

Manna Crespan^{1*}, Francesco Mercati², Gabriella De Lorenzis³, Claudio D’Onofrio⁴, Francesco Sunseri⁵

Two main distinct evolutionary stories describe the Italian grapevine assortment

Affiliations

¹CREA, Research Centre for Viticulture and Enology, Conegliano, Italy²Istituto di Bioscienze e Biorisorse, Consiglio Nazionale delle Ricerche, Palermo, Italy³Università degli Studi di Milano, Dipartimento di Scienze Agrarie ed Ambientali, Milano, Italy⁴Università di Pisa, Dipartimento di Scienze Agrarie, Alimentari e Agro-ambientali, Pisa, Italy⁵Università Mediterranea degli Studi di Reggio Calabria, Dipartimento di Agraria, Reggio Calabria, Italy

Correspondence

Manna Crespan*: manna.crespan@crea.gov.it, Francesco Mercati: francesco.mercati@ibbr.cnr.it, Gabriella De Lorenzis: gabriella.delorenzis@unimi.it, Claudio D’Onofrio: claudio.donofrio@unipi.it, Francesco Sunseri: francesco.sunseri@unirc.it

Summary

A dataset of high-quality 7k SNP profiles of 1,038 unique Eurasian grapevine varieties was used to infer the most likely grapevine migration events, a spatial ancestry estimation, and a model about the origin of Eurasian grapevine germplasm. The comparison of putative gene flow scenarios from Caucasus throughout Europe aided to fit the more reliable spreading routes around the Mediterranean Basin. The same dataset was also used to assess the population genetic diversity, structure, and relatedness of Italian varieties. These data suggested a different history between Northern and Southern Italian grapevines, appearing clearly split into two different clusters.

Interestingly, the Italian genotypes were shown to be distinguishable from all the other Eurasian populations for the first time.

The same SNP panel was used to determine parental relationships, identifying the main parents of traditional Italian and closely related cultivars. The parentage network suggested that Italian germplasm largely originated from a few key parents distributed into several geographical areas of genetic influence, with more or less large overlaps. These key cultivars are ‘Bombino bianco’, ‘Garganega’/‘Grecanico’, ‘Mantonico bianco’, ‘Orsolina’/‘Coccalona nera’, ‘Muscat à petits grains blanc’, ‘Malvasia odorosissima’, ‘Sangiovese’, ‘Sciaccarello’, ‘Visparola’ and ‘Vulpea’. The pedigree reconstruction by full-sib and second-degree relationships highlighted the pivotal role of some cultivars, such as ‘Visparola’, until now scarcely known. A hypothetical migration of this variety from Southern to Northern Italy along the Eastern side, as well as ‘Sangiovese’ migration from Southern to Central Italy along the Western side might be supposed. Moreover, ‘Muscat à petits grains blanc’, mainly through its offspring ‘Malvasia odorosissima’, furnished a consistent contribution to the development of many aromatic grapes grown in the Northern-Western part of the Italian Peninsula.

These results represent the most complete study of grapevine Italian population genetics that has been carried out until now on the Italian germplasm.

Keywords

Vitis vinifera L., SNP markers, migration events, cultivar geographic areas, Italian founder varieties, parent-offspring relationships, second-degree relationships, pedigree

Introduction

Grapevine (*Vitis vinifera* L.) is one of the most important crops around the world. It is indigenous to Eurasia, including Mediterranean, sub-Mediterranean, and Caucasian regions with a spread toward the Pontic, Caspian, and Central Asiatic areas (Mullins *et al.*, 1992). Nowadays, grapevine is cultivated also in Northern and Southern America, South Africa, New Zealand and Australia. Grapevine features a large number of cultivars. At the beginning of 90s, the estimation was around 10,000, but, based on genotyping analysis, this number dropped to 5,000 (This *et al.*, 2006). To date the molecular profiles of more than 6,000 cultivars are available in the *Vitis* International Variety Catalogue (VIVC, <https://www.vivc.de>).

Italy can boast a long winemaking tradition, indeed, the oldest fossil findings attesting the first evidence of Italian viticulture are dated back to the Protohistoric Age (Collesano, 1998). Viticulture is also one of the main Italian agri-food chains. With a vineyard area (680 kha) covering 5.2% of farming land and widespread throughout the Country, Italy is among the leading countries in wine production (59 MhL produced in 2020; <https://www.istat.it/>). The long history of winegrowing and winemaking in Italy resulted in high numbers of cultivars, to date cultivated or preserved in germplasm collections. This large genetic variability has been investigated using different types of molecular markers, amongst the most used are SSRs



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(Simple Sequence Repeats) and SNPs (Single Nucleotide Polymorphisms).

Previous studies were not able to distinguish the Italian grapevine germplasm from that belonging to other European Countries, resulting always in a weak and admixed genetic structure (Cipriani *et al.*, 2010; Bacilieri *et al.*, 2013; Laucou *et al.*, 2018). The first advancement in unraveling the history of Italian grapevine germplasm came from a study on *Magna Graecia* germplasm (De Lorenzis *et al.*, 2019). *Magna Graecia* is the Southern Italy area colonized in ancient times by Greeks. In that paper, for the first time the difference between *Magna Graecia* grapevine germplasm and the rest of European populations was shown. This paper aims to review the last knowledge on the genetic diversity of Italian grapevine germplasm and its origin using high-informative SNP profiles.

Genetic diversity of Italian germplasm

Towards the refinement of knowledge on Italian germplasm genetic diversity, a dataset of high-quality 7k SNP profiles of 384 Italian genotypes was defined and used to study the genetic background of Italian germplasm (Mercati *et al.*, 2021). Cluster analysis, Principal Coordinate Analysis (PCoA), Discriminant Analysis of Principal Component (DAPC) and structure analysis highlighted similar and interesting results: Northern Italian genotypes resulted for the first time distinguished from Southern Italian ones and those from Central Italy appeared more similar to the Northern than Southern genotypes (Fig. 1).

The differentiation of Italian germplasm from all the other Eurasian populations was also obtained when the Italian dataset was merged with the 654 distinctive SNP profiles of cultivars coming from all the Mediterranean Basin and more (Fig. 2). The final dataset accounted for 1,038 unique Eurasian grapevine varieties genotyped at 7k SNP loci and grouped into six geographic populations: i) Balkans; ii) Eastern Mediterranean Sea, Caucasus, Middle and Far East, Russia, Ukraine; iii) Western and Central Europe; iv) Iberian Peninsula; v) Northern-Central Italy; vi) Southern Italy (Mercati *et al.* 2021). Interestingly, Southern Italian genotypes showed a genetic structure different from all the other populations (including Northern-Central Italian cultivars), confirming previous findings (De Lorenzis *et al.*, 2019).

TreeMix analysis investigated the origin of Italian cultivars showing a high proximity between Southern Italy and Balkans germplasm, as well as a supposed migration event from

Southern to Northern Italy (Mercati *et al.*, 2021). These results were in agreement with the most likely gene flow scenarios inferred throughout Approximate Bayesian computation (ABC) analysis. Among the scenarios depicted, two appeared to be the most probable: the first one hypothesized a gene flow from the Balkans to Southern Italy and then to Northern-Central Italy population; the second one assumed that an admixture event between Southern Italian and Western-Central European populations flowed into the Northern-Central Italian population (Mercati *et al.*, 2021). These results strongly reflect the historical, social and economic events occurred in the Italian Peninsula, a country that over the centuries has suffered the domination of different Peoples from the Eastern shores of the Mediterranean Sea and from Western-Central Europe (De Lorenzis *et al.*, 2019).

DAPC on the whole dataset returned nine pools (Fig. 3). Italian genotypes (81%) fall mainly in two groups, pool 6 and pool 7.

Another interesting pool is no. 2: mainly Balkan genotypes are present here (56%), but also a consistent number of Italian ones (23%). For example, the presumed Italian ‘Malvasia bianca lunga’ is located here, a variety shared with the Balkan Countries (under different names, like ‘Pavlos’, ‘Maraština’), possibly introduced in Italy from the Balkans. Another case is ‘Malvasia istriana’, classified as an Italian variety and shared with Dalmatian Countries. In this pool, also 10.5% of Eastern Europe genotypes and some Western-Central Europe varie-

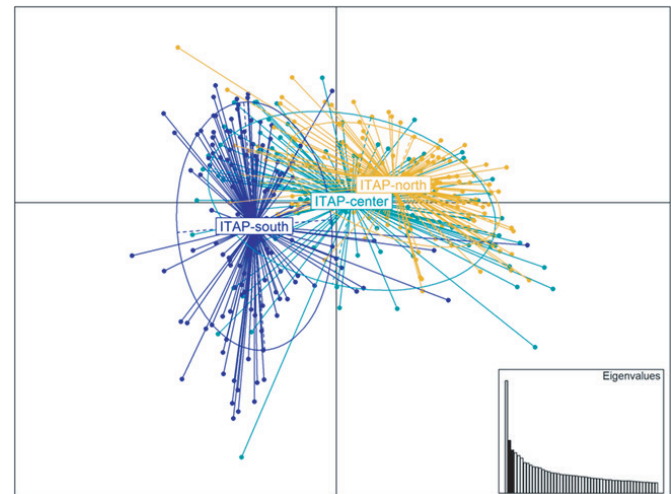


Fig. 1: Principal coordinates analysis (PCoA) of Italian germplasm using SNP profiles (from Mercati *et al.*, 2021).

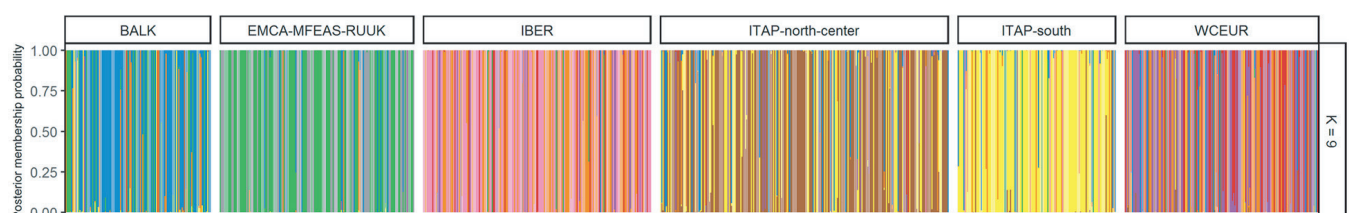


Fig. 2: Barplot of groups assignment obtained with STRUCTURE software for the entire dataset of 1,038 Eurasian varieties genotyped with SNP markers (from Mercati *et al.*, 2021). BALK, varieties from the Balkans; EMCA-MFEAS-RUUK, varieties from Eastern Mediterranean Sea, Caucasus, Middle and Far East, Russia, and Ukraine; IBER, varieties from Iberian Peninsula; ITAP-north-center, varieties from Northern-Central Italy; ITAP-south, varieties from Southern Italy; WCEUR, varieties from Western and Central Europe.

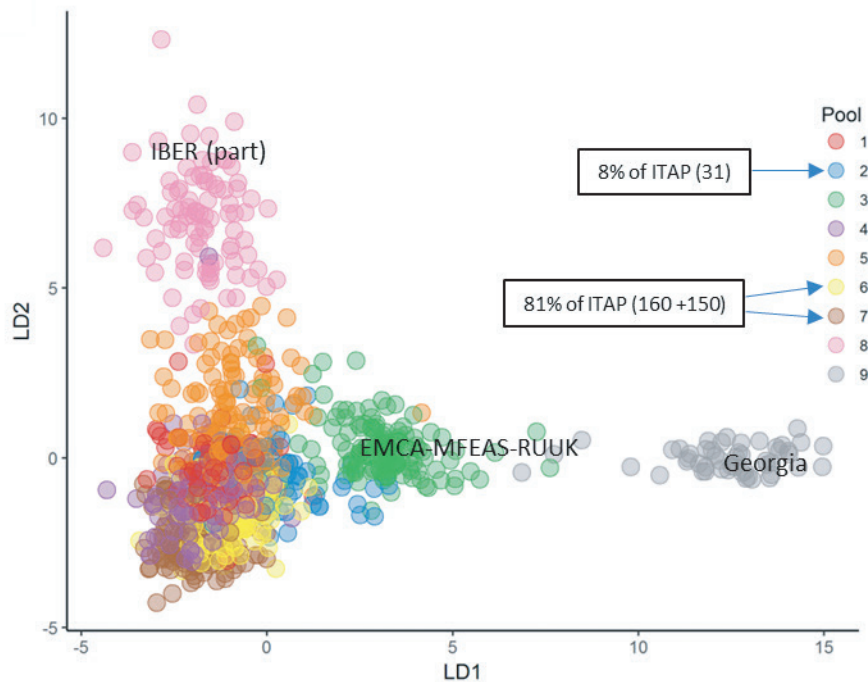


Fig. 3: DAPC scatter plot on the whole dataset of 1,038 Eurasian varieties genotyped with SNP markers (from Mercati *et al.*, 2021, modified). IBER (part): partial Iberian germplasm; ITAP: Italian germplasm; in brackets the number of Italian genotypes in each pool. EMCA-MFEAS-RUUK: Eastern Mediterranean Sea, Caucasus, Middle and Far East, Russia, Ukraine germplasm.

ties (9%) are present, like the by now famous ‘Gouais’/‘Heunisch weiss’, which more probably originated in the Balkans (as already suggested by This *et al.*, 2006) and ‘Blaufränkisch’, recently attributed to Slovenia (Maul *et al.*, 2016). Therefore, pool 2 varieties look like possible ‘bridge’ varieties between Eastern and Western Europe. A clear separation of Georgian genotypes from all the other geographical groups, confirmed the peculiarity of this germplasm, as already found in other studies (De Lorenzis *et al.*, 2015 and 2019), and a likely different evolution.

After enrichment of the Eurasian dataset by adding a small population from Northern Africa (Morocco and Tunisia) to verify its possible role as a bridge between the first domestication center (EMCA-MFEAS-RUUK) and the Iberian Peninsula, increasing the number of unique SNP profile to 1,059, TESS3 program was used to infer ancestral populations and a $K=8$ was obtained. The ancestry coefficients were plotted into a geographical map and, interestingly, Italy was again divided into two parts (Mercati *et al.*, 2021), confirming its peculiarity.

Parentage analyses: a different approach to study grapevine assortment evolution

A different approach for studying the grapevine assortment evolution is the parentage analysis. Crespan *et al.* (2008) referred that ‘Sangiovese’ and ‘Garganega’ were two key varieties for the development of Italian cultivars. Afterwards, large efforts were performed to analyze the parentage relationships in the Italian germplasm. Switching from SSRs to SNPs molecular markers gave the opportunity to obtain more robust results (Ruffa *et al.*, 2016; Crespan *et al.*, 2020; Raimondi *et al.*, 2020; Crespan *et al.*, 2021; D’Onofrio *et al.*, 2021),

mainly confirming and sometimes rejecting those obtained with few dozen SSRs. These studies show that even Italy (as other countries like France, Spain, Montenegro; Lacombe *et al.* 2013, Laucou *et al.*, 2018, Maraš *et al.*, 2020) has its own founder varieties and/or recurring parents, as shown below.

The gene pool assignment for each of the key parents described in the following refers to the DAPC results (Fig. 3) obtained by Mercati *et al.* (2021).

‘Bombino bianco’

‘Bombino bianco’ was assigned to the Italian-specific gene pool 6. It is cultivated mainly in the areas facing the Adriatic Sea and is parent-offspring (PO) related with several Italian and Dalmatian cultivars (Fig. 4), representing a clear bridge connecting the two shores of Adriatic Sea. The lack of its Dalmatian progenies into the SNP dataset in Mercati *et al.* (2021) paper can explain its placement within pool 6.

‘Mantonico bianco’ and ‘Sangiovese’

Another important pair of Italian founders are ‘Mantonico bianco’ and ‘Sangiovese’, both belonging to gene pool 6 (Fig. 5).

‘Sangiovese’ is a well-known grape variety. Grown throughout the Italian Peninsula, it is the main black grape variety grown in Italy and is the basis of famous wines such as Chianti, Morellino di Scansano, Vino Nobile di Montepulciano, Brunello di Montalcino. The regions where it is best known are Tuscany and Emilia Romagna, where it has been known respectively since 1590 and 1672. By contrast, ‘Mantonico bianco’ was at risk of extinction. It is now considered a minor grape variety of Calabria (Southern Italy) and was registered only recently (2014) in the Italian Catalogue (<http://catalogo-viti.politicheagricole.it>, code No. 494).

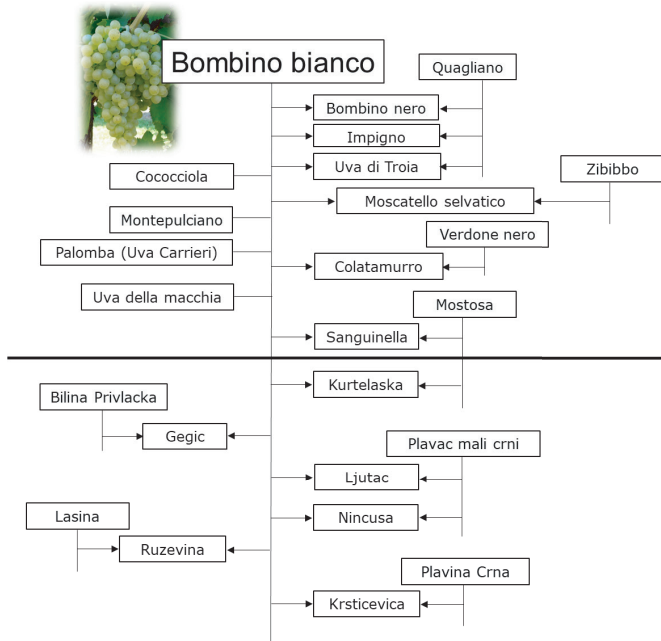


Fig. 4: The progenies of ‘Bombino bianco’ and PO related varieties. The black, horizontal line separates Italian cultivars from Dalmatian ones.

Only Italian varieties were found until now to be progenies of ‘Sangiovese’ and ‘Mantonico bianco’ and they belong mainly to Southern Italy.

‘Mantonico bianco’ played an important role in the generation of grapevine germplasm from both Sicily and Calabria regions. Indeed, this cultivar crossed to ‘Sangiovese’ gave rise to ‘Gaglioppo’ and ‘Nerello mascalese’, which are well-known vines registered in the Italian Catalogue, as well as ‘Mantonicone’/‘Occhi di lepre’ and ‘Lievuso’. ‘Mantonicone’ was found mixed in the same vineyards where ‘Mantonico bianco’ is grown, due to some of its valuable characteristics, such as the lower acidity thanks to which it mitigates the excessively high

values of ‘Mantonico bianco’. ‘Mantonico bianco’ can boast another distinguished descendant, being a parent together with ‘Garganega’/‘Grecanico’, of ‘Catarratto’. ‘Catarratto’ is the most important white berried autochthonous variety of Sicily.

More interestingly, ‘Mantonico bianco’ showed a first-degree kinship with other Calabrian, Basilicata and Sicilian varieties like ‘Ansonica’/‘Inzolia’, ‘Guardavalle’, ‘Brettio nero’, ‘Grecaresse’, ‘Parmisana’/‘Gallico’/‘Pedilongo’, ‘Trebiano antico’, and ‘Truccanosa’, demonstrating that once its distribution area must have been much larger than today.

Similarly, ‘Sangiovese’ also has offspring scattered over a wider area than expected. It is PO-related not only with Tuscan minor varieties (*i.e.*, ‘Morellone’, ‘Vernaccia del Valdarno’, and ‘Foglia tonda’) and Emilia Romagna minor varieties (‘Centesimino’), as expected based on its historically well-known geographical spread, but mainly with the well-known varieties from Calabria, Sicily, and Apulia, such as ‘Perricone’, ‘Frappato’, ‘Susumaniello’ and many minor ones, as ‘Calabrese di Montenuovo’, ‘Lucignola’, ‘Toccarino’, ‘Tuccanese di Turi’, ‘Arbanello’, ‘Orisi’, ‘Negrodolce’/‘Morellino del Valdarno’.

The complex and still uncompleted search for ‘Sangiovese’s parents (D’Onofrio *et al.*, 2021), the recent recognition of many unexpected ‘Sangiovese’ synonyms in Calabria, Sicily and Apulia, proven by DNA analysis (De Lorenzis *et al.*, 2014; Robinson *et al.*, 2012), the discovery of a ‘Sangiovese’ parthenocarpic variant, called ‘Corinto nero’, grown in the Aeolian archipelago, are findings that lead to attribute a Southern Italy area of origin to ‘Sangiovese’.

Sciaccarello

‘Sciaccarello’ (pool 6) is the name used for this cultivar in Corsica. It is also grown in Sardinia, as ‘Niedda Carta’. ‘Sciaccarello’ played a key role in generating progenies in Central Italy, based on the pedigree reconstructions (Fig. 6). Curiously, it

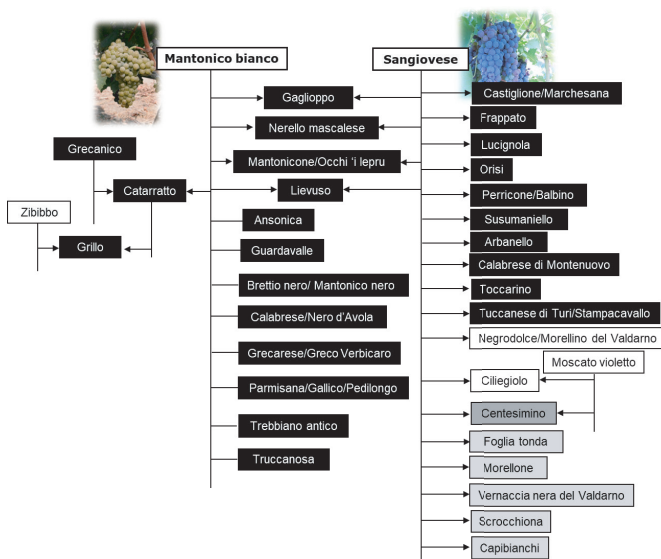


Fig. 5: The progenies of Mantonico bianco and Sangiovese and their PO-related varieties. With black background, South Italy varieties; with grey background, North-Center Italy varieties.

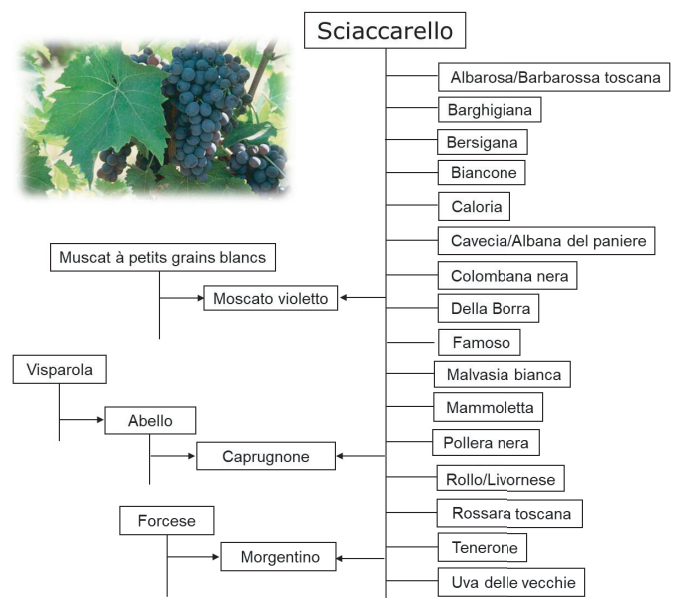


Fig. 6: The offspring of Sciaccarello and its PO-related varieties.

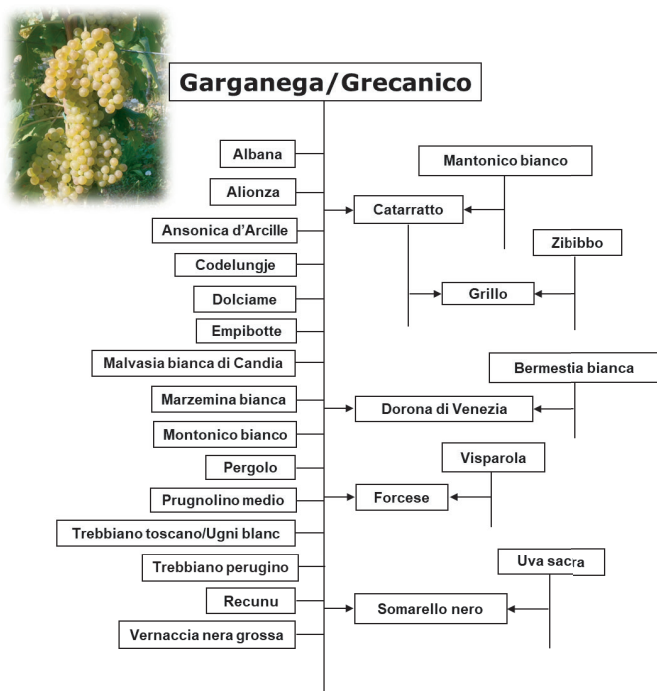


Fig. 7: The offspring of 'Garganega'/'Grecanico' and its PO-related varieties.

almost disappeared in this geographic area, even if a somatic parthenocarpic variant of 'Sciaccarello' was recovered and selected in Emilia Romagna Region, called 'Termarina nera' (Crespan *et al.*, 2016).

'Garganega'/'Grecanico'

'Garganega'/'Grecanico' belongs to pool 7 and generated progeny along all the Italian Peninsula. Among the most renowned ones are 'Catarratto' and 'Trebbiano toscano'/'Ugni blanc' (Fig. 7).

'Orsolina'/'Coccalona nera'

'Orsolina'/'Coccalona nera' (pool 7) is a founder of many Northern Italy cultivars. Among them, the most famous are 'Barbera' and 'Welschriesling' (Raimondi *et al.*, 2020; D'Onofrio *et al.*, 2021) (Fig. 8).

'Visparola'

'Visparola' was assigned to gene pool 2, the 'bridge' between the Balkans and Italy. The pedigree reconstruction, also by full-sib and second-degree relationships, highlighted the key role of 'Visparola' in generating Italian germplasm (D'Onofrio *et al.* 2021, Crespan *et al.*, 2021). 'Visparola' is the name used for this variety in Sicily, together with 'Arvina di Petralia'; additional synonyms were discovered through DNA analysis, like 'Crepolino' and 'Cascarello' in Tuscany, 'Rossola di Tebano' and 'Scacco' in Emilia Romagna. These findings evidenced a wider distribution area of this cultivar, outside both Sicily and Italy, indeed, it was also found in an old vineyard

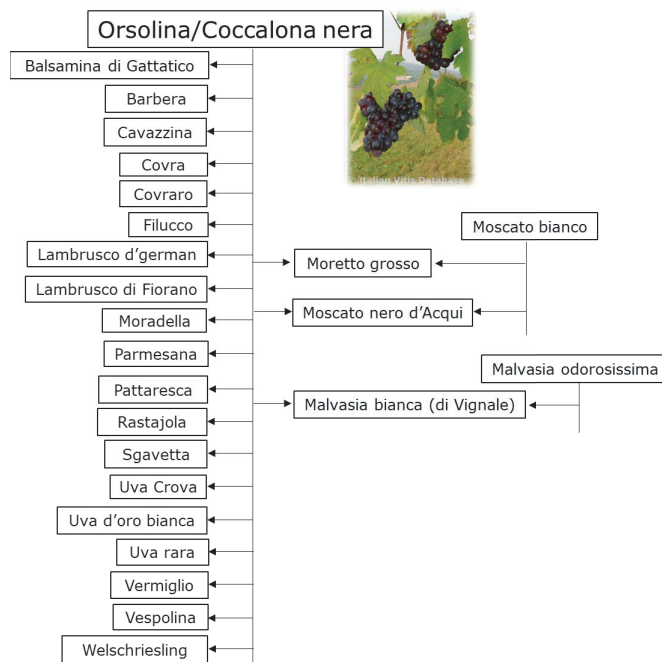


Fig. 8: The offspring of 'Orsolina'/'Coccalona nera'.

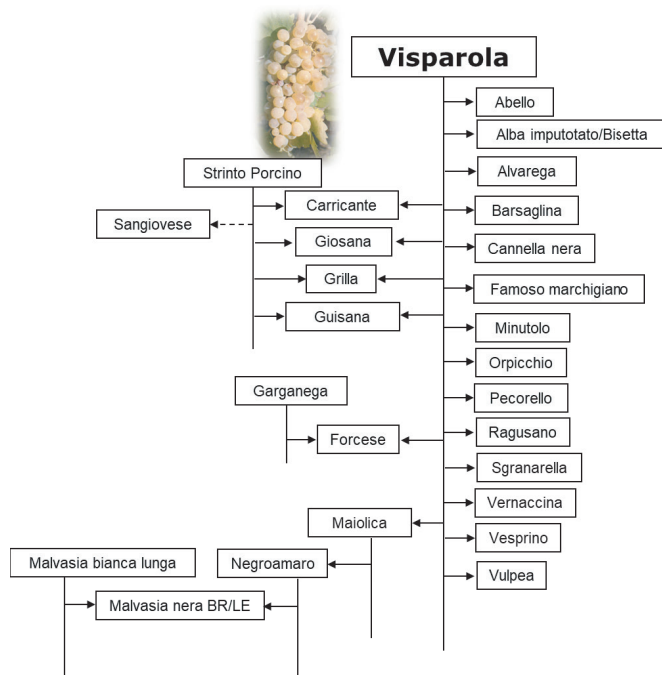


Fig. 9: The offspring of 'Visparola'. Malvasia nera BR/LE: 'Malvasia nera di Brindisi'/'Malvasia nera di Lecce'.

near Lipsia (Germany) as an anonymous vine and called 'Melweiss' (Zdunić *et al.*, 2020). Still in Germany, 'Visparola' was grown in the Geisenheim collection under the wrong name of 'Augster weisser'.

'Visparola' generated progeny along all the Italian Peninsula, and 'Alvarega' also, a variety ascribed to Sardinia (Fig. 9). 'Visparola' seems to be full-sib with the Greek 'Augustiatis', therefore representing a variety linking Greece and Italy (D'Onofrio *et al.*, 2021).

‘Vulpea’

‘Vulpea’ was assigned to the same ‘bridge’ gene pool of ‘Visparola’. A long list of synonyms (115 names) is reported for ‘Vulpea’ in the VVC, testifying its large presence in all Europe. ‘Vulpea’ was frequently a recurrent parent for Veneto and Friuli Venezia Giulia cultivars (Northern-Eastern Italy) (Crespan *et al.*, 2021; D’Onofrio *et al.*, 2021) (Fig. 10). Among the most important offspring is ‘Glera’, used to produce the famous Prosecco wine. ‘Vulpea’ has offsprings also outside Italy, in Croatia, Hungary, Austria, Slovenia, Czech Republic and even in Georgia. More interestingly, ‘Vulpea’ should be a progeny of ‘Visparola’.

‘Muscat à petits grains blancs’ and ‘Malvasia odorosissima’

‘Muscat à petits grains blancs’ (‘bridge’ gene pool) furnished a very strong contribution to generate Italian aromatic cultivars mainly in Piedmont and more in general in Northern Italy, among them, ‘Malvasia odorosissima’ (Ruffa *et al.*, 2016) (Fig. 11).

‘Malvasia odorosissima’ (pool 7) in turn generated additional flavored cultivars in the same area (Fig. 12).

Consequently, many of the Italian aromatic varieties (Muscats and aromatic Malvasias) are Italian autochthonous varieties; in other words, despite their names, these varieties were not imported from Greece.

Conclusions

The Italian genotypes were shown to be distinguishable from all the other Eurasian populations for the first time; interestingly, a different evolutionary history between Northern and Southern Italian grapevines was found.

The parentage network analysis suggested that Italian germplasm largely originated from a few main parents distributed into several geographical areas of genetic influence, even if having more or less large overlaps.

‘Muscat à petits grains blancs’, mainly through its offspring ‘Malvasia odorosissima’, significantly contributed to the development of many aromatic grapes grown in Northern-Western Italy.

These results represent the most accurate and complete study of population genetics that has been carried out until now on the Italian germplasm. In perspective, the analysis of the whole genomes throughout NGS will be able to further clarify the relationships within the Italian germplasm and the other Eurasian grape populations.

Conflicts of interest

The authors declare that they do not have any conflicts of interest.

References

Bacilieri, R., Lacombe, T., Le Cunff, L., Di Vecchi-Staraz, M., Laucou, V., Genna, B., Péros, J.P., This, P., Boursiquot, J.M., 2013: Genetic structure in cultivated grapevines is linked to

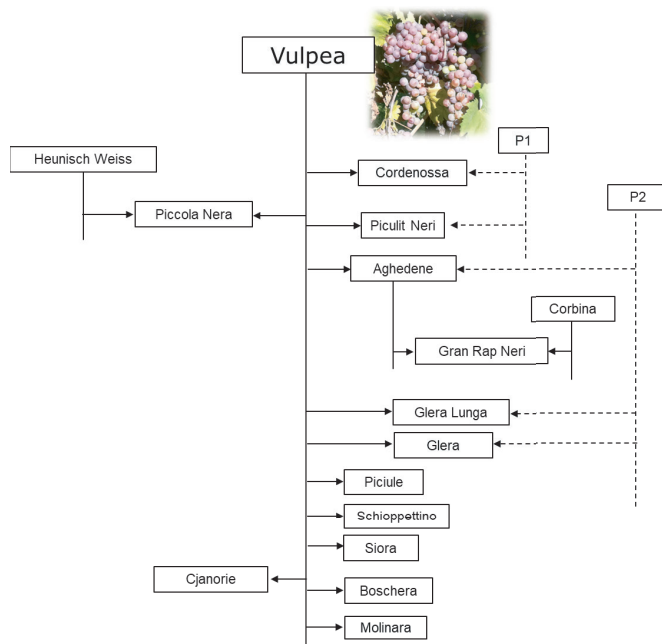


Fig. 10: The Italian offspring of ‘Vulpea’. P1 and P2 are putative common parents, linked to their progeny by dotted lines.

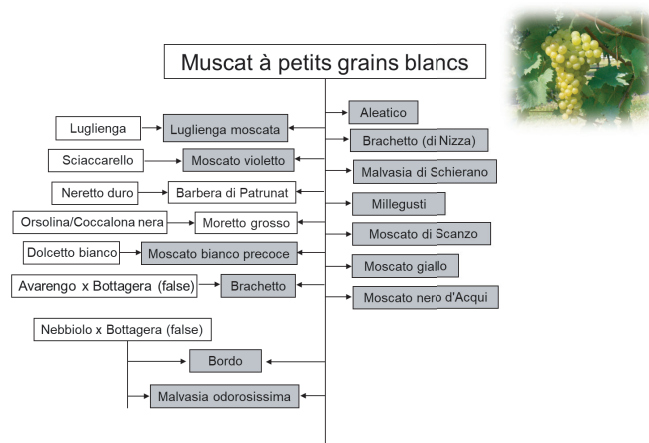


Fig. 11: The Italian offsprings of ‘Muscat à petits grains blancs’. With grey background, aromatic varieties.

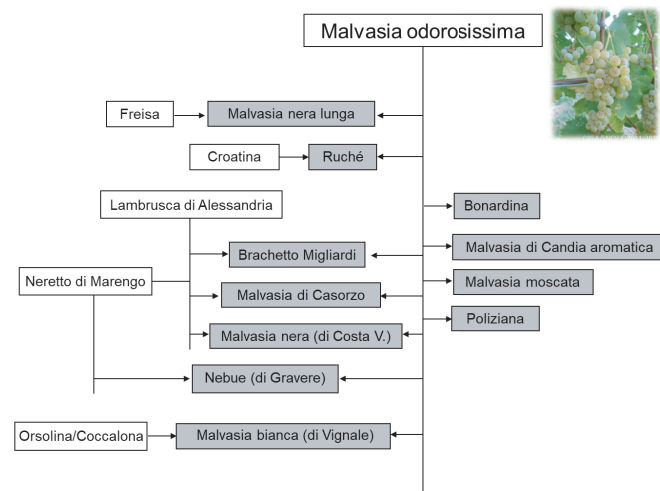


Fig. 12: The Italian offspring of ‘Malvasia odorosissima’. Aromatic varieties have grey background.

- geography and human selection. *BMC Plant Biology* 13, 25, DOI: 10.1186/1471-2229-13-25.
- Cipriani, G., Spadotto, A., Jurman, I., Di Gaspero, G., Crespan, M., Meneghetti, S., Frare, E., Vignani, R., Cresti, M., Morgante, M., Pezzotti, M., Pè, E., Policriti, A., Testolin, R., 2010:** The SSR-based molecular profile of 1005 grapevine (*Vitis vinifera* L.) accessions uncovers new synonymy and parentages, and reveals a large admixture amongst varieties of different geographic origin. *Theoretical and Applied Genetics* 121, 1569-1585, DOI: 10.1007/s00122-010-1411-9.
- Collesano, G., 1998:** Evoluzione varietale della viticoltura da vino in Sicilia. *Vignevini* 25, 27-32.
- Crespan, M., Calò, A., Giannetto, S., Sparacio, A., Storchi, P., Costacurta, A., 2008:** 'Sangiovese' and 'Garganega' are two key varieties of the Italian grapevine assortment evolution. *Vitis* 47 (2), 97-104, DOI: 10.5073/vitis.2008.47.97-104.
- Crespan, M., Carraro, R., Giust, M., Migliaro, D., 2016:** The origin of Termarina cultivar, another grapevine (*Vitis vinifera* L.) parthenocarpic somatic variant. *Australian Journal of Grape and Wine Research*, 22 (3), 489-493. DOI: <https://doi.org/10.1111/ajgw.12236>.
- Crespan, M., Migliaro, D., Larger, S., Pindo, M., Petrusci, C., Stocco, M., Rusjan, D., Sivilotti, P., Velasco, R., Maul, E., 2020:** Unraveling the genetic origin of 'Glera', 'Ribolla gialla' and other autochthonous grapevine varieties from Friuli Venezia Giulia (northeastern Italy). *Scientific Reports*, 10, 7206, DOI: 10.1038/s41598-020-64061-w.
- Crespan, M., Migliaro, D., Larger, S., Pindo, M., Palmisano, M., Manni, A., Manni, E., Polidori, E., Sbaffi, F., Silvestri, Q., Silvestroni, O., Velasco, R., Virgili, S., Camilli, G., 2021:** The grapevine (*Vitis vinifera* L.) varietal assortment and evolution in Marche region (central Italy). *OENO One* 55 (3), 17-37, DOI: 10.20870/oenone.2021.55.3.4628.
- D'Onofrio, C., Tumino, G., Gardiman, M., Crespan, M., Bignami, C., de Palma, L., Barbagallo, M.G., Muganu, M., Morcia, C., Novello, V., Schneider, A., Terzi, V., 2021:** Parentage atlas of Italian grapevine varieties as inferred from SNP genotyping. *Frontiers in Plant Science* 11, 2265, DOI: 10.3389/fpls.2020.605934.
- De Lorenzis, G., Las Casas, G., Brancadoro, L., Scienza A., 2014:** Genotyping of Sicilian grapevine germplasm resources (*V. vinifera* L.) and their relationships with Sangiovese. *Science Horticulturae* 169, 189-98, DOI: 10.1016/j.scienta.2014.02.028.
- De Lorenzis, G., Chipashvili, R., Failla, O., Maghradze, D., 2015:** Study of genetic variability in *Vitis vinifera* L. germplasm by high-throughput Vitis18kSNP array: The case of Georgian genetic resources. *BMC Plant Biology* 15, 154, DOI: 10.1186/s12870-015-0510-9.
- De Lorenzis, G., Mercati, F., Bergamini, C., Cardone, M. F., Lupini, A., Mauceri, A., Caputo, A.R., Abbate, L., Barbagallo, M.G., Antonacci, D., Sunseri, F., Brancadoro, L., 2019:** SNP genotyping elucidates the genetic diversity of *Magna Graecia* grapevine germplasm and its historical origin and dissemination. *BMC Plant Biology* 19, 7, DOI: 10.1186/s12870-018-1576-y.
- Lacombe, T., Boursiquot, J.M., Laucou, V., Di Vecchi-Staraz, M., Peros, J.P., This, P., 2013:** Large-scale parentage analysis in an extended set of grapevine cultivars (*Vitis vinifera* L.). *Theoretical and Applied Genetics* 126, 401-414, DOI: 10.1007/s00122-012-1988-2.
- Laucou, V., Launay, A., Bacilieri, R., Lacombe, T., Adam-Blondon, A.F., Bérard, A., Chauveau, A., de Andrés, M.T., Ludger Hausmann, L., Ibáñez, J., Le Paslier, M.C., Maghradze, D., Martínez-Zapater, J.M., Maul, E., Ponnaiah, M., Töpfer, R., Péros, J.P., Boursiquot, J.M., 2018:** Extended diversity analysis of cultivated grapevine *Vitis vinifera* with 10K genome-wide SNPs. *PLoS One* 13, 1-27, DOI: 10.1371/journal.pone.0192540.
- Maraš, V., Tello, J., Gazivoda, A., Mugosa, M., Persic, M., Raicevic, J., Stajner, N., Ocete, R., Bozovic, V., Popovic, T., García-Escudero, E., Grbic, M., Martínez-Zapater, J.M., Ibáñez, J., 2020:** Population genetic analysis in old Montenegrin vineyards reveals ancient ways currently active to generate diversity in *Vitis vinifera*. *Scientific Reports* 10, 15000, DOI: 10.1038/s41598-020-71918-7.
- Maul, E., Röckel, F., Töpfer, R., 2016:** The "missing link" 'Blauer Zimmettraube' reveals that 'Blauer Portugieser' and 'Blaufränkisch' originated in Lower Styria. *Vitis* 55 (3), 135-143, DOI: 10.5073/vitis.2016.55.135-143.
- Mercati, F., De Lorenzis, G., Mauceri, A., Zerbo, M., Brancadoro, L., D'Onofrio, C., Morcia, C., Barbagallo, M.G., Bignami, M.C., Gardiman, M., de Palma, L., Ruffa, P., Novello, V., Crespan, M., Sunseri, F., 2021:** Integrated Bayesian approaches shed light on the dissemination routes of the Eurasian grapevine germplasm. *Frontiers in Plant Science* 12, 692661, DOI: 10.3389/fpls.2021.692661.
- Mullins, M.G., Bouquet, A., Williams, L.E., 1992:** *Biology of the Grapevine*. Cambridge: Cambridge University Press.
- Raimondi, S., Tumino, G., Ruffa, P., Boccacci, P., Gambino, G., Schneider, A., 2020:** DNA-based genealogy reconstruction of Nebbiolo, Barbera and other ancient grapevine cultivars from northwestern Italy. *Scientific Reports* 10, 15782, DOI: <https://doi.org/10.1038/s41598-020-72799-6>.
- Robinson, J., Harding, J., Vouillamoz, J., 2012:** Sangiovese. In: *Wine grapes. A complete guide to 1.368 vine varieties, including their origins and flavours*, 942-946. Penguin Books Ltd., London, UK.
- Ruffa, P., Raimondi, S., Boccacci, P., Abbà, S., Schneider, A., 2016:** The key role of Moscato bianco and Malvasia aromatica di Parma in the parentage of traditional aromatic grape varieties. *Tree Genetics & Genomes* 12 50, DOI: 10.1007/s11295-016-1006-y.
- This, P., Lacombe, T., Thomas, M.R., 2006:** Historical origins and genetic diversity of wine grapes. *Trends in Genetics* 22 (9), 511-519, DOI: 10.1016/j.tig.2006.07.008.
- Zdunić, G., Luksic, K., Nagy, Z.A., Mucalo, A., Tomislav Radic, K. H., Butorac, L., Györfy Jahnke, G., Kiss, E., Ledesma-Krist, G., Regvar, M., Likar, M., Piltaver, A., Zulj Mihaljevic, M., Maletic, E., Pejic, I., Werling, M., Maul, E., 2020:** Genetic structure and relationships among wild and cultivated grapevines from Central Europe and part of the western Balkan Peninsula. *Genes* 11, 962, DOI: 10.3390/genes11090962.