proposed as an indicator of a noncriolla origin, as the missing parents are assumed to be lost varieties of European origin [17]. However, South American viticulture has not remained unaffected by the genetic erosion experienced in other winemaking regions, and different factors have reduced vineyard diversity [10]. Thus, within the minor traditional varieties lost in the last decades due to cultivar replacement (among other factors), locally born descendants involved in the origin of other living varieties could have disappeared too. In this context, it is essential to carry out broader prospection efforts in old vineyards of historic relevance, as they may still hold key missing links that can reveal the genetic origin of South American varieties, as observed for other European grapevines like the wine grape variety Tempranillo Tinto [48] or, more recently, the table grape variety Dominga [21].

Our pedigree results based on 240 SNP data were also useful to confirm, with higher LOD values, some previously reported family relationships based on SSRs (Table 3). Some examples are the full pedigrees indicated for the Peruvian Criolla varieties Quebranta (Listán Prieto × Mollar Cano) [9] and Moscatel Rosada de Cañete (Listán Prieto × Moscatel Rosado) [11], for which chlorotype information revealed Listán Prieto as the variety acting as mother in the cross (Table 3). Similarly, we confirmed the reported pedigree of the bred varieties Autumn Black (Black Rose × Calmeria) [9], Emperatriz (Sultanina × Emperor) [40], and Perlon (Perlette × Emperor) [40]. We also confirmed the pedigree data for Patricia INTA (Moscatel Rosado × Gargiulo 530), for which no molecular data was available, and we found that Nevado could not have originated from the cross that is described in the literature (Afus Ali × Sultanina). Thus, whilst Nevado shares at least one allele with Sultanina in the SNP and SSR markers studied, it does not happen with its other alleged progenitor, Afus Ali (<https://www.vivc.de>). Thus, our pedigree analyses were useful to confidently correct this information, indicating that Nevado is the offspring of Beba and Sultanina. According to chlorotype information (Table 3), Beba acted as the mother in this cross, which agrees with the fact that the role of Sultanina as a female parent in crosses is not possible (except through artificial embryo rescue) due to its stenospermocarpy [39].

3.3. Morphological Descriptions Identified a Wide Range of Somatic Variation in Listán Prieto and Quebranta, Useful for Cultivar Innovation. Probably reflecting the relevance of Listán Prieto and Quebranta in the Peruvian viticulture sector (especially for the production of Pisco) [19], their molecular profiles were the most frequent in the INIA-EEA-Chincha Collection (Table 1). After the visual inspection of the 20 accessions matching the molecular profile of Listán Prieto, and based on previous notations of the curators of the Collection, we performed a morphological characterization of the clusters and berries of six variant accessions with marked phenotypic differences: Negra Criolla, Ceniza, Moscatel, Cantarilla, La Loca, and Melón. Similarly, we evaluated the phenotypic differences between three variant accessions of Quebranta: Quebranta, Quebranta Rosada, and Quebranta Mollar (Figure 2, Supporting File 4).

Listán Prieto is a black-berried Spanish variety that is considered the first variety introduced to Peru in the 16th century [1, 7]. Likely resulting from its long history in the country, particularly in the valleys of Caravelí and Majes (Arequipa), we found different accessions derived from Listán Prieto with important phenotypic differences. These variant accessions have probably occurred by somatic variation events happening during vegetative propagation processes [3]. The Listán Prieto accession Negra Criolla (Figure 2(a)) was selected as a reference, as it had the expected features of the cultivar, namely long and medium-compact clusters of globose and dark-violet berries of medium size, with no particular flavor (Supporting File 4). In contrast, we found that the accession named Ceniza stood out by its white berries (Figure 2(b)). Grapevine somatic variants for berry color have historically been selected by grape growers as a means of cultivar innovation, given that this trait is appealing for table grape consumers and they allow producing different types of wine (white, red, and rosé) [3]. Berry color variation is genetically determined by a major *locus* on chromosome 2, which colocalizes with the MYB genes *VviMybA1* and *VviMybA2* that regulate the accumulation of anthocyanins in the berry skin of colored cultivars after veraison [49]. Recently, Reynard et al. [50] have indicated that the berry color of the original black-berried Listán Prieto cultivar is due to a combination of two different haplotypes at the berry color *locus*, named *VvMybA1a* and *VvMybA1_SUB*. Following this work, some insertions observed in the sequence of the *VvMybA1_SUB* haplotype generate a lower expression in the *VviMybA1* gene [50], which might explain the low coloration of the berries in Listán Prieto (and in some of its descendants) compared to other black-berried cultivars with other *VviMybA1* haplotype combinations [19]. We propose naming this Listán Prieto white-berried variant as Listán Prieto Blanco, to note its distinctiveness. Further phenotypic and molecular analyses comparing Listán Prieto and Listán Prieto Blanco variants might be of interest to detect the cause of this phenotypic variation. From a practical point of view, the cultivation of Listán Prieto Blanco, would allow diversification of the Peruvian wine sector for the development of Listán Prieto-like white wines, as has been done for the

derived white-berried somatic variants reported for other relevant black-berried cultivars [51, 52].

Two other accessions of interest for the innovation of Listán Prieto wines and Pisco were Moscatel (Figure 2(c)) and Melón (Figure 2(f)), both with Muscat grapes (Supporting File 4). Previous works characterizing grapevines prospected from traditional Peruvian vineyards already indicated the presence of Listán Prieto grapevines with Muscat berries, named Moscatel and Moscatel Negro [11]. In grapevine, the sweet and floral taste and aroma that characterizes the grapes (and wines) of Muscat varieties is due to the accumulation of monoterpenoids (geraniol, linalool, and nerol) in berries [53]. At a molecular level, this trait is due to a major *locus* located on chromosome 5, which co-localizes with a 1-deoxy-D-xylulose 5-phosphate synthase (*VvDXS*) involved in monoterpene biosynthesis. Interestingly, different mutations in the *VvDXS* gene sequence have been linked to the appearance of the muscat trait in somatic variants derived from neutral varieties, like Chardonnay musqué (from Chardonnay), Chasselas musqué (from Chasselas), and Gewürztraminer (from Savagnin/Traminer) [54]. Thus, it might be of interest to explore if the genetic cause of the muscat aroma detected in the aromatic variants of Listán Prieto named Moscatel and Melón derives from somatic mutations at the *VvDXS* gene or if they arose from mutations in alternative genomic regions [55]. In this regard, we propose naming this muscat variant of Listán Prieto as Listán Prieto Moscatel. As previously discussed for Listán Prieto Blanco, the use of Listán Prieto Moscatel represents an important source of cultivar innovation, with a clear application in the production of wines and Pisco with differentiated aromatic profiles.

Lastly, we detected two other accessions of Listán Prieto with the same berry color and aroma but different in cluster compactness: Cantarilla (Figure 2(d)) and La Loca (Figure 2(e)). Compared with the reference accession Negra Criolla, both had looser clusters (Supporting File 4), a beneficial feature for high-quality grape production. Loose clusters are preferred over compact clusters, as they are less susceptible to diverse pests and diseases such as Botrytis bunch rot, which reduces grape production reliance on pesticides [56]. In addition, berries in loose clusters are more sparsely distributed, which favors their even sun radiation and promotes a homogeneous ripening [56]. Based on phenotypic data, the low cluster compactness observed in Cantarilla and La Loca is likely due to the significantly smaller berries in both accessions compared to the reference (Supporting File 4). The small berry size observed in both accessions is an additional beneficial feature in winemaking, since small grapes tend to have a higher skin-to-pulp ratio and a lower seed contribution during winemaking, which turns into wines with deeper color and better phenolic composition [57].

On the other hand, we explored the phenotypic diversity of three of the accessions genetically identified as Quebranta (Figure 2(g)), nowadays the most emblematic Peruvian Criolla grapevine variety that resulted from a natural cross between the varieties Listán Prieto and Mollar Cano (Table 3) [9]. Of interest for cultivar innovation, we found that

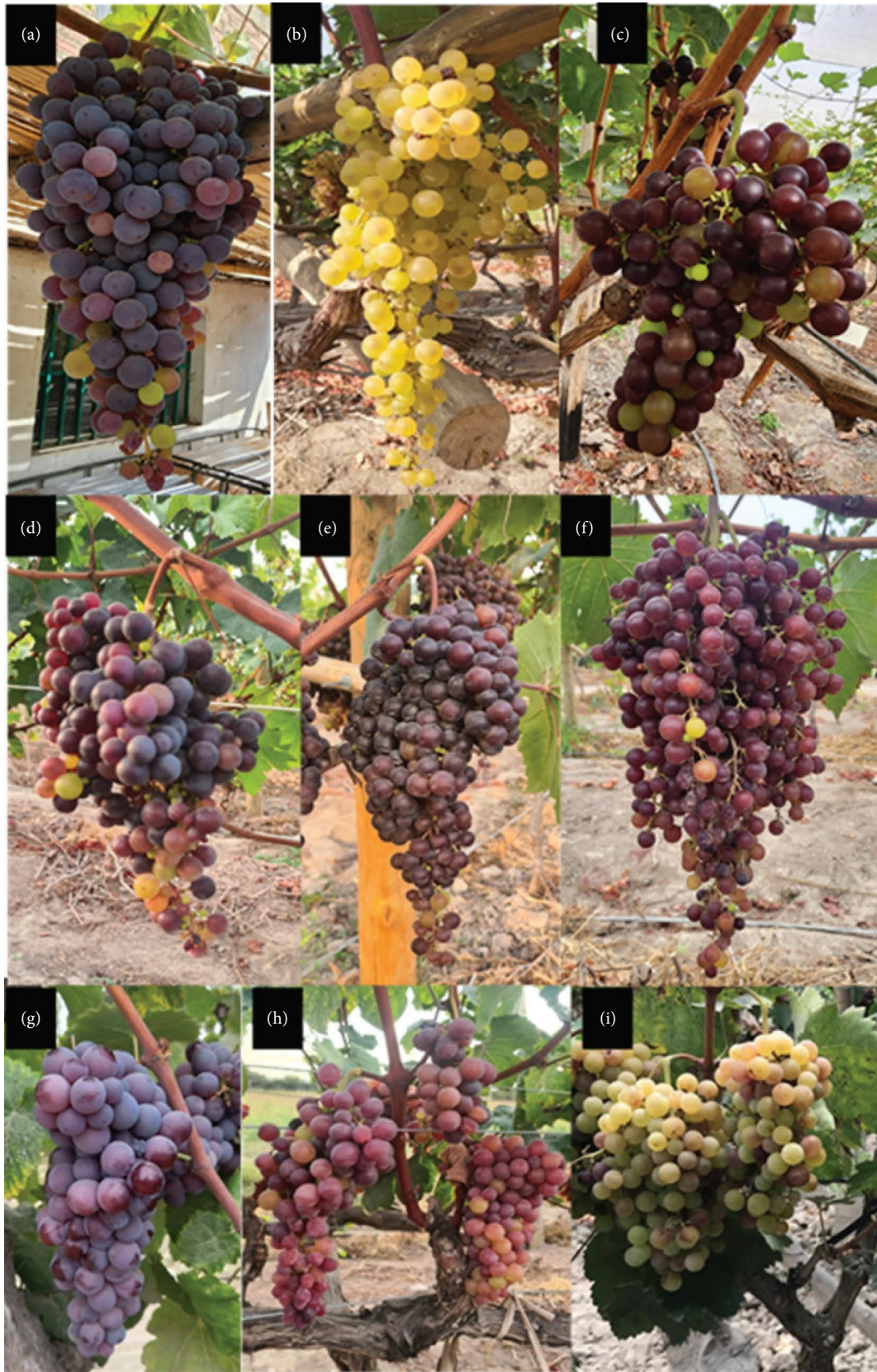


FIGURE 2: Grapevine clusters of some of the somatic variants of Listán Prieto (a–f) and Quebranta (g–i) detected in the ampelographic collection of the Instituto Nacional de Innovación Agraria (INIA-EEA-Chincha), Ica, Peru. (a) Negra criolla, (b) Ceniza, (c) Moscatel, (d) Cantarilla, (e) La Loca, (f) Melón, (g) Quebranta, (h) Quebranta Rosada, and (i) Quebranta Mollar.

the accessions named Quebranta Rosada (Figure 2(h)) and Quebranta Mollar (Figure 2(i)) had different berry colors from that of the accession Quebranta, taken as reference, as it had the expected features of this cultivar. Quebranta has dark-violet berries of similar low color intensity to that observed in the berries of its mother, Listán Prieto (Figure 2). Genetic analyses at the berry color *locus* have proved that Quebranta berry color is also due to the combination of the VvMybA1a and VvMybA1_SUB haplotypes [50]. As discussed for Listán Prieto, the presence of the VvMybA1_SUB in Quebranta (inherited from either Listán Prieto or Mollar Cano [50]) might also explain the low color intensity observed in its berries. In contrast, the phenotypic characterization of the accession Quebranta Rosada revealed that it had rosé berries, whilst Quebranta Mollar was found to have a combination of white and rosé berries (Figure 2). For these two color-berried variants, we propose maintaining the names given by Mendoza et al. [11] (Quebranta Rosada and Quebranta Mollar), who already noted this phenotypic variation after the analysis of Quebranta grapevines of traditional winemaking regions of Peru. The cultivation of Quebranta Rosada and Quebranta Mollar at a commercial level will be an input for the Peruvian production of Quebranta-like wines and Pisco, so it is important to conduct agronomic and oenological works aimed at characterizing the actual potential of these two somatic variants. In addition, their genetic characterization will be useful to reveal the molecular cause underlying their reduced anthocyanin pigmentation phenotypes.

4. Conclusions

Grape growers and wine producers seek new products capable of adapting to evolving environmental conditions and regulations while meeting consumer demands for quality, sustainability, and market innovation. This need can be covered by minor and local cultivars, which provide an opportunity of diversification in the crowded global grape and wine market. The genetic analysis of the grapevine genetic resources preserved at the INIA-EEA-Chincha ampelographic Collection revealed some noncatalogued varieties that can be considered as traditional Peruvian grapevines. Now, the performance of these new-old varieties should be tested to evaluate their potential as novel sources of diversity for market innovation. In addition, pedigree analyses of these varieties revealed that some of them probably derived from the two most relevant founders of local varieties of South America, Listán Prieto and Muscat of Alexandria. This finding increases the existing knowledge in the origin of the Peruvian traditional grapevine diversity. The combination of molecular data with morphological descriptions was useful to detect a series of somatic variants of Listán Prieto and Quebranta that can aid to diversify the production of Pisco, whose regulation limits the varieties that can be used. Within them, the identification of somatic variants with novel berry colors (white, rosé) and aromas (Muscat) are of special interest to produce different products capable to adapt to all consumer needs. Now, it is essential to register the novel varieties (including those generated as

somatic variants) to make this material available to winegrowers, which will favor their cultivation, promote agro-industrial innovation, and strengthen the territorial identity of the Peruvian wine sector.

Data Availability Statement

The data supporting the findings of this work are available in the supporting material of this article.

Conflicts of Interest

The authors declare no conflicts of interest.

Funding

No funding was received for this research. Javier Tello was supported by the Ramón y Cajal Program (RYC2022-037758-I) funded by MCIU/AEI/10.13039/501100011033 and the ESF+.

Acknowledgments

Aybel Almanza Cano thanks Dr. Jorge Jiménez Dávalos, Dean of the Faculty of Agronomy of the Universidad Nacional Agraria La Molina, for his support and for providing access to the facilities used during the development of this research.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. (*Supporting Information*)

Supporting File 1. List of the 122 accessions of the Ampelographic Collection of the Instituto Nacional de Innovación Agraria (INIA-EEA) at Chincha (Ica, Peru) included in this study. For each sample, we indicate its name and origin. Identification results after SSR and SNP genotyping are also included, indicating the molecular profile name and variety number (according to the ICVV and VIVC databases).

Supporting File 2. SSR and SNP profiles obtained for the 45 nonredundant grapevine genotypes found in this study.

Supporting File 3. Neighbor-joining phylogenetic tree between the genetic profiles identified in this study, using molecular data. The varieties Isabella and Niagara were excluded due to their hybrid background. Novel varieties identified here are marked with blue dots, while orange dots indicate previously reported Criolla varieties.

Supporting File 4. Main cluster and grape characteristics of six variant accessions of Listán Prieto and three of Quebranta preserved at the Ampelographic Collection of the Instituto Nacional de Innovación Agraria (INIA-EEA-Chincha), Ica, Peru. Different lowercase letters in the same column indicate significant differences among variant accessions of Listán Prieto ($p < 0.05$). Different capital letters in the same column indicate significant differences among variant accessions of Quebranta ($p < 0.05$).

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