Evidence for a Sympatric Origin of Ribolla gialla, Gouais Blanc and Schiava cultivars (*V. vinifera* L.)

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Ribolla gialla is an autochthonous grape variety cultivated in Friuli Venezia Giulia (Italy) and in Slovenia, and probably originated in Eastern Central Europe. Just like Ribolla gialla, the Gouais blanc and Schiava cultivars also appear to have originated in the same geographical area. To verify this hypothesis, a pool of varieties probably sharing the same historical and geographical origin were taken into account. The fingerprinting, by 35 SSR loci, of Gouais blanc, Ribolla gialla, Schiava grossa and Schiava lombarda (synonyms of Schiava bresciana), is presented and the correlation among historical, geographical and genetic information of these cultivars was investigated. Gouais blanc and Traminer, already suggested as key varieties in the development of European grape diversity and as parents for some French varieties, interestingly enough seems to be linked to Ribolla gialla. The putative parentage was verified using 58 microsatellite markers. The genetic results suggest a common geographical origin for Gouais blanc, Ribolla gialla and the Schiava group: these cultivars appear to be related through sympatric origin. The hypothesis of Ribolla gialla as a progeny of Gouais blanc and Traminer was ruled out. The data proved a second-degree relationship between Gouais blanc and Ribolla gialla and a third or more distant degree of relationships between Ribolla gialla and Traminer.

INTRODUCTION

It is largely documented that the original sites of domestication of wine and table cultivars of *Vitis vinifera* L. are in western Asia, most likely in eastern Anatolia and the Caucasian region (Olmo, 1995; Zohary & Hopf, 2000; This *et al*., 2006a). From the first centres of domestication, the cultivated grapevines moved towards Europe, possible through secondary centres of domestication, following the ancient routes of civilisation (Forni, 2012). The result of the primary and secondary domestication events, and successive local breeding processes, was the huge genetic variability of grapevine varieties, which are widespread in all the traditional winemaking areas, forming a rich germplasm diversity. Commencing from the first decade of the last century, as a consequence of the massive replanting of European vineyards after the devastating attack of Phylloxera (*Daktulosphaira vitifoliae* Fitch, a homopteran insect introduced from North America at the end of nineteenth century), a significant part of these locally bred and grown varieties began to decline and progressively were substituted by a limited numbers of elite local and international cultivars.

Nowadays, projects aimed at the recovery and exploitation of cultivars with historical and geographical relevance are in progress in a number of viticultural regions. Ribolla gialla, a traditional variety of the Collio area (Gorizia province, North-Eastern Italy), is one such example. According to its microsatellite allelic profile, Ribolla gialla is identical to Rebula, a variety from the Slovenian winegrowing area of Brda, on the Italian border (Rusjan *et al*., 2010; De Lorenzis *et al*., 2013). Ribolla gialla is considered an ancient and traditional cultivar of these two neighbouring regions (Cosmo & Polsinelli, 1957), with a strong relationship with their *terroirs* (Calò *et al*., 2006). In Italy, the first documented evidence of a wine made from Ribolla gialla dates back to 1409, when, during a banquet in honour of Pope Gregory XII, Ribolla wine from the Rosazzo Abbey was served (Peterlunger *et al*., 2004). The historical importance of this variety is traceable through the centuries in its usage in the Collio area: for example, Ribolla gialla was offered by municipal authorities to welcome foreign representatives or illustrious visitors, and supplied to the rich Venetian Republic markets (Calò & Costacurta, 2004). In the past few decades it was used to produce wines aimed

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at the local markets and appreciated by consumers for their typicality; now, Ribolla gialla grapes are back in vogue due to the growing interest in traditional and local grapevine landraces.

In the framework of the exploitation of local germplasm, the exploration of inter- and intravarietal genetic diversity is fundamental to define the most appropriated strategies. Some of these autochthonous grapevine varieties could have the same geographical origin (sympatry) and share important events in their cultural and economic history. This could be the case of Ribolla gialla, Gouais blanc, and the group of Italian cultivars called "Schiava".

Gouais blanc, or Heunisch weiss in German, is an old variety that was widespread all over Central Europe. It possibly was introduced from the Eastern Mediterranean Basin along the Danube route in East-Central Europe. It was brought to France by the Roman Emperor Probus during the 3rd century AD as a gift to the Gauls from his Croatian homeland (Aeberhard, 2005). It was cultivated up to the modern age in Austria, France, Germany and Switzerland. In Italy, a few Gouais blanc plants have been identified in Valle d'Aosta and other mountain valleys of Piedmont, attesting to its likely cultivation in the north-west area of the Alps (Schneider & Mannini, 2006). It is considered a qualitatively mediocre variety because of its vigour and high productivity; indeed, "Gouais" has a denigrating meaning, from the old French adjective "gou" (Bowers *et al*., 1999a). At present it is a neglected variety that is only maintained in germplasm collections. Nevertheless, it is a variety that is of paramount importance for the evolution of the West European *V. vinifera* varietal assortment, being the progenitor of several important varieties including the well-known Chardonnay and Gamay (Bowers *et al*., 1999a). Gouais blanc, together with Traminer and Pinot noir, have already been proposed as possible parents for several French varieties (Bowers *et al*., 2000). Based on the molecular analysis of 2 344 unique genotypes by 20 nuclear SSR, Lacombe *et al*. (2012) recently identified 63 genotypes (confirmed and new) related to Gouais blanc through a first-degree relationship, and among the kin group of half kinships the largest was the Gouais blanc kin group.

In Italy, the name "Schiava" (Schiava bianca, Schiava bresciana, Schiava gentile, Schiava grigia, Schiava grossa, Schiava lombarda, Schiava nostrana) is customary to identify a group of varieties possibly sharing some phenotypic traits, as well as a possible common geographical origin in Slavonia, a geographical and historical region in Eastern Croatia (Scienza & Failla, 1996). These cultivars were widely cultivated in Lombardia, Veneto, Trentino Alto Adige and Friuli (Northern Italian regions). Schiava grossa is cultivated as Trollinger in Austria and Germany (Vouillamoz & Arnold, 2010) and Tirolan in Croatia (E. Maletic, personal communication, 2014). It is supposed that the "Schiava" group arrived in Northern Italy and Germany from Pannonia (an ancient province of the Roman Empire bounded north and east by the Danube) with the Longobards, a Germanic population that invaded Italy in the eight century A.D. (Scienza & Failla, 1996). In Italy, these varieties are still cultivated in Trentino Alto Adige and Lombardia, although they have been neglected for decades in the Veneto and Friuli regions (Cosmo & Polsinelli, 1962). The generic varietal name *Sclave* has appeared in the Lombard notarial deeds since the 11th century, and in the Venetian-Lombard region it definitely was the most frequently mentioned variety in land rental documents, in acts of donation and duties and in lease payments (Scienza, 1999). According to molecular analysis reported in Fossati *et al*. (2001), the Schiava accessions collected in the different cultivation areas were classified into two main genotypes: Schiava grossa and Schiava lombarda.

The aim of this work was to investigate the genetic relationship among Ribolla gialla, Gouais blanc and "Schiava" cultivars probably sharing a common historical and geographic origin, based on the results of 35 microsatellite markers (SSR). Moreover, Ribolla gialla as a potential progeny of Gouais Blanc and Traminer was investigated by deep genotyping (58 SSR loci). Nuclear simple sequence repeat (SSR) markers are a useful tool to determine the genetic diversity of *V. vinifera* cultivars (Cipriani *et al*., 2010; Laucou *et al*., 2011; Bacilieri *et al*., 2013; Imazio *et al*., 2013), to solve cases of homonyms (This *et al*., 2006a, 2006b) and synonyms, and to establish pedigree analysis (Bowers *et al*., 2000; Vouillamoz & Grando, 2006; Boursiquot *et al*., 2009; Vouillamoz & Arnold, 2010; De Lorenzis *et al*., 2012; Lacombe *et al*., 2012).

MATERIALS AND METHODS

Plant material

Accessions of Barbera, Bela Glera, Chardonnay, Gouais blanc, Nebbiolo, Pinot noir, Prosecco tondo, Ribolla gialla, Schiava bresciana, Schiava grossa, Schiava lombarda, Syrah, Traminer cultivars were analysed in this study. The samples were collected from the experimental station of Riccagioia scpa (Pavia - Italy), except for Gouais blanc, which was collected from the Agroscope collection (Changins - Swiss).

Gouais blanc, Ribolla gialla and Schiava samples were selected as cultivars sharing a possible common origin; Pinot noir and Traminer as second parents of some Gouais blanc progenies (Bowers *et al*., 2000); Chardonnay as progeny of Gouais blanc and Pinot noir (Bowers *et al*., 1999a); Bela Glera and Prosecco tondo as autochthonous Slovenian and Italian cultivars related to the growing area of Ribolla gialla (Štajner *et al*., 2008); and Barbera, Nebbiolo and Syrah as outgroups.

Molecular analysis

DNA extractions were performed with a DNeasy Plant Mini Kit (Qiagen, Courtaboeuf, France), starting at 0.02 g of dried young leaves. Microsatellite analyses were performed on 35 microsatellite markers (SSR): 20 SSR loci used in Laucou *et al*. (2011), except VVIV37, nine loci selected by the *Vitis* Microsatellite Consortium (VMC1e8, VMC2b3, VMC2b5, VMC2h4, VMC5a1, VMC5c1, VMC5c5, VMC5h2, VMC5h5), VrZag62, VrZag79, VrZag83 and VrZag93 (Sefc *et al.*, 1999), and VVMD17, VVMD34 and VVMD36 (Bowers *et al*., 1999b). For Chardonnay cultivars, the allelic profile reported in Bowers *et al*. (1999a) was taken into account.

To investigate the relationship among Gouais blanc, Ribolla gialla and Traminer, an enhanced pedigree was performed at 23 additional SSR loci up to 58 SSR markers, as in Vouillamoz and Arnold (2010).

PCR amplification conditions and capillary electrophoresis detection were carried out as reported in De Lorenzis *et al*. (2012).

Data analyses

GenAlEx 6.2 software (Peakall & Smouse, 2006) was used to compare and identify samples with an identical allelic profile. The true-to-typeness for each sample was verified. Principal coordinates analysis (PCA, GenAlEx 6.2 software) was used to display genetic divergence among samples based on distance matrix. The dissimilarity matrix obtained by the first three principal coordinates was used to build a Neighbor-Joining dendrogram with MEGA 4.0 software (Tamura, 2007).

Relationship analyses were carried out on 58 SSR loci for Gouais blanc, Ribolla gialla and Traminer. The analyses were performed by calculating the number of loci with at least one allele identical by state (IBS), the identity by descent (IBD: Δ_7 and Δ_8) and relatedness (r) coefficients. Δ_7, Δ_8 and r coefficients were calculated by COANCESTRY 1.0 software (Wang, 2011). A total of 1 000 bootstrapping samples were adopted to estimate the 95% confidence intervals. Allele frequencies were calculated based on the allelic profiles of 87 cultivars that were representative of the European germplasm (Josè Vouillamoz's SSR database, Swiss), genotyped at the same set of markers (data not shown).

TABLE 1
Allelic profiles at 35 SSR loci for identified genotypes.

Locus	Barbera	Bela Glera	Gouais blanc	Nebbiolo	Pinot noir	Prosecco tondo	Ribolla gialla	Schiava grossa	Schiava lombarda	Syrah	Traminer
VMC1b11	181	171	169	165	165	165	171	171	183	165	171
	183	181	183	191	171	181	183	171	185	187	171
VMC1e8	206	208	208	218	226	208	222	208	222	230	226
	208	218	222	222	230	218	228	230	222	232	228
VMC2b3	180	180	164	184	162	164	164	164	164	168	164
	184	186	164	188	168	180	184	188	188	178	184
VMC2b5	193	193	187	185	189	193	193	189	189	193	193
	229	229	189	189	193	193	215	193	193	197	229
VMC2h4	209	203	207	215	203	207	201	203	-[a]	219	201
	225	209	225	215	203	215	221	217	-[a]	219	233
VMC4f3	181	168	172	168	172	168	172	172	172	172	172
	206	168	172	168	178	172	188	182	182	206	178
VMC5a1	168	162	158	166	154	162	164	154	168	164	154
	168	168	168	166	164	168	168	164	168	168	164
VMC5c1	145	145	145	145	145	145	153	151	-[a]	145	145
	145	145	173	145	164	165	153	151	-[a]	171	171
VMC5c5	119	119	119	121	119	119	119	121	119	119	119
	123	125	119	123	121	125	119	123	123	119	121
VMC5h2	193	207	193	207	193	193	193	193	-[a]	193	191
	193	207	193	207	207	207	193	207	-[a]	207	193
VMC5h5	176	176	178	176	168	172	170	168	178	178	170
	194	194	194	188	178	176	194	188	194	194	178
VrZag62	190	188	198	192	188	188	194	192	194	188	188
	198	194	206	198	194	202	198	194	198	194	194
VrZag79	241	249	235	241	235	245	235	237	237	241	241
	255	257	241	249	241	255	247	257	247	247	247
VrZag83	185	185	191	191	189	185	185	197	191	195	185
	191	191	197	197	201	191	191	203	197	201	197
VrZag93	189	199	189	189	189	197	189	189	189	189	189
	229	199	189	189	189	199	189	189	189	199	225
VVIB01	288	292	294	290	288	288	290	298	290	290	290
	294	296	298	298	294	292	294	298	298	294	296

TABLE 1 (CONTINUED)

Locus	Barbera	Bela Glera	Gouais blanc	Nebbiolo	Pinot noir	Prosecco tondo	Ribolla gialla	Schiava grossa	Schiava lombarda	Syrah	Traminer
VVIH54	166	168	150	166	166	166	166	168	168	162	160
	168	176	168	180	168	176	168	168	178	166	166
VVIN16	148	148	150	148	150	148	148	150	150	148	148
	158	152	150	156	158	150	150	156	152	152	156
VVIN73	262	262	262	262	262	262	262	264	262	260	262
	262	262	262	262	264	262	262	264	262	262	262
VVIP31	191	175	175	179	179	179	175	179	183	183	175
	193	179	183	195	183	191	189	191	183	189	189
VVIP60	318	320	320	316	318	320	320	316	320	314	304
	320	320	320	320	320	326	320	320	330	316	320
VVIQ52	79	76	76	83	83	76	76	79	76	81	79
	83	87	83	83	83	83	79	85	85	83	83
VVIV67	355	357	361	359	357	355	355	369	363	357	359
	361	369	361	365	367	359	367	369	369	375	367
VVMD5	224	224	232	230	226	224	230	234	228	224	230
	224	244	238	234	236	244	232	236	236	230	236
VVMD7	247	237	237	247	237	237	237	247	237	237	237
	251	237	247	249	241	245	247	247	251	237	251
VVMD17	211	221	221	211	211	221	221	221	221	211	221
	219	221	223	221	221	221	221	221	221	223	221
VVMD21	239	245	243	247	245	239	239	245	239	245	245
	245	245	245	247	245	245	245	245	245	263	245
VVMD24	205	205	205	205	213	209	205	209	209	205	205
	213	213	205	209	215	213	205	213	213	209	213
VVMD25	238	238	246	240	244	240	252	246	236	246	246
	254	240	262	242	254	244	262	260	246	246	246
VVMD27	183	177	177	181	183	177	177	179	179	185	183
	187	177	179	185	187	191	183	183	183	187	191
VVMD28	233	237	229	235	219	237	229	237	227	219	231
	259	255	247	267	237	245	233	245	245	229	233
VVMD32	250	252	250	240	240	262	250	256	254	240	240
	270	264	270	262	270	264	250	270	270	272	270
VVMD34	236	236	236	236	236	236	236	236	236	236	236
	236	238	238	238	236	238	236	236	236	236	236
VVMD36	249	249	271	259	261	247	271	271	-[a]	261	249
	249	249	283	259	261	249	271	303	-[a]	291	259
VVS2	127	139	129	151	133	131	139	131	131	129	131
	129	143	139	151	147	141	149	151	139	129	149

[a]'-': missing data.

RESULTS AND DISCUSSION

Genetic relationships

A set of 35 SSR loci were used to genotype Barbera, Bela Glera, Gouais blanc, Nebbiolo, Pinot noir, Prosecco tondo, Ribolla gialla, Schiava bresciana, Schiava grossa, Schiava lombarda, Syrah and Traminer. Twelve unique allelic profiles were identified, and only Schiava bresciana and Schiava lombarda shared the same allelic profile. The SSR allelic profiles of the identified genotypes are listed in Table 1. By comparing our results with DNA profiles published in previous works, the true-to-typeness of Barbera (This *et al*., 2004), Bela Glera (Štajner *et al*., 2008), Gouais blanc (Bowers *et al*., 1999a), Nebbiolo (Schneider *et al*., 2003), Pinot noir (Vouillamoz & Grando, 2006), Prosecco tondo (Crespan *et al*., 2007), Ribolla gialla (Rusjan *et al*., 2010), Schiava grossa (Vouillamoz & Arnold, 2010), Syrah (Vouillamoz

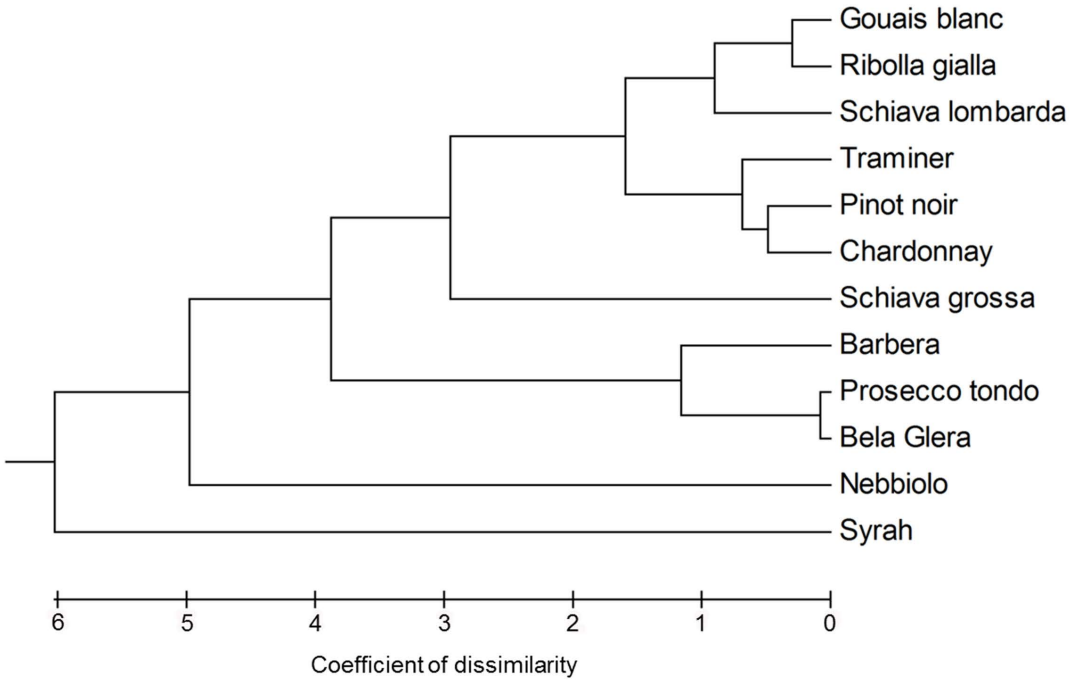

FIGURE 1
Neighbor-Joining dendrogram based on dissimilarity matrix of the first three PCA coordinates, showing the genetic relationship among 12 grapevine cultivars as determined by SSR data.

& Grando, 2006) and Traminer (Regner *et al.*, 2000) was ascertained. The allelic profiles of Schiava bresciana and Schiava lombarda did not match with any genotype in the available databases.

In order to understand the genetic similarity among cultivars, PCA was calculated based on the 35 SSR loci data matrix. The first three coordinates accounted for 68.18% of the total variation (28.09%, 21.03% and 19.06%, respectively). Based on the dissimilarity matrix obtained from the first three coordinates, a dendrogram displaying the relationship among samples was built (Fig. 1). The dendrogram showed two main clusters (threshold of dissimilarity value = 2): i) the first one comprising Chardonnay, Gouais blanc, Pinot noir, Ribolla gialla, Schiava lombarda and Traminer; ii) the second one including Barbera and two varieties cultivated in the north-east of Italy and Slovenia, namely Bela Glera and Prosecco tondo. The other varieties were grouped in minor clusters. Inside the first main cluster, two very distinct subsets were identified: the first one including Gouais blanc, Ribolla gialla and Schiava lombarda, with the second one including Chardonnay, Pinot noir and Traminer. The Schiava grossa variety, clustered without any other samples, appeared to be related more to the first main cluster, while Nebbiolo and Syrah were grouped as outgroups. The dendrogram showed a clear genetic grouping of varieties largely consistent with their geographic origin. As expected, the molecular analysis highlighted the similarity among Gouais blanc, Ribolla gialla and one cultivar of "Schiava" (Schiava lombarda). This result was in agreement with the hypothesis of a common geographical origin for those varieties. The differences in the allelic profiles of the Schiava cultivars were confirmed, but the dissimilarity of these two genotypes was lower than expected if following the results obtained by Fossati *et al.* (2001). Our results, based on the analysis of 35 SSR loci, could reject the Fossati *et al.* (2001) hypothesis that the term "Schiave" more likely refers to a similarity in the vine training system than to a similar genetic background. The latter hypothesis was based on an analysis of only five SSR loci and five AFLP primers combinations, which are known sometimes to produce irreproducible AFLP-banding profiles (Benjak *et al.* 2006).

Furthermore, the dendrogram grouped together the Gouais blanc, Ribolla gialla and Schiava lombarda cultivars, which share some phenotypic and oenological traits: high vigour and high-yielding capacity, large berries and bunches, and medium sugar and high acidity levels in the berry juice (O. Failla, personal communication, 2013). A further indication of the common origin of Gouais blanc and Schiava is linked to the semantics of the variety name. In Germany, the medieval term "Heunisch" was used to identify the local wines in contrast to "Fränkisch" (foreign wine). "Heunisch" and "Schiava" appear to have the same semantic value: "Heunisch" - "Hunnisch" i.e. Huns'; and "Schiava" - "Slavus" i.e. Slavic (from Slavonia), two old populations coming from Eastern Europe (Scienza & Failla, 1996). Following the Venetian meaning of the term "Slavus", the Slavs in particular were considered to be the populations coming from the Northern Balkans.

Moreover, the second main cluster showed a consistent relationship with geographical area. In this cluster we find Bela Glera and Prosecco tondo strongly related to Friuli Venezia Giulia (the Italian region), Istria and Slovenia. Both names sometimes were used erroneously to identify the same variety (Crespan *et al.*, 2007). The name Prosecco tondo could have arisen from the village of Prosecco (Trieste, Friuli Venezia Giulia), and its synonyms are Teran Bijeli in Croatia

(Maletić *et al*., 1999), and Briška Glera and Števerjana in Slovenia (Štajner *et al*., 2011). Varieties called "Glera" are cultivated in Italy (Cividale and Tieste) and in neighbouring countries (Crespan *et al*., 2009; Rusjan *et al*., 2010). The allelic profile of Bela Glera was genetically dissimilar to the other Glera/Prosecco tondo allelic profiles reported in previous works (Štajner *et al*., 2008; Crespan *et al*., 2009; Rusjan *et al*., 2010). This dissimilarity could be explained by the use of the word "Glera" to identify a group of white grapevine varieties (Vertovec, 1844). What was surprising was the presence of Barbera, one of the most important red grape varieties grown in the north-west of Italy, in the third cluster.

Two varieties largely cultivated in the Alpine Arc, Nebbiolo and Syrah, were grouped as an outgroup. Nebbiolo is considered one of the noblest Italian varieties, and its growing area is limited to the mountains of Valle d'Aosta, Piemonte and Valtellina, while Syrah is the famous Rhone Valley red grape cultivar cultivated worldwide. The dissimilarity between the first main cluster and the outgroup varieties was consistent with the genetic distance between Pinot noir and Syrah proved by Vouillamoz and Grando (2006).

Kinship analysis

Considering the broad participation of Gouais blanc and Traminer in the parentship, origin and spread of the grape landraces, Ribolla gialla could be considered a good candidate for having a strong relationship with these two varieties. In order to investigate a possible relationship between Gouais blanc, Ribolla gialla and Traminer, 58 SSR loci were used to generate a deep genotyping and to suggest the most likely pedigree among these varieties. The allelic profile of each analysed cultivar is listed in Table 2.

Gouais blanc and Ribolla gialla shared at least one allele for locus 53 out of 58 loci (IBS = 53), and the IBD and relatedness coefficients values were: Δ_7 = -0.0610 ± 0.0145; Δ_8 = 0.5031 ± 0.0377; and r = 0.1905 ± 0.0023 respectively. These results are not typical of the PO (parent-offspring) relationship, as the IBS value should have been 58 (100% of analysed loci) and the IBD and r values should have been close to the theoretical values 0, 1 and 0.5. The putative PO relationship between Gouais blanc and Ribolla gialla can be ruled out, because it would seem improbable that five discrepancies can be explained by mutations, null alleles or PCR errors (Vouillamoz & Grando, 2006). Nevertheless, these values could explain a second-degree relationship.

At the same time, the supposed close relationship

TABLE 2
Allelic profiles of 23 additional SSR loci for Gouais blanc, Ribolla gialla and Traminer cultivars. Reference variety: 'Pinot noir'.

Locus	Gouais blanc	Ribolla gialla	Traminer	Pinot Noir
VMC1c10	142	156	156	156
	168	168	168	156
VMC2a5	157	157	157	189
	171	171	189	189
VMC2b11	184	168	168	180
	184	184	180	182
VMC2e7	152	156	152	152
	156	160	160	158
VMC2f10	97	93	93	93
	99	99	103	115
VMC3d12	198	205	198	205
	205	205	205	222
VMC4c6	157	163	163	163
	163	165	165	163
VMC5g8	303	303	313	313
	311	317	317	317
VMC6e1	141	165	151	151
	165	170	161	165
VMC6e10	91	109	109	107
	107	132	113	109
VMC6g1	198	191	170	170
	198	198	170	178
VMC8d11	136	126	132	122
	142	136	136	132

TABLE 2 (CONTINUED)

Locus	Gouais blanc	Ribolla gialla	Traminer	Pinot Noir
VMC8f10	197	205	197	195
	205	233	233	197
VMC8g6	147	147	155	147
	155	155	169	169
VMC9b5	248	244	242	244
	262	250	244	248
VMC16f3	177	177	177	177
	181	177	183	183
VrZag21	202	202	200	200
	206	215	206	206
VrZag29	112	112	112	112
	112	116	116	116
VVMD6	194	194	205	205
	214	212	212	205
VVMD26	249	249	249	249
	251	249	251	255
VVMD31	212	210	204	216
	214	212	216	216
VVS4	168	168	151	168
	168	168	151	173
VVS29	171	171	171	171
	179	179	171	179

between Ribolla gialla and Traminer has to be dismissed. Ribolla gialla is genetically dissimilar to Traminer, sharing only 47 out of 58 analysed loci. The IBD and *r* coefficient values calculated for these pair of varieties do not match the theoretical values of the assignment of kinship categories (Δ_7 = -0.1675 ± 0.0732; Δ_8 = 0.3281 ± 0.0165; *r* = -0.0035 ± 0.0282), suggesting that Ribolla gialla and Traminer could be third or more distant relatives. These data provide strong evidence that Ribolla gialla is not a progeny of 'Gouais blanc x Traminer'.

CONCLUSIONS

During the process of domestication, the role of winegrowers was to improve the quality and quantity of the production of grapes by selecting seedlings from spontaneous crosses among different domesticated forms of *V. vinifera* subsp. *sativa*, and possible also among its wild relative forms of *V. vinifera* subsp. *sylvestris*. Gouais blanc has played an important role in the origin of the main grapevines of Central Europe, as is evident from several published research works providing information on the Gouais blanc progeny. Although the hypothesis that Ribolla gialla is a full sibling of two ancient cultivars widely involved in the history of grape breeding (Gouais blanc and Traminer) has been rejected, the genetic data suggest a high correlation among Ribolla gialla, Gouais blanc and the Schiava cultivars. Right now we are not able to determine the hierarchy of or identify the missing links among these varieties, but our results have highlighted the first evidence of a common ancestral variety and the possible sympatric origin of these grapevines in Eastern-Central Europe.

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