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Morphological variation and relationships of Georgian populations of *Vitis vinifera* L. subsp. *sylvestris* (C.C. Gmel.) Hegi

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ABSTRACT

Georgia is considered as one of the regions where for the first time wild growing grapevine plants were used and taken into cultivation by men. An ampelographic and ampelometric study of leaf characters and flower landmark morphometrics was carried out in seven populations of wild grapevine located in four river basins of three geographic regions – Western (1 popul.), Eastern (5 popul.) and Southern (1 popul.) Georgia, and then compared using principal component analysis and multivariate discriminant analysis allowing the populations to be distinguished. Lengths of main leaf veins and nectaries in male flowers were the variables, which allowed the best discrimination among populations. A mutation leading to white-fruited grapevine is found in one population. Pubescence varies within populations and even within an individual genome and could be used as a discriminant trait only in combination with shapes and sizes of leaves and other morphological characters. The results revealed significant differences among populations located in different geographic regions of the Southern Caucasus area, but the five investigated populations from Eastern Georgia differ only insignificantly. The high morphological variability of wild grapevine in Georgia might be considered as characterizing the large gene pool that contributed to the domestication process of grapevine.

Introduction

Populations of wild grapevine – *Vitis vinifera* L. subsp. *sylvestris* (C.C. Gmel.) Hegi – show high genetic and morphological diversity in the Caucasus (Grassi et al., 2006; Kolenati, 1846; Ramishvili, 1988; Woronow, 1925). All five haplotypes detected by using cpDNA microsatellite markers (Grassi et al., 2006) have been found in the Caucasian ecoregion suggesting this area as the possible centre of origin of both wild and cultivated grapevines. However, only one provenance from Georgia has been analyzed in this study, though populations of wild grapevine are here numerous till today and reveal high morphological diversity (Ramishvili, 1988; Sosnovski, 1925).

Nowadays, big attention is paid to elucidate the diversity of the wild grapevine genetic pool used for domestication and to identify the place and period of the original domestication and whether secondary independent domestications also occurred (Arroyo-Garcia et al., 2006; Grassi et al., 2003; Sefc et al., 2003). Special emphasis is given to determine the main events that enabled the morphological transformation from the wild *V. vinifera* subsp. *sylvestris* to cultivated grapevine (Aradhya et al., 2003; Imazio et al., 2006; This et al., 2006; Vouillamoz et al., 2006). The search for ancestors of cultivated varieties has not yet brought unequivocal evidence for place and period of domestication. Most authors accept the opinion that a first domestication event occurred in the South Caucasus (De Candolle, 1885; Negrul, 1946; Olmo, 1976; This et al., 2006; Vavilov, 1931; Vouillamoz et al., 2006) indicated by oldest archaeological findings of grape pips dated from c. 6000 B.C. (vicinity of v. Shulaveri, South-East Georgia; Ramishvili, 1988). Other archaeological evidences of prehistoric winemaking are found in the near proximity of the Caucasian region such as the northern Iran at the Hajji Firuz Tepe site in the northern Zagros mountains, dated circa 5400–5000 B.C. (McGovern, 2003), and in Levant and Jericho in the Near East where archaeological findings are dated from c. 4000 to 3200 B.C. (Zohary and Hopf, 1993, 2000; Zohary and Spiegel-Roy, 1975).

High genetic and morphological variability of both wild and cultivated grapevine might be considered as another indicator of possible origin of cultivated grapevine in the Caucasus. About 500 names of autochthonous grapevine varieties are known from Georgia (Javakhishvili, 1930; Ketskhoveli et al., 1960) characterized by a wide range of color gamma and shapes of berries and pips, which are pointing to an evolutionary centre in this region (Vavilov, 1931). These cultivars show great ampelometric variability and broad adaptability to different climates and soils (Ketskhoveli et al., 1960; Negrul, 1946; Ramishvili, 1970; Tsertsvadze, 1989; Vinogradov-Nikitin, 1929). Kolenati (1846) was the first studying wild and

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Table 1
The seven populations of *Vitis vinifera* subsp. *sylvestris* collected in different locations of Georgia (NCP – number of collected plants; F – female; M – male).

Code	Population	Geographic region	River Basin	Forest type	Coordinates	Elevation (m)	NCP (F/M)
AI03	Jumas-Kure Nature Reserve, Dedoplistskaro distr.	East Georgia	Alazani	Riparian	41°21′34″ N 46°39′01″E	170	3 (2/1)
AI04	Iori Nature Reserve Sagarejo distr.	East Georgia	Iori	Riparian	41°28′12″N 45°39′44″E	370	5 (3/2)
BS01	near v. Godgadzeebi Khulo distr.	West Georgia	Ajaristskali	Beech-coniferous	41°39′16″N 42°20′11″E	785	5 (3/2)
MJ02	Between vv. Atskuri and Likani Borjomi distr.	South Georgia	Mtkvari	Riparian	43°18/20′N 41°47/48′E	830	4 (3/1)
KK02	Gardabani forest-park, Gardabani distr.	East Georgia	Mtkvari	Riparian	41°22′01″N 45°04′31″E	397	5 (1/4)
SK02	near v. Sakorintlo	East Georgia	Mtkvari	Oak-Hornbeam	42°02′45″N 44°22′46″E	772	5 (4/1)
TB02	Suburb of Tbilisi	East Georgia	Mtkvari	Oak-Hornbeam	41°43′42″N 44°43′08"E	604	5 (3/2)

cultivated grapevines in the Caucasus systematically and expressing the opinion that this area might be the centre of origin of cultivated grape. He classified both wild and cultivated grapevines based on the pubescence type of the leaf and distinguished two forms, which he called "Spielarten" – *V. vinifera* subsp. *anebophylla* Kolen. (glabrescent) and *V. vinifera* subsp. *trichophylla* Kolen. (pubescent). Vasilchenko (1947) described one more species of wild grapevine distributed in Talish, Azerbaijan and Iran, characterized by tomentose pubescence on the abaxial surface of the leaf. This species was named *V. hyrcanica* Vass. It shows remarkable similarity to wild grape distributed in the Colchis, Western Georgia. However, according to Ramishvili (1988), the wild grape of Colchis represents a separate taxon discriminated by morphological features from the individuals growing in the Eastern Georgia. The west Georgian wild grape was determined as *Vitis vinifera* subsp. *sylvestris* var. *colchica* Ramishvili. The species of wild grape described by Vasilchenko (1947) in the Caucasus, Iran and Central Asia were later refuted and unified with *V. vinifera* L. (Cherepanov, 1995) and not with *V. sylvestris* C.C. Gmel., which causes some confusion in the taxonomic status of wild grapevines distributed in this part of the world and makes it necessary to conduct more in detail a taxonomic survey of this genus.

At present, wild grapevine occurs mainly in riparian forests on the territory of Georgia and reaches the upper vegetation zones such as oak-hornbeam, beech and spruce forests up to 1000 ma.s.l. (Ramishvili, 1988). The populations are not more as abundant nowadays as it was described by Kolenati (1846) in the middle of XIX c. The invasion of *Phylloxera* and urbanization are major problems diminishing the number of individuals of the wild grapevine in populations. These threats predominantly reduce population sizes of *Vitis vinifera* subsp. *sylvestris*. Individuals of grapevine in the wild are very abundant in Georgia but they belong either to cultivars of *Vitis vinifera* subsp. *sativa* escaped in the course of abandonment of settlements during the quite often wars in the historical past of Georgia, or to introduced American species – *V. riparia* Michx., *V. rupestris* Scheele, *V. berlandieri* Planch., used as rootstocks, and/or to the very popular in Georgia cultivar "Isabella" of *V. labrusca* L. The high diversity of grapevine species led Medvedev (1919) to speculate that all individuals of grapevine growing in the wild in the Caucasus represent escaped cultivars and wild grapevine was completely absent in this region. This opinion was disposed by Woronow (1925) who confirmed that there are both wild and naturalized grapevine individuals. Moreover, Woronow considers both *V. vinifera* subsp. *sativa* and *V. vinifera* subsp. *sylvestris* as species aggregates characterized by high diversity and composed by many races. Due to these circumstances, it becomes more complicated to discriminate the wild grapevine types to which they belong: post cultivated, sub-spontaneous or spontaneous, and within this last group, whether they are colonials, autochthonous, or hybrids.

In this study, we conducted a detailed morphometric study of wild grape populations from the different regions of Georgia for the first time and compared foliar and flower morphology by methods of traditional morphometrics, based on linear measurements of distances and angles of leaf veins based on the descriptor list for grapevine cultivars and wild *Vitis* species proposed by the projects GENRES-081 (2001) and GrapeGen06 (OIV, 2007). Moreover, the shape characteristics of male flowers were analyzed using a landmark-based morphometric study. The aim of this investigation was (1) to assess sites of occurrence of *V. vinifera* subsp. *sylvestris* and conduct an inventory of populations using GPS and GIS methodology; (2) to describe and compare the vegetative and reproductive morphological features using principal components analysis and multivariate discriminant analysis to reveal grouping characters and estimate similarity distances between different populations; (3) to reveal the character of morphological diversity of wild grapevine growing on the territory of Georgia.

Materials and methods

Plant material

Ecological and geographical data of the localities of *V. vinifera* subsp. *sylvestris* in Georgia have been collected from herbarium specimens (TBI and TGM) and literature (Ramishvili, 1988). This data base was used to prepare a map with the program ArcView GIS 3.3 showing the geographical distribution of the populations of wild grapevine (Fig. 1A and B) in Georgia and adjacent regions. The distribution pattern reveals that populations are dispersed along main river basins. Therefore, the populations examined in this study (Fig. 1C and E; Table 1) were chosen on this principle and are located in river basins from different regions of Georgia: (1) Ajaristskali River basin in Ajara, near village (v.) Godgadzeebi, Khulo distr. (2) Four locations are at Mtkvari (Kura) River basin, (a) between vv. Atskuri and Likani, Borjomi distr.; b) at Lekhura River gorge (left tributary of R. Mtkvari) near v. Sakorintlo, Kaspi distr.; (c) at suburb of Tbilisi and (d) at forest-park of Gardabani distr. near boundary with Azerbaijan. (3) Alazani River basin at nature reserve Jumas-Kure, Dedoplistskaro distr. (4) Iori River basin at Iori Nature Reserve, Sagarejo distr. A four-letter-digit code was used for population identification. The first two letters correspond to the areas according to classification schema of Ramishvili (1988), which follows historical-geographic provinces of Georgia: AI – Alazani-Iori; East Georgia; BS – Black Sea Coast including Abkhazeti and Ajara; KK – Kvemo Kartli, South-East Georgia; MJ – Meskhet-Javakheti area, South Georgia; SK – Shida Kartli, East Georgia; and the last two