Historical origins and genetic diversity of wine grapes

Patrice This¹, Thierry Lacombe¹ and Mark R. Thomas²

¹INRA, UMR Diversité et Génoomes des Plantes Cultivées, 2 place P. Viala, 34060 Montpellier, France
²CSIRO Plant Industry, PO Box 350, Glen Osmond, SA 5064, Australia

The genomic resources that are available to the grapevine research community have increased enormously during the past five years, in parallel with a renewed interest in grapevine (Vitis vinifera L.) germplasm resources and analysis of genetic diversity in grapes. Genetic variation, either natural or induced, is invaluable for crop improvement and understanding gene function, and the same is true for the grapevine. The history and vineyard cultural practices have largely determined the genetic diversity that exists today in grapevines. In this article, we provide a synopsis of what is known about the origin and genetics of grapes and how molecular genetics is helping us understand more about this plant: its evolution, historical development, genetic diversity and potential for genetic improvement.

The current status of grape genomic resources
The grapevine (Vitis vinifera L.) is attractive for genomic research because it is diploid and has a small genome size of 475–500 Mb relative to other plants (it is approximately four times the size of Arabidopsis and one sixth the size of the corn genome) [1,2], consisting of 19 chromosomes. The genotypes of grape varieties are highly heterozygous and nearly all modern cultivated varieties (cultivars) are hermaphroditic, self-fertile and out-cross easily. Over the past five years there has been a rapid increase in genomic resources available for grapevine research (Box 1).

Historical overview
The grape is unique: not only is it a major global horticulture crop but it also has ancient historical connections with the development of human culture. The main product, wine, was considered divine, a drink of the gods: even Dionysus and Bacchus were dedicated to this beverage. Other Mediterranean cultures considered that the wine sprang from the blood of humans who had fought the gods [3] and wine has always had a major role in the way of life of Mediterranean people [4].

In the Vitaceae family, it is the Vitis genus that is of major agronomic importance. It consists of ~60 inter-fertile species that exist almost exclusively in the Northern Hemisphere (Table 1). Among them, Vitis vinifera is the only species extensively used in the global wine industry. It is also the only species of the genus indigenous to Eurasia and is suggested to have first appeared ~65 millions years ago [5]. Two forms still co-exist in Eurasia and in North Africa: the cultivated form, V. vinifera subsp. vinifera (or sativa) and the wild form V. vinifera subsp. silvestris (or sylvestris), sometimes referred to as a separate subspecies. This historical separation into subspecies was based on morphological differences [6]. For the purpose of this article, we will refer to the wild-type and cultivated form as subspecies, but it could be easily argued that this distinction is not valid because any differences are most likely the result of domestication over time by humans rather than geographical isolation. Thousands of V. vinifera cultivars exist [7–10] but the global market for wine production is dominated by only a few cultivars owing, in large part, to how wine is currently marketed. The cultivars are generally classified according to their final production: wine grapes, table grapes and raisins. By contrast, the wild form is rare [9] and extends from Portugal to Turkmenistan, and from Rhine riversides to northern forests of Tunisia [3,9,11]. It is believed to be the ancestor of present cultivars [6] and is still observed as wild vines growing on the canopy of surrounding trees (Figure 1a). The domestication of grape seems linked to the discovery of wine, even if it is unclear which process predated the other [3,12]. During domestication, the biology of grapes underwent several dramatic changes (Figure 2) to ensure greater sugar content for better fermentation [13], greater yield and more regular production. In this process, the changes in berry and bunch size and the change from dioecious wild plants (see Glossary) to hermaphrodite cultivated plants were crucial. Changes in seed morphology also occurred [14] and even if its biological significance is unknown, this trait is used in the analysis of archaeological remains to differentiate remains of wild or cultivated grape [15,16]. It is unknown whether these changes occurred over a large period of time through sexual crosses and natural or human selection, or quickly through mutations, selection and subsequent propagation by vegetative multiplication (Box 2).

Uncertainty also remains about the place and period of the original domestication and whether secondary independent domestications also occurred. Although wild grapes were probably present in many places in Europe during the Neolithic period, archaeological and historical evidence suggest that primo-domestication occurred in the Near-East. The earliest evidence of wine production was found in Iran at the Hajji Firuz Tepe site in the northern zagros mountains circa 7400–7000 BP (before present) [3,17]. Seeds of domesticated grapes dated from ~8000 BP were also found in Georgia and in Turkey. Nevertheless, remains of seeds discovered in the Neolithic period in

---

Corresponding author: Thomas, M.R. (Mark.R.Thomas@csiro.au).
Available online 26 July 2006.
Western Europe also suggest exploitation of grape at this time and the remains of wild seeds were also discovered at bronze-age sites in France [14].

From the primo-domestication sites, there was gradual spread to adjacent regions such as Egypt and Lower Mesopotamia (circa 5500–5000 BP) and then further dispersal around the Mediterranean, following the main civilizations (Assyrians, Phoenicians, Greeks, Romans, Etruscans, Carthaginians) [3]. Grape cultivation reached China (2nd century) and Japan (3200 BP) [12]. Under the influence of the Romans, V. vinifera expanded inland and reached many temperate regions of Europe, even as far north as Germany. This expansion often followed the main trade routes (i.e. rivers such as the Rhine, Rhone, Danube and the Garonne). By the end of the Roman Empire, grape growing was common in most of the European locations where they are grown today. The Romans were the first to give names to cultivars [18] but it is difficult to relate them to modern grapes. At this time, the differentiation of table and wine grape was probably already in place in addition to the different colour types [18].

In the middle ages, the Catholic Church replaced the Romans in spreading grape cultivation to new regions and enabled the exchanged germplasm through crusades and spread of their religion through Northern Europe [12]. The extension of Islam to North Africa, Spain and Middle East also had an important role in spreading the grape (particularly table grapes). During the middle ages, the first cultivar names still used today appeared [12].

Following the Renaissance (16th century), V. vinifera colonized new regions (New World countries) where it was not indigenous. The missionaries introduced it to America, first as seeds (because they were easy to transport) and then by cuttings from their places of origin (France, German, Spain, Italy and East Europe). Cuttings were also introduced to South Africa, Australia and New Zealand in the 19th century and introduced later to North Africa [12].

Table 1. Taxonomy of the Vitis genus and use of species in breeding programs during the past centurya

<table>
<thead>
<tr>
<th>Species</th>
<th>Used for breeding new cultivars</th>
<th>Used for breeding rootstocks</th>
<th>Used for breeding inter-specific hybrids</th>
</tr>
</thead>
<tbody>
<tr>
<td>Muscadinia rotundifolia</td>
<td>++</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Vitis aestivalis</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Vitis amurensis</td>
<td>+</td>
<td>–</td>
<td>++</td>
</tr>
<tr>
<td>Vitis berlandieri</td>
<td>+</td>
<td>+++</td>
<td>–</td>
</tr>
<tr>
<td>Vitis candicans</td>
<td>–</td>
<td>+</td>
<td>–</td>
</tr>
<tr>
<td>Vitis caribae</td>
<td>–</td>
<td>–</td>
<td>+</td>
</tr>
<tr>
<td>Vitis champinii</td>
<td>+</td>
<td>+</td>
<td>–</td>
</tr>
<tr>
<td>Vitis cinerea</td>
<td>–</td>
<td>+</td>
<td>++</td>
</tr>
<tr>
<td>Vitis cordifolia</td>
<td>–</td>
<td>–</td>
<td>+</td>
</tr>
<tr>
<td>Vitis labrusca</td>
<td>+++</td>
<td>++</td>
<td>+++</td>
</tr>
<tr>
<td>Vitis longii</td>
<td>+</td>
<td>++</td>
<td>+++</td>
</tr>
<tr>
<td>Vitis riparia</td>
<td>+</td>
<td>+++</td>
<td>+++</td>
</tr>
<tr>
<td>Vitis rupestris</td>
<td>++</td>
<td>+++</td>
<td>+++</td>
</tr>
<tr>
<td>Vitis simpsonii</td>
<td>–</td>
<td>–</td>
<td>+++</td>
</tr>
<tr>
<td>Vitis vinifera</td>
<td>++++</td>
<td>+</td>
<td>+++</td>
</tr>
</tbody>
</table>

aThe grapevine belongs to the botanical family Vitaceae, which consists of almost one thousand species, grouped into 17 genera. Most of which are present in the inter-tropical regions. For example, Virginia creeper (Parthenocissus quinquefolia and P. tricuspidata) are used as ornamentals in gardens, whereas plants grown indoors include Rhodeisus sp. and Tetrastigma sp. In the Vitaceae family, the genus Vitis is the only genus of agronomical importance. It consists of ~60 inter-fertile species living almost exclusively in the Northern Hemisphere, ~30 in America and 30 in Asia. Several species have been extensively used for breeding rootstocks and inter-specific hybrids particularly in the early 20th century.
At the end of the 19th century, after several millennia of geographical expansion, disease-causing agents from America reached Europe (mildews, Phylloxera) resulting in devastation and destruction of many European vineyards, drastically changing the diversity of this species. As a result, a reduction of the diversity most likely occurred for both cultivated and wild grapes. The extent of diversity of V. vinifera found today might be a pale reflection of what existed before the introduction of Phylloxera. European viticulture was saved from extinction by the introduction of several indigenous American, non-vinifera, Vitis species (Table 1) that were used as rootstocks and for breeding

Box 2. Genetic variation in grapevine

Three processes have had a significant impact on the development of cultivated grapevines: sexual reproduction, vegetative propagation and somatic mutations. New genotypes are produced by sexual reproduction, either by crossing or self-fertilization. Because individual grapevine plants have highly heterozygous genotypes any progeny produced from seed is a novel combination of parental alleles, resulting in phenotypic variation and segregation of traits in a progeny population. The selection of a particular phenotype, particularly a berry trait, can be a long process considering the juvenile period (three-to-five years) of grapevine plants and the additional time necessary for evaluation of a trait important for wine production. Furthermore, many generations might be necessary to recover the desired traits. Once identified, vegetative propagation (asexual) by cuttings is a method of maintaining and multiplying a highly desirable genotype so that a vineyard can be planted with a single cultivar. Cuttings are also a convenient method of transporting cultivars from one region to another. Cultivars grown today are maintained by vegetative propagation. Although clonal propagation should ensure that all plants grown from cuttings have the same genotype, the occurrence of a somatic mutation in one cutting and not other cuttings might eventually lead to plants of the same cultivar having a slightly different genotype and sometimes a different phenotype, referred to as clonal variation. This clonal variant thus appeared rapidly over one cycle of vegetative reproduction (three-to-four years). This clonal variation is more complex if the mutation is maintained in only one cell layer of the plant, resulting in genetic chimerism. If the mutation is maintained in only the L1 layer (epidermis) then it will not be passed onto progeny by sexual reproduction [51].
disease-resistant inter-specific hybrids. These inter-specific hybrids were extensively used until the middle of the 20th century (they represented ~50% of the vineyards in 1950 in France [19]), but are now rather scarce.

Over the last 50 years, the cultivated grapevine has undergone another drastic reduction of diversity, owing to the globalization of wine companies and markets, resulting in the emergence of the now familiar worldwide grown cultivars such as Chardonnay, Cabernet Sauvignon, Syrah (Shiraz) and Merlot, and the disappearance of old local cultivars or landraces (see Glossary) [13]. The sanitary selection of healthy disease-free clones has also induced a reduction in clonal diversity for these major cultivars.

Thus, the diversity of grapes existing today has been shaped by human history. Several thousand cultivars exist but most of these are largely confined to germplasm collections.

From the wild grapevine to varieties
How did V. vinifera evolve from the wild to the cultivated form? As already demonstrated for many other plant species [20,21], molecular, genetic and genomic studies can help answer many questions about grape evolution and diversity. A better understanding of the exact status of the remaining wild grape populations and their relationships with existing varieties is important if we are to answer this question.

Does the wild grapevine still exist today?
Wild-growing grapevine individuals have been identified in France [22,23], Spain [24,25], Italy [26,27], Germany, Switzerland, Austria, Romania [28] and Tunisia [29], as well as many other European countries [25], but are they real silvestris individuals, that have never undergone cultivation, or ‘escaped’ individuals from vineyards or hybrids between wild and cultivated forms as described by Levadoux [9]? Genotype analysis could answer this.

Recent analyses focused on the use of microsatellite (SSR) and more recently on single nucleotide polymorphism (SNP) markers [22,23,25,28,30–32] have shown clear distinctions between wild and cultivated individuals. Only one report [31] showed a close affinity between wild samples and cultivars. These divergent results could be due to the differences in sample size and composition between the studies, or the uncertainty in classifying the wild growing individuals. Morphological traits of the plant and seeds are important for the characterization of true silvestris types (Figure 2). Approximately 250 putative silvestris individuals from France are currently being analyzed using 20 well-scattered microsatellite markers selected on a molecular map of V. vinifera [33]. This study should help establish whether true wild individuals with no genetic contribution from cultivated compartment still exist in France. Only when extensive molecular data from wild individuals and cultivars from different regions becomes available will we be able to draw a clearer picture about the existence of silvestris-type individuals in Europe. Analysis of wild grapes from eastern counties such as Turkey, Iran or Georgia, the presumed centre of primo-domestication, will be fundamental in this respect because it might help elucidate the diversity of the grapevine genetic pool used for domestication and identify the main events that enabled the morphological transformation from the wild form to cultivated vinifera.

The wild ancestors and current cultivars differ in several traits, for example, sugar content, flower sex, berry and bunch size. The analysis of allelic diversity for genes involved in these traits would be of great value for the analysis of wild individuals and the definition of their status. Furthermore, as demonstrated for maize [34], the comparison of the level of genetic diversity between the wild ancestor and the cultivated forms could enable the identification of regions of the genome that have undergone a strong selection during the domestication process, and thus identify genes controlling such traits.

Early domestication and propagation by seed
Sexual reproduction and planting of seeds seems to have had an important early role in the domestication and expansion of viticulture into new regions. Seeds are believed to have been the preferred way of long-range transportation of cultivars as suggested by archaeological remains [35]. More direct evidence can now be obtained by DNA analysis and the identification of parentages [36,37]. These parentage studies demonstrate the importance of sexual crosses in the past for the generation of new phenotypes and the adoption and spread, by vegetative propagation (cuttings), of specific genotypes with desirable characters. The Pinot and Gouais varieties of grape were successful in creating progeny [36] that were maintained by viticulturalists of the period and many of these progeny are cultivated in the north east of France and are well-adapted to this environment. However, only one example of a direct relationship between a wild and cultivated individual has been published [31], suggesting the absence of gene flow between wild and cultivated compartments. The flowering times of wild individuals is different from the flowering times of the cultivated forms (Lacome et al., personal communication), reducing the possibility of gene flow through pollen. Characterization of seeds obtained through open-pollination of wild female plants is underway [Di Vecchi et al., unpublished] and will give direct evidence of pollen flux between compartments in areas where they co-exist.

Was there a single domestication event or many domestication events?
Although many studies of genetic diversity have already been published [37], few studies examine a large geographical area that would provide evidence for the existence of diverse domestication pools or a single major domestication event followed by selection of diverse genotypes. An appreciable level of genetic differentiation between table and wine cultivars has been detected using microsatellite markers [31], with Muscat types also somewhat distinct. These differences could be due to divergent selection for berry size and the use of the oriental gene pool for the development of large berry and large cluster table cultivars, and divergent selection for the Muscat flavour for Muscat types [38]. Differences have also been detected between European wine cultivars of those from different regions [39], and the possibility of two independent
domestication events (one in the Near East, one in Western Europe) was shown more recently using chloroplast microsatellite markers [25]. However, this finding was contradicted by Aradhya et al. [31], who found most divergence within groups of cultivars and narrow differentiation between different groups, concluding that there might have been a single complex gene pool with current varieties arising by strong artificial selection. Two limitations however influence this type of analysis. First, a strong geographical structure would imply limited exchange of genetic material between regions and is most unlikely for grapevine, where spread of genetic material between regions has acted to homogenize the pools over time. Chardonnay, often referred to as a French cultivar, is a good example, being the result of a cross between Pinot and Gouais (also called Heunisch weiss) of Croatian origin [36]. Second, because of this exchange of material between regions, the geographical origin of cultivars is not easy to establish. If a French origin of Cabernet Sauvignon is recognized (which is strongly supported by the parentage of this cultivar [40]), the origin of other cultivars is less certain and will probably continue to evolve with new data. Syrah was thought to be of eastern origin [38], but its parentage determined by DNA profiling is now thought to be French [41]. Therefore, deeper sampling from different geographical regions is needed, with concise, accurate information on the geographical and genetic origins of the genotypes and the study of haplotypes rather than genotypes.

It must also be recognized that the origin of many cultivars might not be resolved because of the extinction of the parent. Pinot noir, for example, is sometimes referred to as ‘archaic’ and could have been present in the 1st century, with the Pinot name first recorded in the 14th century [9]. To date, no ancestors have been discovered for this cultivar despite its importance. Does this suggest that Pinot is not too far genetically removed from a wild grapevine or that in the distant past there was a genetic bottleneck with only a few ancient varieties surviving? The numerous progeny of Pinot and Gouais identified (> 275 cultivars [42] M. DiVecchi et al., unpublished) is a strong indication that there was a historical genetic bottleneck in some regions, possibly owing to cultivation practices and/or ownership of the vineyards.

**How old are modern grape varieties?**

Speculation about the historical origins of current cultivars is common in popular consumer wine publications; but is there any evidence that some cultivars that were created during antiquity or the middle ages still exist today as a result of vegetative propagation?

The analysis of ancient plant DNA has made important advances in recent years [43]. DNA of grape seeds between 2600 and 1700 years of age have been successfully analyzed using a few microsatellite markers [44], and this opens the way for analysis of archaeological grape samples. Because seeds could be the result of crosses, analyses on ancient wood remains would be needed to characterize the identity of these old cultivars and compare their DNA profile with those from modern cultivars. Nevertheless, a combination of historical and molecular data can still be useful. For example, the Mission cultivar is grown in many South American countries and was probably introduced into South America by the Spanish missionaries as seeds [19]. The analysis of its DNA and that of many South American cultivars revealed that many of the latter were synonyms and siblings of the Mission variety (Table 2). It is therefore tempting to suggest that the Mission cultivar introduced into South America in

### Table 2. Microsatellite analysis of the Mission cultivar and its relationship with other cultivars from South America and Spain

<table>
<thead>
<tr>
<th>Cultivar name</th>
<th>Origin and use</th>
<th>Use and colour</th>
<th>LOD</th>
<th>Relationship to mission</th>
<th>Parent 1</th>
<th>Parent 2</th>
<th>LOD²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mission</td>
<td>Mexico, California, W, n</td>
<td></td>
<td></td>
<td>Progeny or sibling</td>
<td>Mission</td>
<td>Mission</td>
<td></td>
</tr>
<tr>
<td>Pais</td>
<td>Chile, W, n</td>
<td></td>
<td></td>
<td></td>
<td>Mission</td>
<td>Muscat d’Alexandrie B</td>
<td></td>
</tr>
<tr>
<td>Rosa del Peru</td>
<td>Peru, W, n</td>
<td></td>
<td></td>
<td></td>
<td>Mission</td>
<td>Muscat d’Alexandrie B</td>
<td></td>
</tr>
<tr>
<td>Negra corriente</td>
<td>Peru, W, n</td>
<td></td>
<td></td>
<td></td>
<td>Mission</td>
<td>Muscat d’Alexandrie B</td>
<td></td>
</tr>
<tr>
<td>Criolla chica</td>
<td>Argentina, W, n</td>
<td></td>
<td></td>
<td></td>
<td>Mission</td>
<td>Muscat d’Alexandrie B</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Cultivar name</th>
<th>Origin</th>
<th>Use and colour</th>
<th>LOD</th>
<th>Relationship to mission</th>
<th>Parent 1</th>
<th>Parent 2</th>
<th>LOD²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Perruno</td>
<td>Spain</td>
<td>W, b</td>
<td>32.8</td>
<td>Progeny</td>
<td>Mission</td>
<td>Muscat d’Alexandrie B</td>
<td>63.15</td>
</tr>
<tr>
<td>Torrontes sanjuanino</td>
<td>Argentina, Peru</td>
<td>T, W, b</td>
<td>33.54</td>
<td>Progeny</td>
<td>Mission</td>
<td>Mission</td>
<td></td>
</tr>
<tr>
<td>Quebranta</td>
<td>Peru</td>
<td>T, n</td>
<td>32.02</td>
<td>Progeny</td>
<td>Mission</td>
<td>Negra mole N (Spain)</td>
<td>58.67</td>
</tr>
<tr>
<td>Torrontes riojano</td>
<td>Argentina</td>
<td>T, b</td>
<td>31.99</td>
<td>Progeny</td>
<td>Mission</td>
<td>Muscat d’Alexandrie B</td>
<td>67.08</td>
</tr>
<tr>
<td>Jaen negro</td>
<td>Spain</td>
<td>W, n</td>
<td>30.16</td>
<td>Progeny</td>
<td>Mission</td>
<td>Jaen B (Spain)</td>
<td>61.46</td>
</tr>
<tr>
<td>Criolla San Juanina</td>
<td>Argentina</td>
<td>T, W, n</td>
<td>29.49</td>
<td>Progeny</td>
<td>Mission</td>
<td>Muscat d’Alexandrie B</td>
<td>69.03</td>
</tr>
<tr>
<td>Cereza</td>
<td>Argentina, Uruguay</td>
<td>T, W, n</td>
<td>27.7</td>
<td>Progeny</td>
<td>Mission</td>
<td>Muscat d’Alexandrie B</td>
<td>69.12</td>
</tr>
</tbody>
</table>

*Abbreviations: LOD, log of the odds (lod score); T, table; W, wine; b, white; n, black; B, black.

*LOD score of single parentage with Mission.

*LOD score for parent couples.

*Perruno and Mission share at least one allele at each locus.

www.sciencedirect.com
the 16th century was vegetatively propagated and transported by cuttings to different American countries where it was renamed according to locality. Similarly, in Europe, Chardonnay can be traced back to the middle ages where it was renamed according to locality. Similarly, in the 16th century was vegetatively propagated and moved viticulture from one region to another, has been performed for many centuries.

Despite the importance of vegetative propagation in maintaining cultivars in an almost identical state, recent reports of genetic characterization of existing cultivars have shown that mutations are frequent in grapevines and have had a role in generating genetic diversity.

The role of mutations

Both sexual crossing and natural mutations have been the drivers during grapevine evolution. One of the most important traits in the domestication of grapevine, the appearance of hermaphrodite flowers, seems to be the result of a mutation [45]. It is not known when this form was first selected and used by humans but because it removed the need to maintain both male and female plants the adoption would have been rapid.

Because much of grapevine propagation is performed through cuttings, mutations can accumulate over time and lead to morphological and agronomical differences, and thus the creation of new cultivars.

Many examples of transposon and retrotransposon-based mutations have been published in plants; grapes are no exception and several elements have been identified to date [46,47]. Recently, the insertion of a gypsy-type retroelement (Gret1) in the promoter region of a regulatory gene of the Myb family has been shown to cause the loss of black berry skin colour in homozygous individuals [48]. The original wild grapes are believed to have had black berries [12] and plants with white berries were probably selected and maintained during the domestication process.

The degree of SNP polymorphism is not well known in grapevines. It has recently been reported as being extensive in genes (a mean frequency of one SNP every 78 bp between species and every 119 bp in V. vinifera [49]) but more accurate data for many regions of the genome are needed. It has been shown that a single nucleotide mutation in the VvGAI gene in grapevine not only has an effect on the number of leaf hairs but also reduces the stature of the plant and promotes flowering [50]. The original mutant plant, Pinot Meunier, was a chimera that had a hairy leaf phenotype, with the other phenotypes appearing only after regeneration of plants from the separate cell layers (L1 and L2) [51].

Stable chimeric plants result from somatic mutations if the mutation occurs in a cell of the shoot apical meristem and the mutated cells dominate one cell layer over a period of time. This has previously been discussed in relation to genetic improvement, where depending on which cell layer the mutation occurs, the mutation might be passed onto the next generation [51]. The occurrence of this phenomenon and the maintenance of mutations are due, in a large part, to the age of many grapevine cultivars that have accumulated mutations over time and to the annual pruning of shoots and extensive vegetative propagation that assists in separating mutant cells from wild-type cells. Natural mutants that have leaf, flower or berry changes have been selected in this way (Figures 1b,c). The Pinot family has been particularly well analyzed for vegetative, floral and berry mutants. Pinot noir is the original variety with a black berry, Pinot gris is the grey berry form, thought to be a chimera with a mutation for berry colour in one cell layer, and Pinot blanc is the white berry form, thought to have the mutation in both cell layers (Figure 1b).

Sometimes, independent mutations can lead to identical phenotypes, as suggested for the seedless phenotypes in Sultanina (Sultana, Thompson Seedless), Emperor Seedless and Chasselas apyrène [52]. Humans have selected this mutant seedless phenotype for table grape.

It is now known that non-visual mutations are also present and maintained in grapevine cultivars. Mutations in microsatellite markers have been described and the implications of this for cultivar identity and ancestry determination have been discussed elsewhere [51]. Many of these microsatellite mutations have been shown to exist in a chimeric state with only one cell layer having the mutation [51,53,54].

V. vinifera germplasm and genetic diversity

Molecular evidence shows that both sexual and asexual multiplication and mutations have had a major role in the expansion and diversification of grapevine. The number of different varieties held in germplasm collections around the world is estimated at ~10 000 [7]. Nearly every wine-growing country has its own grapevine germplasm collection, owing to quarantine restrictions and the need to maintain the material in the field as living plants. As already mentioned for Mission cultivar, many names for the same material (synonyms) exist, but because of some peculiar features of the varieties or of the regions where they were grown, a convergence of names for different cultivars (homonyms) has also occurred (Table 3). Microsatellite markers in the early 1990s were first shown to be useful for determining cultivar identity and parentage, and for identifying mistakes [55,56]. Many microsatellite marker studies have since been published identifying synonyms and homonyms that were either previously suspected by ampelography studies or unknown [37,64]. The identification of these ‘onyms’ will also help to determine the true extent of genetic diversity. Based on DNA profiling results, we can speculate that a more accurate estimate of variety numbers might be closer to 5000 varieties with many of them being closely related.

Characterization of diverse germplasm collections using microsatellite markers have been achieved [31,39,57,58] but the cross correlation between all these studies remains to be performed. A coding strategy has been proposed to compare the data between laboratories easily [59]. Reference data for six microsatellite markers and a set of internationally recognized cultivars and rootstocks are now available at http://www.montpellier.inra.fr/vassal.

Additional reference information and tools for the
Table 3. Examples of synonyms, homonyms and mutant forms of popular cultivars

<table>
<thead>
<tr>
<th>Official French name</th>
<th>Main synonyms (country)</th>
<th>Secondary synonyms</th>
<th>Known mutations</th>
<th>Homonyms</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cabernet Sauvignon</td>
<td>-</td>
<td>Bidure, Petite Bidure, Bouchet (FRA); Petit Cabernet (MAR)</td>
<td>Bronze berry form; White berry form</td>
<td>Cabernet franc (FRA)</td>
</tr>
<tr>
<td>Syrah</td>
<td>Shiraz, Hermitage (AUS)</td>
<td>Serine</td>
<td>-</td>
<td>Petit Syrah Durif (USA)</td>
</tr>
<tr>
<td>Sultanine</td>
<td>Sultan (AUS, ZAF)</td>
<td>Serine</td>
<td>-</td>
<td>Sultanine rose Gora Chirine</td>
</tr>
<tr>
<td>Grenache</td>
<td>Garnacha tinta (ESP, Mc); Tokay rosso, Cannonau (ITA); Alicante (ESP)</td>
<td>Serine</td>
<td>-</td>
<td>Garnacha tintorera; Alicante Bouschet (ESP)</td>
</tr>
<tr>
<td>Pinot noir</td>
<td>Blauer Spatburgunder (Mc); Burgundske Modre (CEZ)</td>
<td>Serine</td>
<td>-</td>
<td>Pineau de la Loire (USA); Chenin</td>
</tr>
</tbody>
</table>

*aAbbreviations: AUS, Australia; CEZ, Czech Republic; ESP, Spain; FRA, France; ITA, Italy; JPN, Japan; MAR, Morocco; Mc, Many countries; PRT, Portugal; USA, United States of America; ZAF, South Africa.

The mutation induces a change in the characteristics of the berry and wine and the mutants are often identified as different cultivars.

Concluding remarks

Further research is required to determine accurately the extent and origin of existing genetic diversity, which is mostly confined to germplasm collections. A real possibility exists that some of these germplasm collections will be reduced in size, owing to dwindling resources, and many unique genotypes might be lost. Extensive DNA profiling of the grape varieties found in collections and the development of a common database would seem to be a priority to determine the true number of varieties and the relationships, genetic diversity and identification of unique individuals in these collections. Such data would also assist in historical studies investigating domestication events. Wild grapevines are still poorly characterized. More extensive and combined analyses of wild individuals from a broad geographical area are crucial for understanding the role of V. vinifera silvestris in the domestication process. Until now, most DNA profiling studies in grapevine have been performed using neutral markers (such as non-coding microsatellite markers) but the availability of numerous grapevine ESTs and the increasing characterization of genes should encourage the analysis of allelic diversity in genes involved in the genetic control of important traits. This would not only help us understand the biology of the grape but would have direct application for crop improvement.

Acknowledgements

This work was supported in part by CSIRO Plant Industry, the Commonwealth Cooperative Research Centre Program, specifically the Cooperative Research Centre for Viticulture (CRCV) and the Grape and Wine Research and Development Cooperation (GWRDC), INRA and the French Ministry of Research and Agriculture. We thank J.P. Bruno for assistance with Figure 2.

References

5 de Saporta, G. (1879) *Le monde des plantes avant l'apparition de l'homme.* Masson
519


Five things you might not know about Elsevier

1. Elsevier is a founder member of the WHO’s HINARI and AGORA initiatives, which enable the world’s poorest countries to gain free access to scientific literature. More than 1000 journals, including the Trends and Current Opinion collections and Drug Discovery Today, are now available free of charge or at significantly reduced prices.

2. The online archive of Elsevier’s premier Cell Press journal collection became freely available in January 2005. Free access to the recent archive, including Cell, Neuron, Immunity and Current Biology, is available on ScienceDirect and the Cell Press journal sites 12 months after articles are first published.

3. Have you contributed to an Elsevier journal, book or series? Did you know that all our authors are entitled to a 30% discount on books and stand-alone CDs when ordered directly from us? For more information, call our sales offices:

   +1 800 782 4927 (USA) or +1 800 460 3110 (Canada, South and Central America)
   or +44 (0)1865 474 010 (all other countries)

4. Elsevier has a long tradition of liberal copyright policies and for many years has permitted both the posting of preprints on public servers and the posting of final articles on internal servers. Now, Elsevier has extended its author posting policy to allow authors to post the final text version of their articles free of charge on their personal websites and institutional repositories or websites.

5. The Elsevier Foundation is a knowledge-centered foundation that makes grants and contributions throughout the world. A reflection of our culturally rich global organization, the Foundation has, for example, funded the setting up of a video library to educate for children in Philadelphia, provided storybooks to children in Cape Town, sponsored the creation of the Stanley L. Robbins Visiting Professorship at Brigham and Women’s Hospital, and given funding to the 3rd International Conference on Children’s Health and the Environment.

Endeavour

Coming soon in the quarterly magazine for the history and philosophy of science:

Disputed discovery: vivisection and experiment in the 19th century by C. Berkowitz
Engineering fame: Isambard Kingdom Brunel by P. Fara
‘But man can do his duty’: Charles Darwin’s Christian belief by J. van der Heide

Endeavour is available on ScienceDirect, www.sciencedirect.com