Genet Resour Crop Evol (2014) 61:1507-1521
DOI 10.1007/s10722-014-0125-2

RESEARCH ARTICLE

Genetic diversity of *Vitis vinifera* in Georgia: relationships between local cultivars and wild grapevine, *V. vinifera* L. subsp. *sylvestris*

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Received: 29 October 2013 / Accepted: 14 April 2014

Abstract The Caucasus and Middle East regions are considered to be the primary centre of origin of cultivated grapevine, and, as confirmed by archaeobotanical, archaeological, and cultural evidence, Georgia belongs to this earliest centre of winemaking. This study aims to investigate the genetic diversity, population structure and relationships of local autochthonous wine cultivars and wild grapevine, *Vitis vinifera* subsp. *sylvestris*. Multiple accessions of 15 Georgian aboriginal cultivars and 42 individuals of wild grapevine from different regions of Georgia and adjacent Turkey were genotyped at 17 nuclear microsatellite loci. A total of 160 alleles were detected with a mean number of 9.41 alleles and the effective number of 4.6 alleles (r) per locus, indicating that the SSRs were highly informative. Despite high genetic diversity, the level of genetic differentiation among defined wild and cultivated populations is low (F_{st} = 0,05; P***), which together with the outcome of model-based cluster analyses and genetic assignment methods point to gene flow among wild populations, as well as among cultivated and wild accessions. Besides, the data presented here suggest that local cultivars 'Saperavi' and 'Tavkveri' are independently derived from different local wild populations, while the majority of Georgian cultivars seem to have a single origin. Overall, the present study takes important steps for better characterization of Georgian cultivated and wild grapevines, and supports Georgia as one of the important centres of grapevine domestication still harbouring valuable genetic resources for grapevine breeding.

Keywords Domestication · Genetic diversity · Genetic similarity · Georgian grape cultivars · Microsatellites · *Vitis vinifera* subsp. *sylvestris* · *V. vinifera* subsp. *vinifera*

Electronic supplementary material The online version of this article (doi:10.1007/s10722-014-0125-2) contains supplementary material, which is available to authorized users.

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Introduction

Grapevine (*Vitis vinifera* L.) is one of the most valuable crops worldwide and consists of two forms, domesticated *V. vinifera* L. subsp. *vinifera* and wild *V. vinifera* L. subsp. *sylvestris* (C.C.Gmel.) Hegi. The Caucasus region is considered to be within the primary centre of origin of domesticated grapevine, with high relevance

Published online: 08 May 2014

for the further distribution of the crop throughout the Mediterranean basin and for the development of modern European cultivars (De Candolle 1885; Potebnia 1911; Negrul 1946; Mullins et al. 1992; Jackson 1994; Damania et al. 1997; Sefc et al. 2003; Constantini 2004; Forni 2006; This et al. 2006; Vouillamoz et al. 2006). Grapevine was among the first fruits to be cultivated in Georgia (Javakhishvili 1930). Confirmations for long-lasting cultivation of grapevine in Georgia stem from archaeological remains of berries and seeds of domesticated grapes dated ~8,000 years before present (yBP) in southeastern Georgia (Ramishvili 1988; McGovern et al. 1997). Other archaeological evidences of prehistoric winemaking are found in near proximity of the Caucasian region in northern Iran at the Hajji Firuz Tepe site in the northern Zagros Mountains dated to about 7,400–7,000 yBP (McGovern 2003) and in the Levant where archaeological findings are dated to ~6,000 yBP (Zohary and Spiegel-Roy 1975; Zohary and Hopf 2000).

Another indicator of a possible origin of cultivated grapevine in the Caucasus region is high genetic and morphological diversity of both wild and cultivated grapes in this area (Vavilov 1931; Grassi et al. 2006; Ekhvaia and Akhalkatsi 2010). About 500 names of autochthonous grapevine varieties, including the centuries-old cultivars 'Rkatsiteli', 'Ojaleshi', and 'Saperavi,' are known from Georgia (Javakhishvili 1930; Ketskhoveli et al. 1960). They show great ampelometric variability and broad adaptability to different climates and soils (Vinogradov-Nikitin 1929; Negrul 1946; Ketskhoveli et al. 1960; Ramishvili 1970; Tsertsvadze 1989; Ekhvaia and Akhalkatsi 2006). However, only half of these cultivars have been conserved in some national collections, and today only a small number of local varieties are still cultivated (Chkhartishvili and Tsertsvadze 2004). This causes genetic erosion on this rich ampelographic heritage, involving loss of a valuable gene pool before it could be evaluated.

Wild grapevine occurs in the Caucasus region mainly in riparian forests and reaches upper vegetation zones such as oak-hornbeam, beech and spruce forests at up to 900 m a.s.l. (Ramishvili 1988). Like in other parts of the world, the distribution area of the subspecies was dramatically reduced in Georgia due to human activities. Therefore, investigation and preservation of genetic variability of wild grapevine populations has become a priority to avoid genetic erosion and maintain invaluable genetic resources for cultivated grapevines (Arnold et al. 1998).

In recent years, particular attention has been paid to elucidate the domestication history of cultivated grape (Grassi et al. 2003; Sefc et al. 2003; Arroyo-Garcia et al. 2006; Myles et al. 2011). Myles et al. (2011) supposed a Near East origin of subsp. *vinifera*, while others argue that at least a second independent domestication centre exists in the Mediterranean (Grassi et al. 2003; Sefc et al. 2003; Arroyo-Garcia et al. 2006; Lopes et al. 2009). Special emphasis has been given to evaluation and genetic characterization of different cultivars and/or determination of the main events that enabled the morphological transformation from wild subsp. *sylvestris* to cultivated grapevine (Aradhya et al. 2003; Vouillamoz et al. 2006; Imazio et al. 2006; This et al. 2006; D'Onofrio et al. 2010; Bacilieri et al. 2013). Unfortunately, the above-mentioned studies included none or only a few autochthonous varieties from the Caucasus region. A recent work of Imazio et al. (2013) evaluated the genetic diversity of Georgian cultivars from European germplasm repositories and investigated their relationships with some worldwide distributed, mainly European varieties. However, there is very limited knowledge about genetic diversity and population structure of Georgian wild grapevine. Consequently, it is of high importance to study aboriginal grape varieties from the supposed domestication area and determine their genetic relationships to the local wild populations. In addition, knowledge about genetic variation in natural populations may provide relevant information for biodiversity conservation strategies of the region. In the present study, we have performed a comprehensive comparative study of the native populations of wild subsp. *sylvestris* and the local autochthonous cultivars. We employed 17 nuclear microsatellite (SSR) markers to (1) study genetic diversity of Georgian wild and domesticated grape germplasm and (2) assess the relationships among autochthonous cultivars and wild grapevine populations in order to shed light on the origin of the locally cultivated varieties.

Materials and methods

Plant material

A total of 99 samples representing 57 accessions were studied: 15 Georgian autochthonous cultivars (*V.*