

Article

Comparison between the Grape Technological Characteristics of *Vitis vinifera* Subsp. *sylvestris* and Subsp. *sativa*

David Maghradze ¹, Shengeli Kikilashvili ^{2,3}, Olan Gotsiridze ², Tamar Maghradze ², Daniela Fracassetti ^{4,*} , Osvaldo Failla ⁵ and Laura Rustioni ⁶ 

¹ LEPL Scientific-Research Center of Agriculture, 6 Marshal Gelovani Ave, 0159 Tbilisi, Georgia; david.maghradze@gmail.com

² Faculty of Viticulture and Winemaking, Caucasus International University, Chargali Street 73, 0141 Tbilisi, Georgia; shengeli.kikilashvili@ciu.edu.ge (S.K.); olan.gotsiridze@ciu.edu.ge (O.G.); tamar_maghradze@ciu.edu.ge (T.M.)

³ Faculty of Agrarian Sciences and Biosystem Engineering, Georgian Technical University (GTU), 17, David Guramishvili Ave, 0192 Tbilisi, Georgia

⁴ Department of Food, Environmental and Nutritional Sciences, Università degli Studi di Milano, Via G. Celoria 2, 20133 Milan, Italy

⁵ Department of Agricultural and Environmental Sciences—Production, Landscape, Agroenergy, Università degli Studi di Milano, Via G. Celoria 2, 20133 Milan, Italy; osvaldo.failla@unimi.it

⁶ Laboratorio di Colture Arboree, DiSteBA (Dipartimento di Scienze e Tecnologie Biologiche e Ambientali), Università del Salento, Via Provinciale Monteroni, 73100 Lecce, Italy; laura.rustioni@unisalento.it

* Correspondence: daniela.fracassetti@unimi.it



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Abstract: Wine has been produced in Georgia since the 6th millennium BC. The processes of cultivar selection and breeding started with wild grapes *Vitis vinifera* L. ssp. *sylvestris* Gmel. and included multiple introgression events—from the wild to domestication. This article aims at improving the knowledge concerning the history of winemaking through a comparison of the *Vitis vinifera* subsp. *sylvestris* and subsp. *sativa*. Grapes of *Vitis vinifera* subsp. *sylvestris* were grown in an ampelographic collection and vintages 2017–2020 were analyzed. The obtained data were compared to a wider dataset available in literature concerning *Vitis vinifera* subsp. *sativa*, demonstrating the central role of grape morphology in the domestication process. This evidence suggests that the technological value of the cultivars played an important role in the selection process. In vintages 2017, 2018, and 2019, wines were produced with *Vitis vinifera* subsp. *sylvestris* grapes and compared with Cabernet Sauvignon and Saperavi vinifications. For all the vintages, the fermentations took shorter time for wild grape, despite the highest content of total phenols. Learning from the past, *Vitis vinifera* subsp. *sylvestris* might still be an interesting genetic resource for future breeding programs. Furthermore, the possible combination of wild and domesticated grapes can make possible the production of wines with long ageing, exalting their own characteristics.

Keywords: wild grapes; Caucasus; Neolithic wines; genetic resources; grapevine domestication; viticulture; winemaking

1. Introduction

A recent bio-archeological multidisciplinary research confirmed that the earliest evidence of wine production from grapes (*Vitis vinifera* L.) in large-capacity jars was in the Georgian territory [1]. The research demonstrated that Neolithic *Shulaveri-Shomu Tepe* culture grew grapevine plants near their villages in 6th millennium BC, as confirmed also by numerous pollen grains of grapes extracted from the archaeological sites of *Gadachrili Gora* and *Shulaveri Gora* since 2014 [2]. According to this data, we have to consider that grapevine domestication, with the processes of cultivar selection and breeding, was initiated 8000 years ago in the South Caucasian area.

It is not fully understood how Neolithic population managed grapevine cultivation. Based on the available information of later historical periods, we can also assume that the Neolithic people used to protect and improve the wild grapevine populations, together with their support trees, by cleaning the surrounding forest from trees and shrubs in competition with grapevines for light and soil resources (nutrient and water). The management of these wild grapevine populations can be considered as the first stage of grape domestication named as ‘Embryonic viticulture’ [3].

The domestication of grapevine *Vitis vinifera* L. is still to be clarified. Based on the theory proposed by Vavilov [4], the crucial role of *Vitis vinifera* wild relative is the starting point of the process. The wild relative of the Eurasian cultivated grapevine *Vitis vinifera* ssp. *sativa* DC. is the wild grape *Vitis vinifera* ssp. *sylvestris* Gmel. Actually, these two taxa are so close to each other that botanists recognize them as a sub-species of the same Linnaean species. Beside the wild grapevine role in initiating the domestication process, it took an important follow-up part in different historical periods, regions, and cultures, for both winemaking and possibly multiple introgression events from the wild to the domestic compartment. This role is well documented, thanks the possibility of tracing the grape domestication through the botanical remains, mainly the seeds, from archaeological sites. An updated table concerning the archaeobotanical records of grapevine in Georgia is reported in Table S1. The well-established method used to distinguish wild and cultivated grapevine seeds is based on a range of morpho-biometric criteria, including the ratio of width and length [5]. More recently, several morphometric measurements can be processed by multivariate analysis [6]. In the initial stage of domestication, in the Early Neolithic period, the wild morphotype was usually found in the archeological sites of Caucasus. The presence of a wild seed morphotype, alone or together with domesticated morphotype, has also been dated in the following protohistoric and historic periods, until the Middle Ages, not only in Caucasus, but also in Greece, Sardinia, and France [6–9].

Archaeologists mainly infer to the simultaneous presence of wild and domestic grape seed morphotypes as a marker of primary or secondary grapevine domestication centers or as a consequence of the introduction of domesticated grapevines in regions where wild grapevines were already proto-cultivated [6,7]. According to these authors, wild grapevines might have been cultivated and used to make wine. With cultivation, we refer to grapevine management, including pruning, selective propagation, and planting to improve fruit production. Cultivation of the wild grapevine might be considered as one of the first steps in the domestication process [9]. This exploitation provides a solid basis for the initial periods of grape cultivation, but the presence of both wild grape seeds with cultivated morphotype in the following historical periods can be ascribable to other reasons. According to the literature, the probable reasons why wild grapes were used for winemaking together with domestic grapes could be: (i) the abundant availability of wild grapes in the forest and wild vegetation of Europe and minor Asia until the mid-19th century [10,11]; (ii) the scarcity of grapes from cultivated vineyards due to economic and political instability in Sardinia during the 14th century [12], in Georgia in the 18th century [13], in Germany and Italy until recent times [14–16]; (iii) the improved durability, taste, and flavor of wines obtained with wild and cultivated grapes [14]; and (iv) the production of vinegar that was one of the main products used with salt for food preservation in the past [14]. Moreover, (v) wild grapevines were also collected and employed as a medicinal plant [14,17].

Currently, wild grapevines are considered as a rare and endangered plant subspecies, despite the scientific community agreeing to consider *Vitis vinifera* L. subsp. *sylvestris* Gmel. as a precious genetic resource [18].

The production of wine with wild grapevines, known also as ‘wild wine’, can find justification and support due to their oenological traits. Even if certain characteristics seem to be of particular interest from a winemaking perspective, data concerning wines produced with wild grapes is still limited to make definitive assumptions. Nonetheless, previously published research has showed promising results. The wine made from the wild grapes of the river Ega (Santa Cruz de Campezo, North Spain) was characterized by high color

intensity (26.57) and total acidity (19.3 g of tartaric acid/L) that the authors indicated of importance thinking about breeding of red cultivars in areas under a temperate climate [19]. Similarly, wild wine produced in Sardinia (Italy) had good acidity and color intensity [12]. Arroyo-García et al. [10] made wine using wild grapes from Rivera de Huelva (Andalusia, Spain); the authors indicated that microvinification led to a wine with good acidity and medium color intensity, two interesting characteristics in a warm climate. These traits of wild wines can be considered the two main characteristics for improving viticulture in current climatic conditions [20]. Lara et al. [14] reported that wild wine showed ethanol content up to 14.5% (v/v), good degree of acidity with pH values in the range 3.1–3.5, and a high level of total polyphenols (about 80 g/L), suggesting the suitability of must from wild grape for prolonged winemaking process. More recently, a study of seven accessions of wild wines made with grapes harvested in the forests of the South Caucasus countries, including Armenia, Azerbaijan, and Georgia, also demonstrated the diversity of enological parameters, providing the idea that the must of wild grape could be used to improve traditional wines, resulting in color intensity [21]. This data also suggests that the possible combination of wild and domesticated grapes can make a wine suitable for long ageing.

However, the wines made with wild grapes collected in the forests can only provide general information about the wild wines [21,22]. Various limiting factors, such as non-uniform berry maturation, geographical differences in plant locations, and birds picking ripe berries, can limit the effective demonstration of the maximum enological potential of wild grapes. The harvest of grapes cultivated in vineyards allows to overcome these constraints. Derosas et al. [23] studied the wines prepared from five accessions of wild grape of Sardinia located in a field collection (AGRI Sardinia, Cagliari). The authors showed the wines had an adequate amount of ethanol and the variability of certain enological characters (like polyphenols) made the wild grapes interesting for winemaking purposes as well for further enological investigation.

Due to the important innovation in molecular biology of the last decades, research is mainly focused on plants' genetic aspects. In fact, it has been shown that the identification and study of genetic diversity using SSR markers is the most studied aspect concerning wild grapevine populations [18]. To add to current knowledge, this study aimed to provide enocarpological characteristics of wild grapevine *Vitis vinifera sylvestris* from Georgia. These data were then compared to the similar data of the large set of cultivated grapevines of *Vitis vinifera sativa* from Georgia and other European countries. Moreover, the composition of wines produced with wild and cultivated grapes was evaluated in order to better understand the role of grape breeding in enology during millennia. The interest of studying wines made from wild grapes in comparison to cultivated grapes becomes evident by analyzing both grapes and wines. The long-term goal will be to increase the knowledge about wild grapes and wines and to evaluate the suitability and potentiality of wild grapes for wine production.

2. Materials and Methods

2.1. Experimental Design: Experimental Site Description, Plant Material, and Maintenance

The experiment was conducted in the *Vitis vinifera* subsp. *sylvestris* collection established during 2014–2016, facilitated by the research program of the National Wine Agency for the “Study of Vine and Wine Culture of Georgia”. The plant materials grown in that vineyard were discovered during expeditions to the territory of Georgia in 2003 under the framework of various national and international projects. Molecular fingerprinting based on SSR and SNPs markers have been used to identify the true-to-type of *Vitis sylvestris* accessions [24].

This vineyard belongs to the Jighaura collection (FAO code GEO038) named after academician S. Cholokashvili of LEPL Scientific-Research of Agriculture (Mtskheta, Kartli Province of Eastern Georgia). The *Vitis vinifera* subsp. *sylvestris* collection site (Latitude 41.90, Longitude 44.76, Elevation 513 m a.s.l.) accumulates 2100–2350 °C of Growing Degree Days (GDD) and 540–590 mm of average annual precipitation [25]. The soil of the

site is meadow brown, and it has good physical properties and the ability to retain water. The content of lime increases deeper into the soil (up to 18–20%); its pH is 7.8–8.1 and the humus content is 1.40–1.65%. It is poor in nitrogen and phosphorus and contains potassium in medium amounts. The planting layout is 2.3 m (between rows) x 1.3 m (between plants). The pruning system is Double-Guyot (20–24 buds/vine). The soil is managed with a natural grass-cover system. If necessary, a drip-irrigation system is available. Nutritional supply and pesticide control are managed to guarantee the good development and production of plants, as well as their healthy conditions during all vegetative seasons. All the vines are grafted on Kober 5 BB (*Vitis berlandieri* x *Vitis riparia*) rootstocks.

The collection maintains 60 wild grapevine accessions (3–5 plants/accession), including both male and female plants. However, only plants having female type of flowers and producing grapes were considered in this research.

2.2. Eno-Carpological Description

The analyses were carried on the 2017–2020 period. Most of the accessions were studied for 3–4 vintages, however, this number varied depending on the availability of grapes in each accession. Details concerning the number of measurements for each parameter are available in Table S2.

The standard phenotyping protocol proposed by the COST action FA1003 “East-West Collaboration for Grapevine Diversity Exploration and Mobilization of Adaptive Traits for Breeding” has been adopted for eno-carpological evaluation of wild accessions [26–29]. Briefly, 3 replications of 3 representative bunches for each accession were collected at maturity stage (upon stable sugars concentration) and weighted. From each replicate, 10 berries were selected and their diameters measured. These berries were also used to quantify the berry weight, skin weight, seed number, and weight. Skins and seeds were extracted in a hydrochloric ethanol solution (ethanol/water/hydrochloric acid 37% 70/30/1), to quantify the total phenolic and anthocyanin concentrations. Phenols were analyzed separately for skin and seed extracts, using the Folin–Ciocalteu reagent. The absorbance for total anthocyanins (at 540 nm) and total polyphenols (at 700 nm) was measured by using a UV-1100 Spectrophotometer (Jiangsu, China) and respectively expressed as malvidin-3-O-glucoside (mg/kg of grape) and (+) catechin (mg/kg of grape) concentration [30,31]. The surplus of the bunches was pressed to obtain musts. The total soluble solids (°Brix) were measured by a digital refractometer and total acidity by titration with sodium hydroxide 0.1 N with bromothymol blue as the indicator.

2.3. Wine Production and Characterization

During vintages 2017, 2018, and 2019, wines were produced with *Vitis vinifera* subsp. *sylvestris* grapes. Due to the low yield of wild grapevines, all the productive accessions were mixed. As comparison, aliquots of Cabernet Sauvignon and Saperavi grapes were also harvested at the Jighaura collection of the LEPL Scientific-Research Center of Agriculture and microvinifications were carried out. The amounts of the three grape cultivars considered and vinified for each vintage are reported in Table S3.

Vinifications were carried out by using the red winemaking method (with grape skin maceration) [32]. Briefly, grapes were hand-harvested and destemmed to remove the stalks. Crushing was carried out manually and the obtained musts were added with potassium metabisulfite (60 mg/L) in order to prevent spontaneous and undesired fermentations. Inoculum was performed with a commercial yeast (IOC 18-2007, 0.2 g/L) that was prepared by dissolving the yeast powder in 100-times volume of water. The yeast suspension was kept at 36 °C for 15 min under shaking, and the same amount of grape must was added in order to adapt the yeast cells to the temperature of must. After 10 min, the yeast suspension was added to musts contained in three separate small tanks (10–20 L). The alcoholic fermentation was carried out at 20 ± 2 °C and it lasted up to 25 days (Table S2). Fermentations were conducted to dryness. At the end of the alcoholic fermentation, grape pomaces were separated by pressing and the obtained wines were added with potassium

metabisulfite (60 mg/L). The wines were kept in the microvinification tanks at 15–20 °C for 6 months; after stabilization and clarification, they were racked and bottled in green bottles (750 mL) closed with an agglomerated cork cap after the addition of potassium metabisulfite (60 mg/L). The wines were stored at 15–20 °C and analyzed six months after the bottling.

The analyses of musts and wines were carried out following the official protocols reported by the International Organization of Vine and Wine (OIV). In particular, the analyzed parameters in both musts and wines were sugar content (g/L; OIV-AS311-01A), pH (OIV-MA-AS313-01) and total acidity (g/L of tartaric acid; OIV-MA-AS313-01). Volatile acidity (g/L of acetic acid; OIV-MA-AS313-02), ethanol (% (v/v); OIV-MA-AS312-01A), malvidin diglucoside (mL/L; OIV-MA-AS312), total phenol content (mg/L of catechin; OIV-MA-E-AS2-10-INDFOL; spectrophotometer SP-Carry-50—Los Angeles, CA, United States), and total dry extract (g/L; OIV-MA-AS2-0315-11; equipment- KNAUER thermo chromatography) were determined in wine samples.

2.4. Statistic Data Processing

The software SPSS (SPSS, Chicago, IL, USA) version 22.0 was used for the statistical data processing.

The description of the Georgian population of *Vitis vinifera* subsp. *sylvestris* was compared to the *Vitis vinifera* subsp. *sativa* dataset collected during the COST action FA1003 “East-West Collaboration for Grapevine Diversity Exploration and Mobilization of Adaptive Traits for Breeding” [26–28,33]. Differences and similarities are shown overlapping the frequency distribution graph of the two populations for each studied parameter. Descriptive analysis (average, minimum, maximum, quartiles—25, 50, 75) of the Georgian *Vitis vinifera* subsp. *sylvestris* population was compared to the data available in literature concerning the Georgian [33] and Euro-Asiatic [26] *Vitis vinifera* subsp. *sativa* populations.

Data related to the composition of must and wine samples were averaged among vintages as only negligible differences were found. One-way ANOVA was carried out and significant differences among must and wine samples produced from different grapes were determined by F-test (LSD) considering $p < 0.1$ and $p < 0.05$.

3. Results

3.1. Grape Characterization

Vitis vinifera subsp. *sylvestris* had smaller fruits than *Vitis vinifera* subsp. *sativa*. The bunches were smaller (Figure 1a), made by smaller berries (Figure 1b–d). However, the shape of the berry remained similar, with a dominance of round berries (Figure 1e). Obviously, the smaller berries had a higher ratio of surface with respect to the sphere volume and, thus, the contribution of skins to the total berry weight was higher in the subsp. *sylvestris* (Figure 1f).

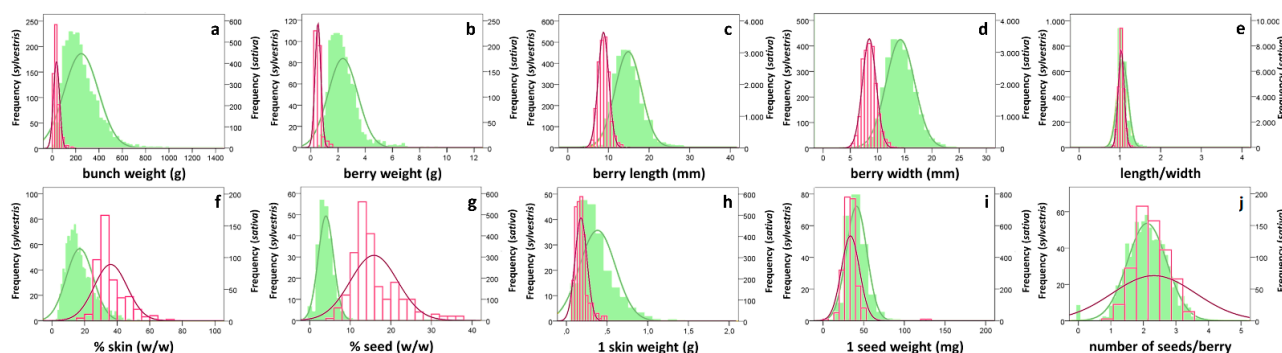


Figure 1. Carpological characteristics of *Vitis vinifera* subsp. *sylvestris* (in pink) and subsp. *sativa* (in green). *Vitis vinifera* subsp. *sativa* data are already published in Rustioni et al. [26]. (a): bunch weight (g), (b): berry weight (g), (c): berry length (mm), (d): berry width (mm), (e): length/width, (f): % skin (w/w), (g): % seed (w/w), (h): one skin weight (g), (i): one seed weight (mg), (j): number of seeds/berry.

The number of seeds per berry was similar among the subspecies (Figure 1j), with a slightly larger number in the subsp. *sylvestris* (Table S2). Nevertheless, despite the seed weight being generally lower in subsp. *sylvestris* (Figure 1i), the contribution of seed to the total berry weight was higher in the subsp. *sylvestris* (Figure 1g) due to the smaller berries with less pulp.

The *Vitis vinifera* subsp. *sylvestris* musts were more concentrated than *Vitis vinifera* subsp. *sativa* in both sugars and acids (Figure 2a,b).

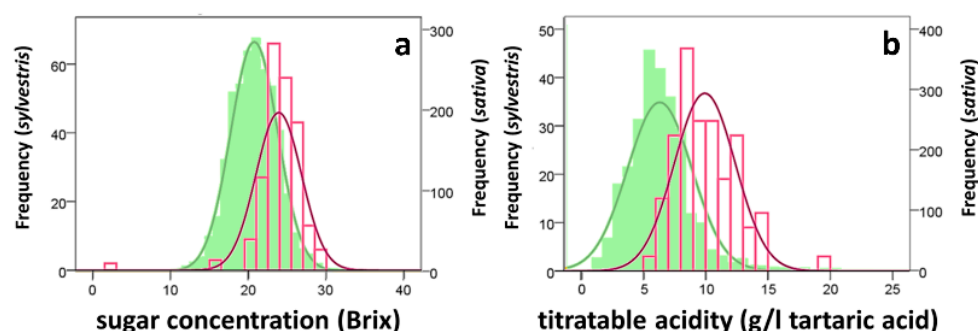


Figure 2. Technological parameters of the must of *Vitis vinifera* subsp. *sylvestris* (in pink) and subsp. *sativa* (in green). *Vitis vinifera* subsp. *sativa* data are already published in Rustioni et al. [26]. (a): sugar concentration (Brix), (b): titratable acidity (g/L tartaric acid).

The grapes of *Vitis vinifera* subsp. *sylvestris* had a higher concentration in anthocyanins than *Vitis vinifera* subsp. *sativa* (Figure 3a). However, this is mainly due to the carpological features of the grapes, with higher proportions of pigmented skins in subsp. *sylvestris*. In fact, the accumulation of pigments in the skin tissue was very similar among the two subspecies (Figure 3c) and, thus, a small *sylvestris* berry had a lower amount of anthocyanins (Figure 3b), having a smaller skin.

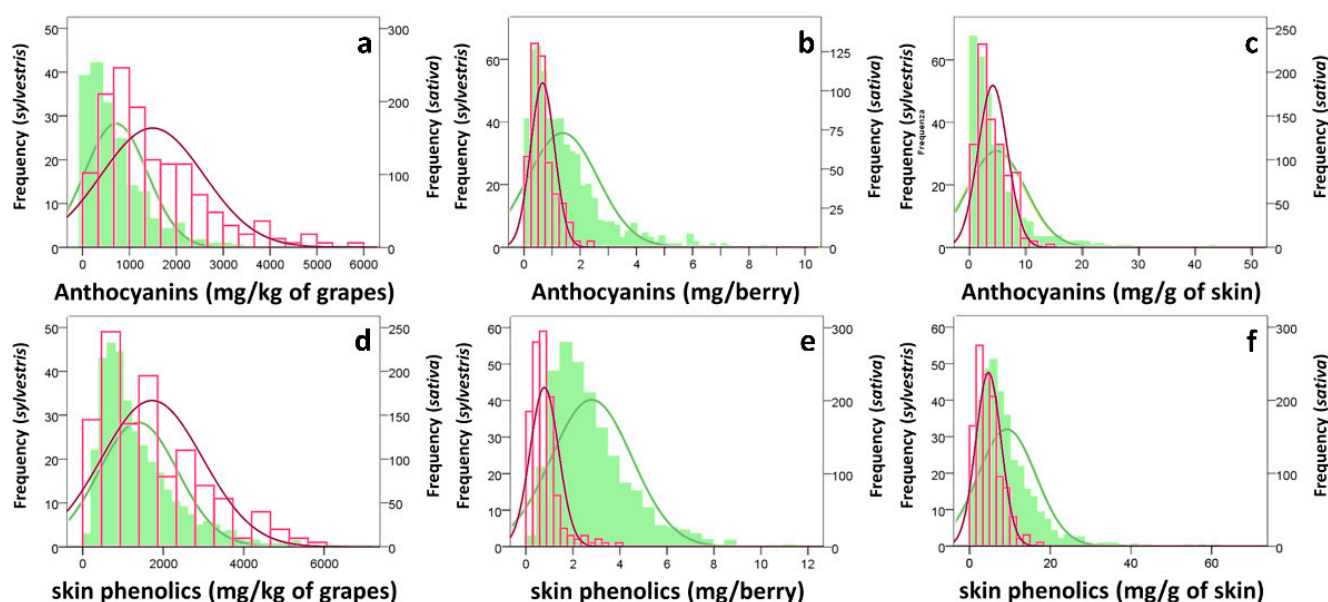


Figure 3. Anthocyanins and phenolics in skins of *Vitis vinifera* subsp. *sylvestris* (in pink) and subsp. *sativa* (in green). *Vitis vinifera* subsp. *sativa* data are already published in Rustioni et al. [26]. (a): anthocyanins (mg/kg of grapes), (b): anthocyanins (mg/berry), (c): anthocyanins (mg/g of skin), (d): skin phenolics (mg/kg of grapes), (e): skin phenolics (mg/berry), (f): skin phenolics (mg/g of skin).

Concerning the skin phenolics, the lower concentration in the small *sylvestris* berries (Figure 3e) was exacerbated by a lower ability of the skin tissue in their synthesis (Figure 3f).

Nevertheless, the higher skin percentage of the berry weight (Figure 1f) ensured a slightly higher phenolic concentration in *sylvestris* grapes (Figure 3d).

The grapes of *Vitis vinifera* subsp. *sylvestris* had a higher concentration in seed phenolics than *Vitis vinifera* subsp. *sativa* (Figure 4a), due to the higher seed percentage of the berry weight (Figure 1g), despite the generally lower ability of *sylvestris* seeds to accumulate phenolics (Figure 4b–d).

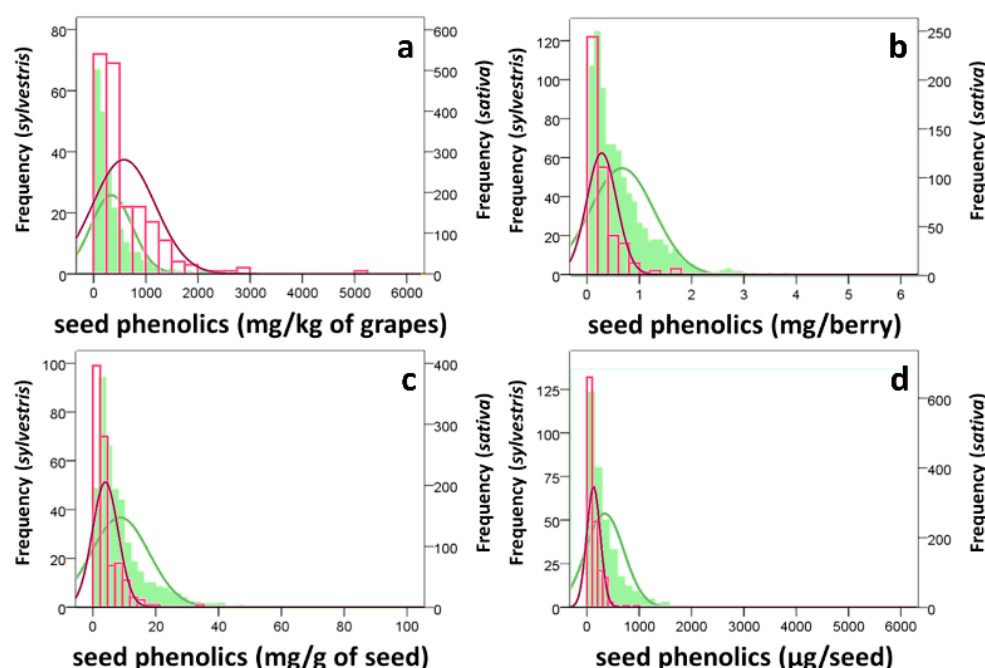


Figure 4. Seed phenolics in *Vitis vinifera* subsp. *sylvestris* (in pink) and subsp. *sativa* (in green). *Vitis vinifera* subsp. *sativa* data are already published in Rustioni et al. [26]. (a): seed phenolics (mg/kg of grapes), (b): seed phenolics (mg/berry), (c): seed phenolics (mg/g of seed), (d): seed phenolics (µg/seed).

Despite the lower accumulation of phenolics in the small *sylvestris* berries (Figure 5d), the carpological features ensured a slightly higher total phenolic amount in *sylvestris* grapes (Figure 5c). These phenolics came mainly from skins (Figure 5a), still the proportion rising from seeds was higher in *sylvestris* with respect to *sativa* (Figure 5a,b).

Enlarging the comparison of the *sativa* grapes cultivated in Georgia (Table S2), it is worth noticing that these grapes were characterized by carpological descriptors with values often in between the ones recorded for *sylvestris* and *sativa*, with values obviously closed to the ones recorded in *sativa*. However, Georgian cultivars were characterized by thicker skins and heavier seeds, and this has impacts on the phenolic components.

3.2. Composition of Musts and Wines

The sugar concentration of all the three musts samples investigated in this study indicated the ripeness of the grapes and the suitability of harvest time for wine production. The sugar concentration was slightly higher in wild grapes, while acidity and pH were higher in Saperavi grape (Table 1). However, no significant difference was found in the chemical parameters of must samples.

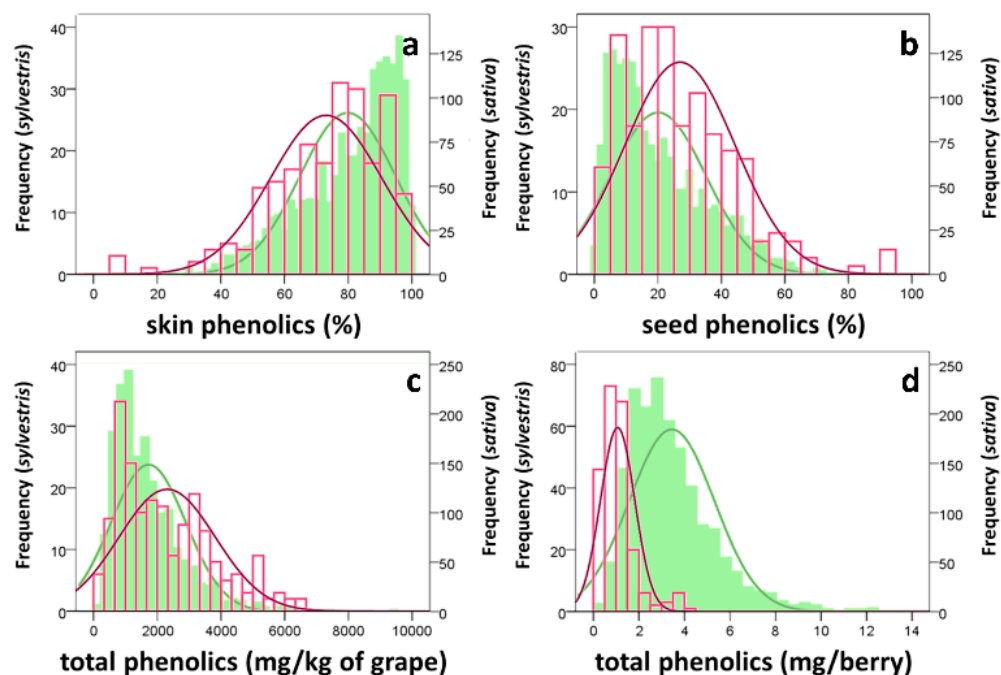


Figure 5. Total phenolics and their origin proportions in *Vitis vinifera* subsp. *sylvestris* (in pink) and subsp. *sativa* (in green). *Vitis vinifera* subsp. *sativa* data are already published in Rustioni et al. [26]. (a): skin phenolics (%), (b): seed phenolics (%), (c): total phenolics (mg/kg of grapes), (d): total phenolics (mg/berry).

Table 1. Sugar concentration, total acidity, and pH for the musts produced with wild grape, Cabernet Sauvignon, and Saperavi grapes. Data is expressed as average \pm standard error of the three vintages investigated. Different letters mean significant differences (F-test). #: LS, level of significance: ns, non-significant.

Must	Wild Grape	Cabernet Sauvignon	Saperavi	LS #
Sugar concentration ($^{\circ}$ Brix)	25.1 \pm 0.9 ^a	24.1 \pm 1.4 ^a	22.1 \pm 1.2 ^a	ns
Total acidity (g/L of tartaric acid)	7.8 \pm 0.8 ^a	6.7 \pm 0.7 ^a	9.2 \pm 1.3 ^a	ns
pH	3.4 \pm 0.2 ^a	3.4 \pm 0.2 ^a	3.2 \pm 0.2 ^a	ns

In all the microvinifications carried out on vintages 2017, 2018, and 2019, the alcoholic fermentations were completed after maximum 25 days. For all the vintages, the fermentations took shorter time in case of wild grape, while they were the longest with Saperavi grape. Only negligible differences were found in the residual sugars, except for Cabernet Sauvignon wine produced in 2018 (8.1 g/L vs. 1.8 g/L in both 2017 and 2019 wine samples). As expected, malvidin diglucoside was not detected in Cabernet Sauvignon and Saperavi wines, while its concentration was 2.5 ± 2.1 mL/L in wild grape wines. The concentration of ethanol, volatile acidity, and pH did not show any significant differences between the wine samples produced with the grapes investigated (Table 2). Total acidity was the lowest in Cabernet Sauvignon wine being significant ($\alpha = 0.05$) in comparison to both wild grape ($p = 0.013$) and Saperavi ($p = 0.022$) wines. Saperavi wines showed the lowest total dry extract, which was significantly lower. Wild grape wines had the highest content of total phenol (3.1 ± 1.1 g/L), significant for $\alpha = 0.01$ in comparison with both Cabernet Sauvignon and Saperavi wines. Nonetheless, preliminary sensory data indicated the difference was not significant for the perception of acidity or for phenolic-related attributes (i.e., astringency, bitterness, phenols) and sapidity (data not shown).

Table 2. Chemical parameters for the wines produced with wild grape, Cabernet Sauvignon, and Saperavi grapes. Data is expressed as average \pm standard error of the three (2017, 2018, 2019) vintages investigated. Different letters mean significant differences (F-test). #: LS, level of significance: ns, non-significant; *, $p < 0.1$; **, $p < 0.05$.

Wine	Wild Grape	Cabernet Sauvignon	Saperavi	LS #
Residual sugars (g/L)	3.0 \pm 0.9 ^a	5.0 \pm 4.5 ^a	1.9 \pm 0.2 ^a	ns
Total acidity (g/L of tartaric acid)	7.1 \pm 0.5 ^a	6.2 \pm 0.2 ^b	7.2 \pm 0.5 ^a	**
Volatile acidity (g/L of acetic acid)	0.5 \pm 0.2 ^a	0.6 \pm 0.1 ^a	0.6 \pm 0.0 ^a	ns
pH	3.6 \pm 0.0 ^a	3.3 \pm 0.4 ^a	3.3 \pm 0.2 ^a	ns
Ethanol (% v/v)	14.2 \pm 0.8 ^a	13.8 \pm 1.0 ^a	13.7 \pm 0.9 ^a	ns
Total phenol content (g/L of catechin)	3.1 \pm 1.1 ^a	1.7 \pm 0.4 ^b	1.7 \pm 0.4 ^b	*
Total dry extract (g/L)	33.6 \pm 3.7 ^a	31.4 \pm 5.3 ^a	25.2 \pm 1.9 ^b	*

4. Discussion

Coherently with most of the cultivated crops, grapevine selection during millennia of viticulture was mainly aimed at the increase of production yield, both in the field and in the winery. It means bigger bunches and bigger juicy berries with a reduced proportion of solid parts.

Our results indicate that wild grapes have a higher proportion of seeds with respect to *Vitis vinifera* subsp. *sativa* population. It is worth noticing that this result was obtained in an ampelographic collection, where the dioecious character of *Vitis vinifera* subsp. *sylvestris* was counterbalanced by the high presence of male wild and also other grapevine plants producing sufficient quantity of pollen for guaranteed pollination of female wild grapes. In fact, when the *Vitis vinifera* subsp. *sativa* population was compared to *Vitis vinifera* subsp. *sylvestris* populations grown in the wild, a lower number of seeds per berry was observed in the *sylvestris* grapes [34]. Thus, when pollination occurs, *Vitis vinifera* subsp. *sylvestris* seems to have a more performing reproductive physiology, resulting in a higher number of seeds/berry, with respect to cultivated grapes. We can suppose that, during domestication, humans selected juicy berries, with a lower percentage of seeds. This hypothesis is coherent with the domestication syndrome characteristics, that includes changes in the reproductive systems towards increased selfing (hermaphrodite flowers of subsp. *sativa*) and replacement of sexual reproduction by vegetative reproduction, maintaining the trueness to type and improving the appetizing characters [35]. In fact, the extreme case of seedless grapes was appreciated since the birth of our culture, by Greek philosophers and ancient Egyptians, and seedlessness (both parthenocarpy and stenospermocarpy) is still attracting the interest of both the industrial and the scientific communities [36]. The reproductive anatomy of cultivated grapes includes a series of steps, and partial dysfunctions could occur at different stages of the reproductive cycle, modulating the intensity of the disorders [37]. Thus, a less pressing selection on this trait may have resulted in a slightly lower number of seeds in cultivated grapes, even when seedlessness is not fully achieved.

Considering the other carpological traits, it is clear that the domestication process was focused on grape and wine production, not only selecting bigger bunches and berries, but also choosing the juiciest fruits, with a higher percentage of pulp with respect to seeds and skins. Different studies confirmed the central role of agricultural yield in the domestication process of different crop species [35,38]. Nevertheless, highlighting the different carpological proportions of pulp, skin, and seeds in *Vitis vinifera* subsp. *sativa* and subsp. *sylvestris*, we can hypothesize that the technological value of the cultivars

also played an important role in the selection process. In addition, the technological use of cultivated plants played a central role in the selection of other crops. For example, different methods used for rice harvest imposed different selective pressures, and the same species have been domesticated for different food organs in different regions (e.g., lettuce is used for edible leaves in the Mediterranean regions and for enlarged edible stem in China) [39]. However, considering grapevine, we can suggest that this evidence confirms the predominant use of *Vitis* fruits for winemaking purposes since the birth of its cultivation and that the plant domestication evolved together with oenological technology. This hypothesis is also coherent with the archeological artifacts found in Georgia related to the ancient history of winemaking [40–42]. Finally, the central role of Caucasian territories in the grapevine domestication devoted to wine production is confirmed by the intermediate values observed in Georgian cultivated grapes between *Vitis vinifera* subsp. *sativa* and subsp. *sylvestris* [33].

We observed that in *Vitis vinifera* subsp. *sylvestris*, berry pulp generally has higher concentrations of sugars and acids, with respect to the *Vitis vinifera* subsp. *sativa*. Considering sugars, it is worth noting that this work does not deepen the dynamics of accumulation and further studies could point out subtler differences based, for example, on the mechanisms of sugar accumulation in the two subspecies or on the impact of the harvesting time on the obtained wine flavors [43,44].

Considering phenolics, the main differences between *Vitis vinifera* subsp. *sylvestris* and subsp. *sativa* should be ascribed to the differences in the carpological traits, despite specific disfunctions in the phenylpropanoid biosynthetic pathway taking away the attention of winegrowers during the selection of specific white and pink cultivars [45–49]. Of course, beside genetic characteristics, (micro-)environmental conditions and vineyard management affect the vine phenotype and grape enological potential, especially when we deal with secondary metabolisms, such as phenolics [50–53]. Unfortunately, knowledge concerning the impact of prehistoric viticulture practices on grape quality is not available. However, we can suppose that ‘embryonic viticulture’ management co-evolved together with plant domestication and cultivar selection.

The yield-based selection that occurred during domestication resulted in a loss of traits that could be of interest in the light of current knowledge concerning the importance of plant resilience to climate changes or modern enological objectives. These traits could be of particular interest in the perspective of new breeding purposes [54].

The domestication of grapes did not seem to play a role in the composition of musts investigated. Nevertheless, even if the sugar concentrations in musts were comparable and similar fermentation conditions were applied (i.e., starter yeast, temperature), the longer time observed for Saperavi must suggests the high acidity could slow down fermentation. Considering the chemical parameters determined in wines, that obtained with wild grape were characterized by a high total acidity and total phenol content. Other authors found that wines produced with wild grape had high acidity, making the grape suitable for growing in temperate and warm climate [10,12,19]. Moreover, the high level of phenols allowed to perform prolonged winemaking process [14].

5. Conclusions

This article enhances current knowledge of wild grape and wine. The changes that occurred in grape berries as a consequence of the domestication process involved the number of seeds, the carpological traits, as well content of phenolics. These characteristics are of particular interest for an effective response against climatic changes and the development of modern viticulture through new breeding activities.

Wines obtained with wild grape can be suitable for prolonged winemaking in which wood aging can be also expected in order to allow its evolution. The possible combination of wild and domesticated grapes can make possible the production of wine with long ageing, exalting their own characteristics. The possibility to produce wine with grape being more tolerant to the environmental stresses could represent an advantage due to the lower

input requirements in viticulture and in terms of grape characteristics and wine quality. As a consequence, the production of high-level wine could be sustainably maintained, effectively responding to consumers' requests. The interested differences among the grapes investigated, especially for phenols, evidence the possibility of the oenological use of wild grape enriching the phenolic content and making long aging suitable even for those varieties that are poorer in mouthfeel and body.

Further investigation will study the determination of aroma profile from both analytical and sensory points of view, as well as a more detailed characterization of phenolic compounds.

Supplementary Materials: The following are available online at <https://www.mdpi.com/2073-4395/11/3/472/s1>, Table S1: Archaeobotanical records of grapevine in Georgia, Table S2: Comparison in the data distribution of *Vitis vinifera* subsp. *sylvestris* and subsp. *sativa*, with details of sativa plants cultivated in Georgia. *Vitis vinifera* subsp. *sativa* data are already published in Rustioni et al [26] and Georgian cultivars are described in Sargolzaei et al. [33], Table S3: Amounts (kg) of grapes vinified in vintages 2017, 2018, and 2019. The duration of alcoholic fermentation (days) is reported in brackets.

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