

Ecological and sanitary characteristics of the Eurasian wild grapevine (*Vitis vinifera* L. ssp. *sylvestris* (Gmelin) Hegi) in Georgia (Caucasian region)

Rafael Ocete Rubio¹, Elvira Ocete Rubio¹, Carlos Ocete Pérez¹, M. Ángeles Pérez Izquierdo¹, Laura Rustioni², Osvaldo Failla², Ramaz Chipashvili³ and David Maghradze^{3*}

¹Laboratorio de Entomología Aplicada, Universidad de Sevilla, Avenida Reina Mercedes, 6, 41012 Sevilla, Spain, ²Department of Crop Production, University of Milan, Via Celoria 2, 20133 Milan, Italy and ³Institute of Horticulture, Viticulture and Oenology (IHVO), 6 Marshal Gelovani Ave. 0159, Tbilisi, Georgia

Received 5 January 2012; Accepted 5 June 2012 – First published online 12 July 2012

Abstract

This paper shows the results of the investigation on some ecological aspects and on the sanitary status of the wild Euroasiatic native grapevine (*Vitis vinifera* L. ssp. *sylvestris* (Gmelin) Hegi) in Georgia (South Caucasus). This taxon is seriously endangered by human activities such as forest cleaning and setting fires. Moreover, invasive *Vitaceae* of the North American origin, imported after phylloxera (*Daktulosphaira vitifoliae* Fitch) when vineyards were being replanted, increase the risk to lose these spontaneous vines. The survey includes collection of data on the population structure, the plant sex ratio, the main botanical supporters of the vines and the associated flora, the presence of invasive vines of the North American origin and the incidence of phytophagous arthropods and pathogens. The phytosanitary study showed that monophagous eriophyid mites and exotic fungal diseases, such as downy (*Plasmopara viticola* (Berkeley and Curtis) Berlese and de Toni) and powdery mildews (*Erysiphe necator* –(Schweinitz) Burrill), cause symptoms on all the observed populations. The absence of symptoms caused by phylloxera, root-knot nematodes and root rot is remarkable. However, the level of detected injuries caused by these parasitic organisms does not seem to be a real problem for the survival of the populations.

Keywords: associated flora; downy and powdery mildew; eriophyid mites; North American *Vitaceae*; phylloxera

Introduction

The Eurasian native wild grapevine is taxonomically classified as *Vitis vinifera* L. ssp. *sylvestris* (Gmelin) Hegi. This sub-specific taxon constitutes the dioecious ancestor of grapevine cultivars belonging to *V. vinifera*

L. ssp. *sativa* (DC.) Hegi (De Candolle, 1883; Arnold, 2002). Currently, this strain is considered a threatened plant genetic resource, and it is quickly disappearing through direct and indirect human intervention (Red Book, 1982; Arnold *et al.*, 1997). The causes are mainly attributed to deforestation and building activities in deforested locations. In the past, wild grapevines were used for the production of juice, wine, vinegar, tartaric acid, medicines, fishing traps and rootstocks among other things. These traditions have been carried out by

*Corresponding author. E-mail: d_maghradze@geo.net.ge

different cultures throughout centuries, from the Hindu Kush mountain range in Asia to the Iberian Peninsula in Europe (Ocete *et al.*, 2007).

Wild vines are woody lianas that through their tendrils climb up on the nearby vegetation in order to obtain the best canopy architecture. The resulting adaptive advantage contributes to enhanced exposure to direct solar radiation and reducing competition disadvantage with other surrounding species.

Georgia is situated between the Caucasian mountain range, with some peaks over 5000 m in height, and the Black Sea. Due to its particular geographical location, the area constituted a unique refuge habitat for several plants, including *Vitis*, during Pleistocene ice ages (Ramishvili, 2001).

The main natural habitats of the wild grapevine populations are river-bank forests and some colluvial positions situated on the slopes of hills and mountains (Ramishvili, 1998; Arnold, 2002; Maghradze *et al.*, 2010), where soils are often renewed by flooding or by gravity.

Wild vines show a high foliar polymorphism. The fruiting plants produce small inflorescences with feminine flowers with reflected stamens. The male plants have bigger inflorescences constituted only by staminate flowers. Wild berries are usually small, roundish and black (Arnold, 2002). These plants have some interesting features of biotic and abiotic stress resistance that could be transferred, by selective breeding, to cultivars and rootstocks (Ocete *et al.*, 2007).

Ocete *et al.* (2011) carried out an investigation of the current state of phylloxera infestation in European countries. Data from the Caucasus region were not available at that time. Studies assaying microsatellite (short sequence repeat (SSR)), chloroplast microsatellite (cpSSR) and single nucleotide polymorphism markers on the genetic sequence of the wild grapevine from the

South Caucasus region, which also includes Georgia, have stressed a high genetic drift compared with European populations (Arroyo-García *et al.*, 2006; Imazio *et al.*, 2010; Myles *et al.*, 2011). This increases the interest in the study of the main pests and diseases affecting the wild grapevine populations in this geographical area. In addition, this would contribute to the evaluation of their sanitary status after 150 years of infestation of phylloxera and American fungal diseases. Thus, the main aim of this study was to survey the sanitary status of this taxon in Georgia, with particular interest in the incidence of pests and diseases, and an evaluation of the possible competition from North American species.

Materials and methods

Field expeditions were organized to characterize the wild grapevine populations in the eastern regions of Georgia during the summer in 2008. Each population had previously been observed at the flowering time in May–June. Differentiation between *V. vinifera* wild vines and North American species was carried out by observing the main morphological discriminant descriptors. Attention was particularly focused on leaves and flowers, following the methods of Larrea (1978) and Ocete *et al.* (2006). Plant classification, including the supporting trees of the wild vines and the accompanying vegetation, was determined following the local Florae (Grossgeim, 1937–1967; Makashvili, 1991; Flora Georgia, 1971–2007) and then validated by Dr Benito Valdés from the Botanical Department of the University of Sevilla (Spain).

The observation of symptoms caused by pests and diseases was carried out on shoots, leaves and bunches of up to 3 m of canopy height. To detect any possible subterranean phytophagous and pathogens, roots were unearthed down to 40–50 cm of depth. They were

Table 1. Location of the wild populations in Georgia

Site name	Position ^a	Interval of latitude	Interval of longitude	Elevation (m.a.s.l.)
Delisi	C	41°43'27.3"–41°43'38.4"	44°42'14.3"–44°42'18.3"	648–654
Shirikhevi	A	41°57'50.5"–41°57'53.6"	44°43'0.1"–44°43'17.6"	698–707
Bagichala	C	42°2'17.3"–42°1'16.9"	44°44'17.6"–44°44'52.5"	706–718
Zhinvali reservoir	AC	42°8'39.8"	44°45'58.8"	677
Meneso	C	42°2'17.3"–42°7'24.8"	44°40'31.6"–44°46'31.5"	927
Ninotsminda	C	41°44'17"–41°44'20.8"	45°17'5.9"–45°17'8.6"	878–880
Kvetari	C	42°3'17"–42°3'38.2"	45°6'17.6"–45°6'47.6"	700–793
Sabue	C	42°2'53.4"–42°3'21.4"	45°7'8.2"–45°7'32.1"	621–649
Chachkhriala	AC	42°2'42.5"	45°9'2.4"	618
Samebis seri	AC	41°56'29.1"–41°56'32.7"	45°46'2.1"–45°46'30.6"	358–366

m.a.s.l., metres above sea level.

^a Positions are defined as follows: A, alluvial position; C, colluvial position; AC, both alluvial and colluvial positions.

Table 2. Status of wild populations in their natural habitat

Populations	No. of sites	Total plants	Plants per site	Plant range
In this study	10	89	8.9	1–20
Georgia total	50	189	3.8	1–20
Italy ^a	277	1032	3.7	–
Spain ^b	378	2041	5.4	1–260

^aData from Biagini (2011). ^bData from Ocete *et al.* (unpublished).

evaluated as done previously by Ocete *et al.* (2007) in the case of mite infestation and according to the OIV (2009) descriptors in the case of mildews.

Results

Ecological aspects

In this study, ten locations were surveyed (Table 1). They were considered independent populations when the distance between two sites was more than 10 km. It has to be taken into account that the male pollen grain of the studied species has a medium weight, hence it cannot be transported by wind over long distances as described by Arnold (2002). The number of vines varied between 1 and 20 plants in the different sites, with an average value of 8.9 (Table 2). The number of vines of each sex from each population is indicated in Table 3.

The data demonstrated that 18 out of 89 observed wild plants had female-type flowers (20.2%), and 24 plants had male-type flowers (24.0%). A large group of plants (48) are still unidentified, because of the short flowering period which impeded the complete field observation over the large area to survey.

The main non-vinifera grapevines were classified as American rootstock hybrids escaped from cultivation. *Vitis rupestris* and *Vitis riparia* like-to-type plants were detected in the Bagichala and Kvetari region sites. *Vitis* × *labruscana* cultivar Isabella like vines were found only in the Kvetari region.

The plant supporters and the accompanying vegetation are listed in Supplementary Table S1 (available online only at <http://journals.cambridge.org>).

Evaluation of pests

Data on the presence of phytophagous arthropods are reported in Table 4.

The observations carried out on roots demonstrated that, in natural habitats, no damage caused by phylloxera, *Daktulosphaira vitifoliae* (Fitch) (Homoptera,

Phylloxeridae), was found on roots and leaves. All roots showed a complete absence of symptoms caused by root-knot nematodes, such as galls and secondary rootlets (Raski, 1994). Damages caused by *Meloidogyne* were not found.

Concave felty galls situated in the lower leaf surface, which induce swellings on the lower leaf side, caused by the erineum strain of *Colomerus vitis* (Pagenstecher) (Acari, Eriophyidae), were observed on all the populations studied in the present survey. Symptoms were very frequent, affecting almost all of the vines, but damages caused by this pest were not serious (levels 1–3), and did not affect the viability of the liana.

Another mite found on the leaves of most of the prospected populations was the grape rust mite, *Calepitrimerus vitis* (Nalepa) (Acari, Eriophyidae). Its distribution and level of infestation, usually scored at level 1, was lower compared with *C. vitis*.

Evaluation of diseases

Data on the presence of symptoms caused by diseases are shown in Table 4. Symptoms of root rot were absent on all samples.

On the parts of the plants above ground level, symptoms of infection were caused by North American fungal species which included powdery and downy mildews, *Erysiphe necator* (Schweinitz) Burrill and *Plasmopara viticola* (Berkeley and Curtis) Berlese and de Toni, respectively.

Symptoms of powdery mildew on wild vines were found on leaves, shoots (Chleistotecia) and, far more rarely, on the bunch. These symptoms affected virtually all the populations studied in Georgia. The degree of intensity of the infection on wild vines was rated between 1 and 3 through observing the leaves according to the descriptors. This corresponds to a low infection.

Table 3. Sex of flowers of wild vines

Site name	No. of plants	Female	Male	Not yet identified
Delisi	7	1	3	3
Shirikhevi	8	3	5	0
Bagichala	18	4	9	5
Zhinvali reservoir	4	–	1	3
Meneso	2	2	–	0
Ninotsminda	12	2	3	8
Kvetari	20	2	2	16
Sabue	8	3	–	5
Chachkhriala	1	1	–	–
Samebis seri	9	–	1	8
Total	89	18	24	48
%	100	20.2	27.0	53.9

Table 4. Number of affected plants and evaluation of infestation/infection by parasites^a

Site name	No. of plants	<i>Colomerus vitis</i>	<i>Calepitrimerus vitis</i>	<i>Erysiphe necator</i>	<i>Plasmopara viticola</i>
Delisi	7	7 (1–3)	3 (1)	5 (1–3)	2 (1)
Shirikhevi	8	8 (1–3)	3 (1)	4 (1–3)	1 (1)
Bagichala	18	18 (1–3)	5 (1)	11 (1–3)	3 (1–3)
Zhinvali reservoir	4	4 (1–3)	1 (1)	3 (1–3)	0
Meneso	2	2 (1)	0	2 (1–3)	0
Ninotsminda	12	12 (1–3)	3 (1)	7 (1–3)	3 (1–3)
Kvetari	20	20 (1–3)	7 (1–3)	11 (1–3)	4 (1)
Sabue	8	8 (1–3)	3 (1–3)	3 (1–3)	2 (1)
Chachkhriala	1	1 (1)	0	0	0
Samebis seri	9	9 (1–3)	2 (1)	3 (1)	1 (1)
Total	89	89	27	49	16
%	100	100	30.3	55	17.9

^a For each species, the number of affected plants and level of infestation (in parentheses) are indicated, following the scale of Ocete *et al.* (2007) for mite infestation, and the OIV (2009) descriptors for mildews. In the case of mites, the evaluation situated between 1 and 3 means that the mite affected 10–25% of the leaves.

Typical symptoms of downy mildew were found in Georgian wild vines on leaves (similar to oil spots) and shoots longer than 10 cm; this also occurs in the case of cultivars. Damage on bunches was less frequent. Finally, symptoms caused by this fungal species were less frequent than those caused by powdery mildew, as indicated by the degree of infection rated as 1 on average.

Discussion

The evaluation of the status of wild populations in this survey demonstrated a higher density of plants per site (8.9) compared with data from the whole of Georgia (3.8 plants per site) (Maghradze *et al.*, 2011), Italy (3.7) and Spain (5.7) (Table 2). In both Western European countries, the number of populations is higher than in Georgia and, as a consequence, a higher number of vines have been identified. This is probably also due to the fact that in the Italian and Spanish surveys, several natural reserves have been involved, whereas the investigation in Georgia was done outside the boundaries of protected areas.

Usually, the number of males identified in each population was higher than the number of females. In the sites of Zhinvali and Sabue, there are no female plants. This makes seed reproduction impossible. In general, populations are very small so their short- and medium-term viability is expected to be very low (Table 3).

It is necessary to underline that in the Caucasian region, where Vavilov (1926) found the highest diversity of vines in the cradle of viticulture, there were 55 productive female cultivated varieties (13.3% of total germplasm; Ampelography, 1970; Maghradze *et al.*, 2010). Among these, the two cultivars 'Asuretili Shavi' and

'Tavkveri' are included in the official list of cultivated varieties of Georgia (Law, 1998) and are spread throughout the Kartli province of East Georgia. The female cultivars can be pointed as a relict step in the history of Georgian viticulture: they show the passage from the domestication of wild vines to the cultivation of selected hermaphrodite varieties during an early development phase of this crop.

The accompanying vegetation of the vines is the characteristic flora of the Caucasian natural areas under 1000 m of altitude with low human impact, where several species of fruit trees took refuge during the Quaternary ice age. This flora is typical of temperate forests in the Palaearctic ecozone, where there is great biodiversity due to the confluence of Central European, Central Asian and Middle Eastern botanical provinces. This alluvial formation with deciduous species constitutes the Euxine–Colchic forest of the South Caucasus, which stretches eastward towards the shores of the Caspian Sea, where the Tertiary botanical species took refuge (Moore, 1982).

Supported trees and bushes with thorns (such as *Crataegus* ssp. and *Prunus* ssp.) are supposed to have played an important role in the protection of wild vines from wild or domestic animals.

As in Europe, some of the American rootstock hybrids and *Vitis* × *labruscana* are gradually colonizing the river banks and slopes of the hills in Georgia, taking over the niche of autochthonous wild vines (Cholokashvili, 1983), as it was observed in several European populations (Arrigo and Arnold, 2007). Such is the situation in the Bagichala and Kvetari sites. Such plants are more invasive and show a higher resistance to North American imported mildews compared with native wild vines: this is why they are involved in the extinction of wild autochthonous grapevines in

the Valencia region (Spain; Laguna, 2003a, b), Têt river valley (France), Montseny Reserve of the Biosphere (Spain), and in several parts of the Rhone, Rhine, Danube, Ebro, Guadalquivir, Duero and other important European rivers and their tributaries (Terpó, 1969, 1974; Ocete *et al.*, 2007). This is another reason for the urgent need of protection of the biodiversity of the Georgian wild grapevine, which is the earliest known domestication centre of the vine. In the Eastern part of the Iberian Peninsula, it was one of the main causes for wild grapevine disappearance (Laguna, 2003a, b).

The absence of phylloxera infestation is due to the temporary flooding of soil profiles in all of the European locations. These lianas grow in sites where edaphic conditions such as permanent or temporary anoxic conditions caused by flooding make them unsuitable for the development of phylloxera. Meanwhile, laboratory experiments with artificial infestation indicated that Eurasian wild grapevines exhibited nodosities and tuberosities on roots caused by a homopteran under induced artificial infestation in pots (Ocete *et al.*, 2011).

In spite of considerations on the infestation of roots of wild grapevines found in France by Camille St. Pierre and included in De La Branchere (1876), phylloxera had little direct impact on the remaining wild vines (Ocete *et al.*, 2006).

Around Georgia, a homopteran was detected in Southern Russia in 1863 (Negrul, 1952). In 1881, it was cited in the West Georgian province of Abkhazeti, close to the city of Sokhumi located on the Black Sea coast. Between 1889 and 1891, the vineyards situated in Western Georgia were infested. In Eastern Georgia, the pest was found in Tbilisi in 1884 (but it was immediately eliminated) and in the province of Kartli in 1893. Later, between 1906 and 1910, the symptoms were found in the province of Kakheti (Kantaria and Ramishvili, 1983; Ramishvili, 2001). The damage throughout the country was extensive, and losses were so high that viticulture and winemaking ceased to be prosperous activities. The vineyard acreage was dramatically reduced. To control phylloxera and other diseases, the 'Caucasus Phylloxera Committee' was established in 1880, playing an important role in the detection of infested vineyards, introducing innovative methods to fight against parasites and describing local varieties under the threat of extinction. The method of grafting local varieties on American rootstocks was introduced in the last decade of the 19th century, playing a very important role in saving Georgian viticulture and wine-making (Lomineishvili and Gaprindashvili, 1990).

The absence of damage caused by nematodes is probably due to the action of water contained in the

profile of the soil mentioned previously, according to Palm and Walter (1991).

The erineum strain of *C. vitis* caused symptoms on 100% of the studied vines, with a low (1–3) intensity of attack, as occurred in the case of the Spanish and French populations (Lara and Ocete, 1992; Ocete *et al.*, 2007, 2008). It is a monophagous species (Arnaud and Arnaud, 1931), widely distributed in the vineyards of both hemispheres (Keifer *et al.*, 1982; Dennil, 1986). This mite has two strains which are more commonly found on cultivars: the bud strain and the leaf curl strain (Reyes, 2004). Through the genetic research approach and characterization, the two strains would belong to distinct species (Carew *et al.*, 2004). In those nests, several natural enemies of the erineum strain mite can be found, mainly *Phytoseiidae*, *Tydeidae* and *Cecidomyida*, and all of them constitute a new target to be investigated in the future. Some predatory species belonging to the cited families cannot be found in vineyards due to the use of pesticides (Ferragut *et al.*, 2008).

C. vitis is another monophagous species detected in 62% of the European populations sampled between Portugal and Hungary (Ocete *et al.*, unpublished data). It caused a low level of infestation on 30.3% of the vines found in Georgia belonging to eight populations observed, with an overall lower level of infestation compared with other mite species. After bud burst (D phenophase according to Baggiolini (1952)), females that have broken the diapause begin to feed, resulting in small spots that can be seen against light. Symptoms caused by this phytophagous were found in different vineyards of Europe, America, South Africa and Australia. Usually, it is considered as a secondary pest (Sazo Rodríguez *et al.*, 2003). Injuries caused by a high infestation of both cited mites on Australian vineyards were referred to as restricted spring growth (Bernard *et al.*, 2005).

Because of the impossibility of long migrations of the two obligatory monophagous parasitic eriophyids and their wide presence on the majority of wild grapevines, we can assume that these mites have always coexisted with their primary host since ever and were transferred to cultivars during the domestication processes.

Several support trees, belonging mainly to the *Populus* and *Quercus* genera, are infected by *Armillaria mellea* (Vahl: Fr.) Kummer in Georgia. This fungal disease caused the hyphae to produce abundant white mats between the hardwood and the bark, but it is absent in the roots of the vines. It is an interesting fact when focusing on the possibility of getting new rootstocks using wild vines in breeding programmes.

Powdery mildew symptoms were detected in 55% of the studied vines. This percentage is similar to Southern Spanish populations, according to data from Ocete *et al.* (2007). Its level of infestation varied between low and

medium. Only one population was free from the disease, perhaps due to the fact that it contained only one vine.

In the Old World, the first damages caused by powdery mildew were discovered in England by Berkeley (1847), and were later detected on cultivars situated in France (Cortés, 1854; Müller, 1882). Eight years later, the fungal disease had invaded the vineyards of Europe, Northern Africa and Asia Minor (Le Canu, 1862). In Georgia, this disease was discovered in the middle of the 19th century (1857 in Guria province) in Western Georgia: it destroyed high vineyards in the provinces of Guria and Samegrelo (Kantaria and Ramishvili, 1983; Ramishvili, 2001). Nowadays, the pathogen can be found in all wine-producing areas, under dry weather conditions and average temperatures between 15 and 35°C (Pérez de Obanos, 1992; Pearson and Goheen, 1996).

On the other hand, downy mildew affected 18% of the vines, usually with a lower intensity than *E. necator*. No symptoms were found in the three populations with a lower number of vines. In the case of Southern Spanish populations, this disease affected about 60% of the 200 populations studied by Ocete *et al.* (2007).

Downy mildew was detected in the south of Western France, near Bordeaux in about 1878 (Millardet, 1885). Four years later, the disease affected all French vineyards and adjacent countries (Urien de Vera and Diego-Madrazo, 1891) and reached South Caucasus in the last two decades of the 19th century (Kantaria and Ramishvili, 1983; Ramishvili, 2001).

The presence of both North American mildews on Georgian populations and in the rest of the Eurasian wild grapevines studied in Europe is a legacy from cultivars infected by the massive importation of American vines occurred in the 19th century. All cultivars of *V. vinifera* are susceptible to this fungus. Only the North American species, mainly *V. rupestris* and *Vitis rotundifolia*, exhibited an important level of resistance because they had evolved with this pathogen (Leroux and Clerjeau, 1985). The easy transportation of the spores from vineyards to natural habitats induces the infections of wild vine populations situated in remote sites.

This phytosanitary study demonstrates that, today, parasitic organisms are not the main problem for the survival of relic populations. This is a very important conclusion, as it was widely believed that phylloxera was one of the main causes of the reduction of wild grapevine populations in Georgia. Despite this fact, the fungal diseases probably had a heavy impact on wild grapevine individuals, leading to the death of many plants growing in sites which are more suitable for the development of these pathogens. The remaining wild plants could be descendants of those that exhibited a higher tolerance

or were situated in habitats under conditions which were not suitable for heavy mildew infection.

Acknowledgements

This study is a joint publication of the COST Action FA1003 'East-West Collaboration for Grapevine Diversity Exploration and Mobilization of Adaptive Traits for Breeding' (http://w3.cost.eu/index.php?id=181&action_number=FA1003). The authors wish to thank Dr Nicole Ortega and Dr Agnes Minnery for the critical review of the manuscript, Dr Marina Olwen Fogarty and Adolfo Molejón-García for the accurate and passionate revision of the English text, and Dr Benito Valdes (Botanical Department of the University of Sevilla, Spain) for helping with the determination of vegetation.

References

- Ampelography (1970) Varieties with female type of flower. In: Negrel AM (Editor of Chief) *Reference Book of the Ampelography of the Soviet Union in Ten Volumes*. Moscow: Pishchevaia promishlennost, pp. 406–408 (In Russian).
- Arnaud G and Arnaud M (1931) *Traité de pathologie végétale*. Paris: Tomo I.
- Arnold C, Gillet F and Gobat JM (1998) Situation de la vigne sauvage, *Vitis vinifera* ssp. *silvestris* en Europe. *Vitis* 37 (4): 159–170.
- Arnold C (2002) *Ecologie de la vigne sauvage, Vitis vinifera* L. ssp. *silvestris* (Gmelin) Hegi, dans les forêts alluviales et colluviales d'Europe. PhD Thesis, University of Neuchâtel.
- Arrigo N and Arnold C (2007) Naturalised *Vitis* rootstocks in Europe and consequences to native wild grapevine. *PLoS One* 2: e521. doi:10.1371/journal.pone.0000521.
- Arroyo-García R, Ruiz-García L, Bolling L, Ocete R, Lopez MA, Arnold C, Ergul A, Söylemezoglu G, Uzun HI, Cabello F, Ibañez J, Aradhya MK, Atanassov A, Atanassov I, Balint S, Cenis JL, Costantini L, Gorislavets S, Grando MS, Klein BY, McGovern PE, Merdinoglu D, Pejic I, Pelsy F, Primikiriou N, Risovannaya V, Roubelakis-Angelakis KA, Snoussi H, Sotiri P, Tamhankar S, This P, Troshin L, Malpica JM, Lefort F and Martinez-Zapater JM (2006) Multiple origins of cultivated grapevine (*Vitis vinifera* L. ssp. *sativa*) based on chloroplast DNA polymorphisms. *Molecular Ecology* 15: 3707–3714.
- Baggiolini M (1952) Les stades réperes dans le développement annuelle de la vigne et leur utilisation pratique. *Revue Romande d'Agriculture, Viticulture et d'Arboriculture* 8: 4–6.
- Berkeley J (1847) Sur une nouvelle espèce d'oidium, *O. tuckeryi*, parasite de la vigne. *Gardener's Chronicle* 27 de novembre.
- Bernard M, Horne P and Hoffmann A (2005) Eriophyoid mite damage in *Vitis vinifera* (grapevine) in Australia: *Calepitrimerus vitis* and *Colomerus vitis* (Acari: Eriophyidae) as the common cause of the widespread 'Restricted Spring Growth' syndrome. *Experimental and Applied Acarology* 35: 83–109.

- Biagini B (2011) La vite selvatica in Italia. In: Biagini B (ed.) *Proceeding of the International Conference "Origini Della Viticoltura: Dalla Vite Selvatica Alle Varietà Coltivate"*, 25 June 2010, Castiglione d'Orcia, Italy, pp. 183–203.
- Carew ME, Goodisamn MAD and Hoffmann AA (2004) Species status and population structure of grapevine eriophyoid mites (Acari: Eriophyidae). *Entomologia Experimentalis et Applicata* 111: 87–96.
- Cholokashvili N (1983) Genus *Vitis* L. In: *Flora of Georgia*. vol. 8 2nd edn. Tbilisi: Metsniereba, pp. 274–278 (in Georgian).
- Cortés B (1854) *Salvación de las viñas ó historia del oidium-tuckeri*. Imp. De Manuel Minuesa, 1854.
- De Candolle A (1883) *Origine des plantes cultivées*. Paris: Baillière.
- Dennil GB (1986) An ecological basis for timing control measures against the grape vine bud mite *Eriophyes vitis* PGst. *Crop Protection* 5: 12–14.
- Flora Georgia (1971–2007) Flora of Georgia. In: Ketskhoveli N and Gagnidze R (Editors of chief) *15 Volumes*, 2nd edn. Tbilisi: Mecniereba (in Georgian).
- Ferragut F, Gallardo A, Ocete R and López MA (2008) Natural predatory enemies of the Erineum strain of *Colomerus vitis* (Pagenstecher) (Acari, Eriophyidae) found on wild grapevine populations from southern Spain (Andalusia). *Vitis* 47: 51–54.
- Grossgeim AA (1939, 1940, 1945, 1950, 1952, 1962, 1967) *Flora of the Caucasus in 7 Volumes*, 2nd edn. Baku and Moscow-Leningrad (in Russian).
- Imazio S, Maghradze D, Bacilieri R, De Lorenzis G, Scienza A, This P and Failla O (2010) Molecular survey of Georgian traditional grapevine genetic resources. In: *Book of Abstracts for the 10th International Conference on Grape Genetics and breeding*, 1–5 August 2010, Geneva, USA. pp. 70.
- Kantaria V and Ramishvili M (1983) *Viticulture*. Tbilisi (In Georgian): Ganatleba.
- Keifer HH, Baker EW, Kono T, Delfinado M and Styer WE (1982) An illustrated guide to plant abnormalities caused by Eriophyd mites in North America. In: *US Department of Agriculture, Agriculture Handbook No. 573*. 178 pp.
- Laguna E (2003a) Sobre las formas naturalizadas de *Vitis* en la Comunidad Valenciana. I. Las especies. *Flora Montibérica* 23: 46–82.
- Laguna E (2003b) Datos sobre la producción de frutos de las especies e híbridos invasores de vides (*Vitis* L.). *Toll Negre* 2: 10–15.
- Lara M and Ocete Rubio R (1992) Erinosi, una constante de las poblaciones españolas de *Vitis vinifera silvestris* (Gmelin) Hegi. *Viticultura Enología Profesional* 29: 11–16.
- Larrea A (1978) *Vides americanas portainjertos*. Madrid: Ministerio de Agricultura.
- Law (1998) *Law of Georgia about Grapevine and Wine*. Tbilisi (In Georgian).
- Le Canu RL (1862) *Instrucción popular para el azufrado de las vides*. Madrid: Imprenta de Manuel Alvarez.
- Leroux P and Clerjeau M (1985) Resistance of *Botrytis cinerea* Pers. and *Plasmopara viticola* (Berk. and Curt.) Berl. and de Toni to fungicides in French vineyards. *Crop Protection* 4: 137–160.
- Lomineishvili R and Gaprindashvili G (1990) Sakara testing station after 100 years of its establishment. In: *Proceedings of the Georgian Research Institute of Horticulture, Viticulture and Oenology. Special Issue 'Sakara Testing Station is 100 Years Old'*, Tbilisi, pp. 3–40 (In Georgian).
- Maghradze D, Ocete Rubio ME, Pérez Izquierdo MA, Chipashvili R, Osete Pérez CA and Ocete Rubio R (2010) El patrimonio vitícola de Georgia: el estado sanitario de sus poblaciones silvestres. In: *Materials of the Congress "XXXI Jornadas de Viticultura y Enología de Tierra de Barros"*, 4–8 Mayo 2009, Badajoz. Almedralejo: Centro Universitario Santa Ana de Almedralejo, pp. 113–126.
- Maghradze D, Failla O, Imazio R, Bacilieri R, Chipashvili R, Quattrini E, This P and Scienza A (2011) Wild grapevine of Georgia. In: *Proceeding of the International Conference "Origini della viticoltura: dalla vite selvatica alle varietà coltivate"*, 25 June 2010, Castiglione d'Orcia, Italy, pp. 183–203.
- Makashvili A (1991) *Lexicum botanicum–Nomina plantarum*. 3rd edn. Tbilisi (In Georgian, Russian, Latin): Metsniereba.
- Millardet A (1885) *Historie des principales variétés et espèces de vignes d'origine américaine qui résistent au Phylloxera*. Paris/Bordeaux: Masson/Feret.
- Moore D (1982) Green planet. In: *The Story of Plant Life on Earth*. Cambridge/Melbourne: Cambridge University Press.
- Müller JTV (1882) *Guía teórico-práctica para combatir las enfermedades de la vid*. Madrid: Biblioteca Agrícola Ilustrada.
- Myles S, Boyko AR, Owense CL, Browna PJ, Grassi F, Aradhya MK, Prins B, Reynolds A, Chia J-M, Ware D, Bustamante CD and Buckler ES (2011) Genetic structure and domestication history of the grape. In: *PNAS (Proceedings of Academy of Science, USA)*. Early edn. Available at www.pnas.org/cgi/doi/10.1073/pnas.1009363108, p. 6.
- Negrul AM (1952) *Viticulture with Basic Ampelography and Breeding*. Moscow (In Russian): Agricultural Literature, p. 427.
- Ocete R, Gallardo A, Lara M, López MA and Pérez MA (2006) *Una perspectiva histórica sobre la crisis filoxérica y su impacto en el viñedo andaluz*. Sevilla: Instituto de Investigación y Formación Agraria y Pesquera, Consejería de Innovación, Ciencia y Empresa, Consejería de Agricultura y Pesca, Junta de Andalucía, pp. 187.
- Ocete R, Cantos M, López MA, Gallardo A, Pérez MA, Troncoso A, Lara M, Failla O, Ferragut FJ and Liñán J (2007) *Caracterización y conservación del recurso fitogenético vid silvestre en Andalucía*. Consejería de Medio Ambiente, Junta de Andalucía, Sevilla.
- Ocete R, López MA, Gallardo A and Arnold C (2008) Comparative analysis of wild and cultivated grapevine (*Vitis vinifera*) in the Basque Region of Spain and France. *Agriculture, Ecosystems and Environment* 123: 95–98.
- Ocete R, Arnold C, Failla O, Lovicu G, Biagini B, Imazio S, Lara M, Maghradze D and Angeles-Lopes M (2011) Consideration on European wild grapevine (*Vitis vinifera* L., ssp. *silvestris* (Gmelin) Hegi) and Phylloxera infestation. *Vitis* 50: 97–98.
- OIV (2009) *Descriptor List for Grape Varieties and Vitis Species*, 2nd edn. Paris: The OIV, 179 pp.
- Palm CE and Walter WD (1991) *Control of Plant-parasitic Nematodes*. vol. 4. Washington, DC: National Academy of Sciences, pp. 219.
- Pearson RC and Goheen AC (1996) *Plagas y enfermedades de la vid*. Mundi-Prensa: The American Phytopathological Society, pp. 91.
- Pérez de Obanos J (1992) Plagas en viñedos: acariosis y erinosi. *Navarra agraria, No. 12*. Pamplona: ITGC.
- Ramishvili R (1988) *Wildly Growing Grapevine of the Trans-Caucasus*. Tbilisi, p. 124 (in Russian).

- Ramishvili R (2001) *History of Georgian Grape and Wine*. Tbilisi, p. 240 (in Georgian).
- Raski DJ (1994) Nematodos parásitos de la vid. In: Pearson RC and Goheen AC (eds) *Plagas y enfermedades de la vid*. Mundi-Prensa: The American Phytopathological Society, pp. 55–56.
- Red Book of Georgia (1982) Krikina, Forest grape, Usurvazi, *Vitis silvestris* Gmel. In: Kacharava W (Editor of Chief). *Rare and Endangered Species of Animals and Plants*. Tbilisi: Sabchota Sakartvelo, pp. 155–156 (in Georgian).
- Reyes J (2004) *ERINOSIS (Eriophyes vitis* Pgst. *Sin Colomerus vitis* Pgst.) En *Los parasitos de la vid: Estrategias de Protección Razonada*. Madrid: Mundi-Prensa & MAPA.
- Saint Pierre C (1876) Les ravegours des verges et des vignes. In: De La Branchère, H. Paris. J. Rothschild (ed.) pp 67.
- Sazo Rodríguez L, Agurto L, Contador F and Mondaca AC (2003) Nuevas especies de Acaros fitófagos asociados a la vid vinífera en Chile . Available at <http://www.gie.uchile.cl/pdf/Luis%20Sazo/acaros.pdf>
- Terpó A (1969) A *Vitis silvestris* Magyar Középhegységi termőhelyi Viszonyainak vizsgálata. Budapest. *Botanikai Közlemények* 56: 27–35.
- Terpó A (1974) A ligeti szőlő- *Vitis vinifera* L. (Taxonomic key of the wild and feral vine species occurring in Hungary). Budapest. *Magyarország Kultúrflórája* 4: 15–16.
- Urien de Vera E and Diego-Madrado C (1891) *Las enfermedades de la vid*. Salamanca: Imp. de Fco. Núñez Izquierdo.
- Vavilov NI (1926) Cemtry proiskhozhdenia kulturnikh rastenii (The centres of origin for cultivated plants). *Trudi po prikladnoi botanike, genetike i selektsii (Proceedings of Applied Botany, Genetics and Breeding)* 16: 133–137 (in Russian).