

Origins of Viticulture

Subjects: Agriculture, Dairy & Animal Science

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The grapevine (*Vitis vinifera* L.), besides being one of the most extensively cultivated fruit trees in the world, is also a fascinating subject for evolutionary studies. The domestication process started in the Near East and the varieties obtained were successively spread and cultivated in different areas. Whether the domestication occurred only once, or whether successive domestication events occurred independently, is a highly debated mystery. Moreover, introgression events, breeding and intense trade in the Mediterranean basin have followed, in the last thousands of years, obfuscating the genetic relationships. Although a succession of genomic studies has been carried out to explore grapevine origin and different evolution models are proposed, an overview of the topic remains pending.

Keywords: *Vitis* ; origin ; domestication ; grapes ; grapevine ; Viticulture

1. Introduction

Vitis vinifera L. is one of the most economically important fruit crops in the world. It is used in the global wine industry, covering approximately 7.5 million hectares in 2019 and producing more than 67 million tons of grapes ^[1]. Two subspecies are recognised: the wild form, *V. vinifera* subsp. *sylvestris*, and the domesticated one, *V. vinifera* subsp. *vinifera* (or *sativa*). Subspecies *sylvestris* is considered the progenitor of the subspecies *vinifera* and, phenotypically, the two subspecies differ in some traits relating to the morphology of flower, seed and leaf, to berry and bunch size (Figure 1) and sugar content ^[2]. The flowers of *sylvestris* individuals are dioecious (male and female flowers), while those of the *vinifera* are monoicous (hermaphrodite flowers) ^[3]. The subspecies *sylvestris* was neglected for several years, but recent studies have evidenced a great morphological variability and a presumed subdivision in different variants ^[4,5]. Moreover, ecological studies have shown that the wild populations, differently than *vinifera*, can grow in a wide range of habitats with wide adaptability to different soils, including forested wetlands, along seasonal rivers in closed forests and sand dune shrublands.

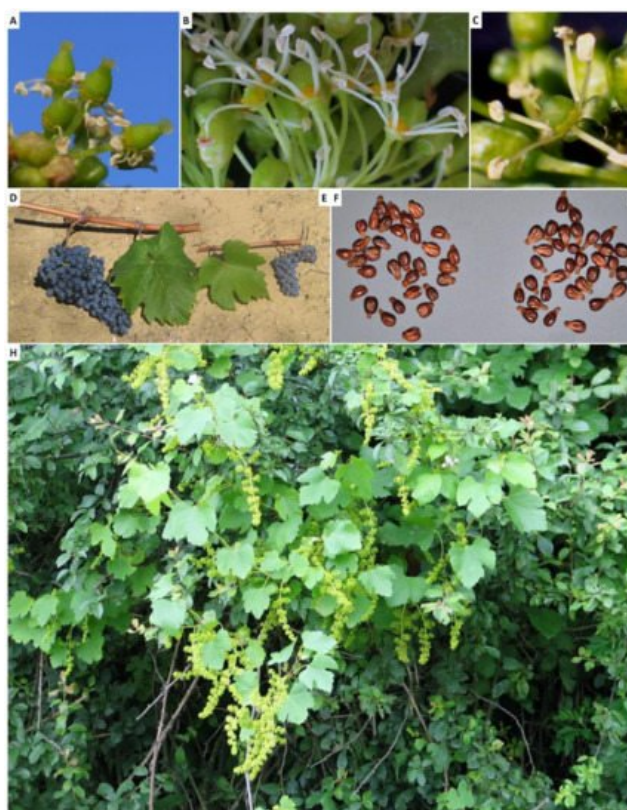


Figure 1. Phenotypical traits of *sylvestris* and *vinifera*. Female (A) and male (B) flowers of *sylvestris* individuals. Hermaphrodite flower (C) of *vinifera* individuals. Leaf and bunch of *vinifera* (D) and *sylvestris* (E) individuals. Seed of *sylvestris* (F) and *vinifera* (G) individuals. (H) Plant of *sylvestris* individual. Seeds of *sylvestris* are small, with a rounded outline and short stalks, while the *vinifera* ones are large, elongated, pyriform with elongated stalk. Leaves of *sylvestris* are smaller than the cultivated ones. *Vinifera* shows berries and bunches bigger than those of *sylvestris*, with a higher sugar content.

The grapevine domestication process occurred in the Near East, in some place along a large area that ranges between Central Asia and the Black Sea. Archaeological and archaeobotanical evidence suggest that viniculture began in the Near East, ca. 6000–5800 BC during the early Neolithic Period [4]. However, some questions about where and when the process of domestication began, remain elusive. The study of domestication is a research area that does not only concern how plants were modified by humans in the past but allows us to understand how to design ideal crops for more sustainable agriculture. This aspect is essential because the genetic diversity of crops has been reduced throughout the process of domestication resulting in the loss of several traits. Moreover, breeding processes that have involved the selection of desirable traits to improve the crop productivity, have aggravated the situation, causing the loss of disease-resistant traits. The depletion of diversity has a serious impact on agriculture, constraining the possibility of the cultivation of crops in more extreme environments or in alternatively increasing the input of pesticides and water, with severe cost to the environment. To reverse this situation, it is necessary to identify the wild relatives of crops which are known to tolerate biotic and abiotic stress, a trait lost during human selection. To date, the subsp. *vinifera* is cultivated in Europe, Asia, Northern America, Southern America, Northern Africa, South Africa, New Zealand and Australia. The domesticated form includes a huge number of varieties, with more than 10,000 cultivars believed to exist in the world, complicating the identification of cultivar and the tracking of the species origins. In the last two decades, molecular studies have led to a deeper knowledge of the evolution of grapevines and the domestication process continues to be at the centre of debate in several studies.

2. The Domestication of the Grapevine in the Near East

Whether the grapevine was domesticated only once, or whether some varieties were domesticated independently, is a mystery hotly debated and different scenarios are proposed. The main hypothesis defined as the “Noah hypothesis”, so named in honour of the biblical patriarch who planted the first vineyard on Mount Ararat after the flood, proposes that grapevine domestication processes took place in a well-defined restricted area (Single-origin model). In addition, a multiple-origin hypothesis that provides for the foundation of independent lineages originating from wild progenitors spread some place along the entire distribution range has been proposed (Multi-origin model).

Genetic relationships between wild and domesticated forms can be traced by molecular analysis and several markers are widely used to show the genetic structure and domestication history of crops. One of the modern challenges in plant science is to improve the access to and use of genetic variability hidden in the genomes. In the genomic era, efficient genotyping tools should be able to cover a large part of the genome. In the last years, several authors have observed a reduction of genetic variability, confirming that the grapevine has suffered from a weak domestication bottleneck in the Near East followed by diffusion towards Europe [7,8,9]. However, studies carried out on germplasm resources collected in the Caucasus have shown an unexpected diversity and richness [5] raising some doubts about the correct geographic place of the main domestication area.

Plastid microsatellites have been used to explore the haplotype diversity from grapevine cultivars distributed from the Near East to the Mediterranean basin. Even though conclusions cannot be drawn about the domestication area from the results, the existence in the past of an intensive varietal exchange of germplasm and propagation throughout Europe have been evidenced [10]. On the other hand, Arroyo-García et al. [11], have examined the haplotype relationships under a network model in a large sampling of wild and domesticated accessions. The results supported the existence of at least two centres of domestication, one in the Near East and another in the Western Mediterranean region, confirming the involvement of several founders recruited throughout a prolonged time period. However, further studies are needed to understand the contributions made by the wild populations located in the Italian and Iberian Peninsulas, France and Greece (including the main islands of the Mediterranean basin) and to understand whether these locations have had a role of secondary domestication or were diversification centres.

In recent years, molecular studies have proved that interspecific hybridisation and introgression are central processes in the evolution of *Vitis* genus [6]. Introgression is considered a process mediated by the transfer of genes through repeated backcrosses and when occurring from crops to its wild relatives can have deleterious consequences on the genetic structure and conservation of populations. On the other hand, the inverse process of introgression from wild to crop may

be considered a rapid method for the crop to adapt to new environments. The admixture between perennial crops and wild progenitors has hardly been studied and genetic analysis was not always able to trace the gene flow, especially if an elevated number of generations have elapsed. Recent molecular studies have shown that the role of introgression appears to have been fundamental in grapevine [13,14,15]. Today, little is known about the effect of introgression, but the continuing extinction of *sylvestris* plants with a significant reduction in gene diversity and heterozygosity of populations in respect to *vinifera*, is causing a serious demographic decline of wild grapevine. An increasing number of studies have proposed that the maintenance and the conservation of wild populations should be a primary aim in Europe because these plants are a unique and fundamental genetic resource for the improvement of the cultivated grapevine in the future [16,17]. Some molecular studies have been proposed recently with the aim of studying genomic divergence between the two subspecies, but greater efforts should be made to explore the real level of introgression. Moreover, some urgent issues which are still pending should be examined such as the effective direction and intensity of gene flow between wild and domesticated forms as well as the accurate estimation of admixture times. Future works should be directed to identify which genomic regions are involved in gene flow. For example, signals of introgression might not be diffused in the entire genome but localised in specific chromosomes.

A limit of the research aimed to investigate the origin of grapevine domestication is, undoubtedly, the interpretation of the past through the study of modern cultivars. An important contribution in dealing with this issue comes from archaeological remains. So far, the most common method used to study the diversity of archaeological pips has been based on morphometric analysis. Wild and domesticated grapevine seeds can be distinguished based on seed shape, contributing greatly to connecting past to present diversity. Basically, *sylvestris* seeds are spherical with a small beak, while the *vinifera* seeds are pyriform-shaped with a well-developed beak. Thanks to morphological analysis of archaeological seeds, new insight on secondary domestication centre has been suggested, such as a domestication centres in the Languedoc region in France [7], and an early local grapevine domestication in prehistoric Greece [8]. The combination of seed morphological and genetic characterisation should allow a better understanding of the grapevine domestication process. Nevertheless, if the genetic characterisation of modern varieties had a great impact among researchers with very successful results, the same could not be said about the study of ancient DNA (aDNA). The first results on genetic diversity of grapevine aDNA were not completely satisfactory for several reasons. First, aDNA from archaeobotanical specimens must be correctly preserved and only charring and waterlogging samples are a good source for DNA amplification. Secondly, aDNA should not be contaminated by exogenous DNA. Thirdly, a high amount of template DNA is needed. The next-generation sequencing techniques provide a significant boost to aDNA studies. Indeed, short read length makes this new technology ideal for aDNA research, guaranteeing reliable results. Wales et al. [9], for the first time, have high-throughput sequenced aDNA from archaeological grape specimens coming from Armenia, England, Israel, Italy and Turkey, dating ca. 4000 BCE–1500 CE.

Moreover, all genetic variations, that ranging from SNPs to large genomic structural variants (SVs) such as duplications, inversions and transpositions, are the result of selection through time. The origin of SVs in plants is relatively poorly understood as are the mechanisms that govern the gene gain and loss, even though many important agronomic traits may be determined by these changes [21]. Due to domestication, the grapevine has experienced a bottleneck and vegetative reproduction led to the accumulation of recessive deleterious mutations. On the other hand, the stability of phenotype has made the clonal propagation attractive in agriculture. Grapevine is an ideal candidate to study genetic variations in clonal systems and, over the last few years, many resequencing studies focus on the effects of SVs throughout domestication. Zhou et al. [10] showed that domesticated grapevine, compared with its wild dioecious progenitor, has accumulated SVs and suggest that these modifications are a major driving force in the domestication process. In the future, comprehensive evolutionary studies need to resequence an extensive number of genomes including wild relatives of crops. Unfortunately, a part of genetic diversity included in the wild grapevine lineages may be lost due to climate changes that occurred in the past or the anthropogenic pressures in the recent times. Accessions which originate from different geographical regions or that show different phenotypes, should be collected to maximise the diversity. Moreover, to acquire full knowledge of genetic diversity and to gain full understanding of genomic variations, the pan-genome of grapes should be planned. Generally, the pan-genome refers to a full complement of genes of a species, but in grapes the concept could be expanded to the clade that includes the wild species of *Vitis* genus. Recent studies propose to produce a super-pan-genome for each crop, using at least one *de novo* assembly from each species. In this way, it is possible to reduce the bias that could be produced mapping the sequencing data from genetically distant species. The *Vitis* genus counts around 60–70 taxa widespread throughout Eurasia and Northern America and several of them are inter-fertile. Wild grapes are adapted to a wide range of climatic conditions and harbour genes resistant or tolerant towards both biotic and abiotic stresses, and several taxa are used today, as in the past, to produce rootstocks resistant to pathogens and pests, to drought and salinity, as well as cultivars characterised by a good quality of fruit and suitable for winemaking. Thus, the genetic material conserved in wild grapes is a source of resistance to several stresses useful to improve the cultivars by traditional agronomic strategies or modern genomic editing methodologies.

3. Conclusions

Over the last two decades, an increasing number of studies aimed to examine the genetic resources of grapevine and to investigate its ancestries. Several studies proposed that the main domestication occurred in the Southern regions of Caucasus, but recent insight suggests that a primo-domestication centre could be extended to Central Asian countries. In these areas, the grapevine has suffered from a history of protracted cultivation, thus, the pre-domestication phase may have begun earlier than previously thought. Even if these results fit well with the protracted model of crop domestication, successive studies are needed to define the times of transition between different domestication phases. Grapevine cultivars were introduced to the Mediterranean basin only successively, but secondary centres of domestication and diversification are also highly debated. Several years of breeding seem to have obfuscated the signatures of the secondary domestication processes and recent molecular studies have shown that the role of introgression appears to be fundamental. Introgression from *sylvestris* to *vinifera* aided by human activity have contributed to the domestication processes. Wild populations have had enough time to adapt to local environments and they harbour desirable traits useful for the improvement of the varieties. On the other hand, gene flow from *vinifera* to *sylvestris* has been widely detected and it can have a significant impact on the conservation of wild populations. On the basis of data reported, the introgression is far from uncommon, thus, we propose that a detailed screening of gene flow which occurred between *sylvestris* and *vinifera* germplasms should be conducted urgently. Today the grapevine domestication process is a challenge which is far from being completely solved and some issues remain pending. We argue that the realisation of a pan-genome of grapes could be a useful resource to track the change of genes which have occurred during different phases of domestication. In the future, whole-genome resequencing analysis will make it possible to explore a large portion of the variabilities in grapevine and some of the above mentioned pending issues are expected to be solved. However, we are also aware that only by increasing the sampling of landraces and wild populations distributed in remote regions and particularly in Central Asian countries, will it be possible to increase the chance to obtain a complete picture of genetic relationships and go back to the roots of the domestication process.

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