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CHAPTER 15

Exploiting *Vitis* genetic diversity to manage with stress

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Abstract

The genus *Vitis* contains more than 60 species with *Vitis vinifera* as the most renowned domesticated one. More than 5000 *V. vinifera* cultivars are available. These, together with fertile interspecific hybrids obtained by crossing, provide a reservoir for genotypes performing better under environmental stress. Aiming the management of the grapevine germplasm to cope with stress, *Vitis* species with special emphasis on *V. vinifera* cultivars are being characterized for the performance under the main environmental challenges, namely abiotic stress by extreme temperature, light and UV radiation, drought, salinity and nutritional deficits. Due to concerns on the environmental impact of fungicides and fertilizers, on the problem of water scarcity, as well as on the impact of climate change on grape production, characterizing and exploiting grapevine genetic resources is essential for a sustainable viticulture. Breeding strategies and tolerance genetic source possibilities to face with abiotic stress in viticulture are presented and discussed.

Keywords: abiotic stress, breeding strategies, climate change, clonal selection, genetic diversity, germplasm, stress tolerance, somatic variation, sustainable viticulture, *Vitis* species, *Vitis vinifera* cultivars

Grapevine in a Changing Environment: A Molecular and Ecophysiological Perspective, First Edition. Edited by Hernâni Gerós, Maria Manuela Chaves, Hipólito Medrano Gil and Serge Delrot.
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List of abbreviations

ABA	Abscisic acid
Ctr	Copper transporter
DOP	Protected designation of origin
DREB	Dehydration responsive element binding
IAC 766	Agronomic Institute of Campinas 766
QTL	Quantitative trait locus
SNP	Single nucleotide polymorphism
SO4	Selection Oppenheim 4
USVIT 7-8	University of Stellenbosch Viticulture 7-8
UV	Ultraviolet
VvCBF4	*Vitis vinifera* C-repeat binding factor 4
VvMYBA	*Vitis vinifera* Myeloblastosis oncogene A transcription factor

15.1 Introduction

Nowadays the conservation of grapevine genetic diversity is a huge concern. The genus *Vitis* contains more than 60 species that can be divided into distinct geographical groups. The most renowned species is *Vitis vinifera*, domesticated more than 7000 years ago somewhere in Transcaucasia, where it spread to other regions. The high morphological and genetic diversity of *V. vinifera* and the ease with which it is asexually propagated gave rise to an estimated number of more than 5000 cultivars. Currently, scientists and breeders are working together at an international level to generate knowledge about the valuable diversity of grapevine, its patterns, processes, adaptations to the environment and correlations among traits such as stress tolerance and grape quality. Taking advantage of the grapevine reference genome and current resequencing projects, a large number of SNPs and other polymorphisms have already been identified in *V. vinifera* varieties, which will be valuable for the assessment of the genotype–phenotype relationship when combined with phenotypic data in genetic analyses approaches. These tools will help to optimize the search and selection of genotypes joining stress tolerance together with grape quality features.

15.2 Grapevine diversity

The genus *Vitis* is the only genus of the *Vitaceae* family that produces edible fruits (Bouquet, 2011). Paleontological remains suggest that the genus *Vitis* first appeared in the tertiary age, more than 55 million years ago (Tiffney and Barghoorn, 1976). Nowadays almost 60 species are considered within this genus (Galet, 1988), which are naturally distributed in three major areas: (1) Eurasia, which includes southern Europe, Asia Minor and the Caucasus up to Afghanistan, (2) Far East, including East China, Korea and Japan, and (3) America, where it extends from the east of Canada to the United States and from Central America to the Equator. The vast extent of these areas cannot make us forget that the current diversity is decreasing, at least in the peripheral regions. The causes of this phenomenon called 'genetic erosion' are multiple, but are mostly related to the impact of human activity on nature, namely the advent of new arable areas.

The genus *Vitis* is divided into two subgenus or sections based on anatomical and caryological differences: *Muscadinia*, represented by three species that are under discussion (Comeaux et al., 1987) and *Vitis*, which contains 56 species (Galet, 1988). However, the number of species in this section could even be lower based on recent botanical classifications (Comeaux et al., 1987). The *Vitis* section is thought to have diversified after the Quaternary ice ages (Viala and Vermorel, 1910) in the absence of genetic barriers (Levadoux et al., 1962). Thus, in spite of their high morphological diversity, all species remain interfertile, which facilitates the use of their genetic diversity in the genetic improvement of *V. vinifera* cultivars and rootstocks.

Apart from *V. vinifera*, domesticated in Eurasia (see below), several species in the two sections, such as *V. labrusca and V. rotundifolia*, were domesticated in North America during the eighteenth century (Olien, 1990) or used to provide special traits to grapevine cultivars. In this way, species such as *V. labrusca* and *V. aestivalis*, which are resistant to diseases affecting *V. vinifera* in North America, were used in crosses to *V. vinifera* to generate well-known American cultivars such as Concord (Tukey, 1966) and Norton (Reisch et al., 1993). Other species such as *V. riparia*, *V. rupestris* and *V. berlandieri* were used in rootstock breeding mostly to generate Phylloxera resistance in Europe at the end of the nineteenth century (Pouget, 1990). The use of *V. rotundifolia* has been more restricted, given the presence of genetic barriers between the *Vitis* and *Muscadinia* sections impairing natural hybridization (Bouquet et al., 2000).

From the point of view of tolerance to abiotic stresses, many species in the *Vitis* section have shown tolerance traits useful in rootstock breeding that could also be relevant to improve tolerance in newly bred cultivars of *V. vinifera*. Among abiotic stress tolerance it is important to mention: (i) the tolerance to cold stress of *V. amurensis* and possibly *V. labrusca* and *V. aestivalis*; (ii) the drought tolerance observed in several North American species like *V. californica*, *V. champinii*, *V. doaniana*, *V. longii*, *V. girdiana* and *V. arizonica*, (Padgett-Johnson et al., 2003) and the Chinese species *V. yeshanesis* (Yuejin et al., 2004); (iii) the salinity stress tolerance observed in rootstocks derived from *V. rupestris* and *V. riparia* showing a chloride excluder phenotype; (iv) the tolerance to calcareous soils shown by *V. berlandieri*, *V. cinerea*, *V. champinii* and *V. californica* (Bavaresco, 1994; Bavaresco et al., 1995); (v) the tolerance to low pH soils of *V. labrusca* as well as rootstocks derived from *V. berlandieri* × *V. rupestris* (Conradie, 1983; Himelrick, 1991); (vi) the tolerance to aluminium toxicity identified among rootstock genotypes from *V. berlandieri*, *V. riparia* and *V. rupestris* (Cançado et al., 2009).

V. vinifera is the only species naturally found in the Eurasian area, and two subspecies *V. vinifera* subsp. *vinifera* and *V. vinifera* subsp. *sylvestris* are considered to distinguish domesticated from wild forms. Up to the nineteenth century the wild subspecies *V. vinifera* subsp. *sylvestris* was widely distributed along the Eurasian region. In 1857 Bronner (cited in Alleweldt, 1983) reported 'thousands of wild vines vegetate in the forests along the banks of the Rhine'. Unfortunately, one hundred years later, in-depth studies conducted by Schumann (1968) (cited in Alleweldt, 1983) showed that, in this region, there were only a few examples that survived the intensive exploitation of forests, the import of new pests and pathogens (see below) and other actions taken by mankind. Very small populations of wild vines can still be found in some areas of riparian woods and riverside areas in Central and Southern Europe, North Africa, Middle East and other Asian regions located between the Black Sea and the Hindu Kush (Ocete Rubio et al., 1999). These wild populations still maintain some genetic diversity that could be relevant in terms of environmental adaptation of cultivars to specific geographical areas, although it is rapidly being reduced due to the decrease of genetic flow among different populations, the hybridization with plants in commercial vineyards and increased rates of inbreeding (De Andres et al., 2012).

Domestication of *V. vinifera* likely began more than 7000 years ago in Transcaucasia, currently involving countries such as Georgia, Armenia, Azerbaijan, Turkey and Iran. This is the area where there is greatest genetic diversity for the species and where the oldest wine production archaeological remains have been found, including grape seeds and artefacts, which show a very ancient 'wine culture' (McGovern, 2003). From these *primo* domestication locations wine culture and grapevine production expanded to the nearby Taurus or Zagros Mountains, later to Southern regions and eventually to the west, along the Mediterranean Sea. Vine vegetative propagation enabled their dissemination to other regions and the expansion of viticulture during the Chalcolithic and Early Bronze ages in the Middle East (Zohary and Hopf, 1994). Available archaeological data indicate that Phoenicians and Greeks introduced vines in various areas of the Western Mediterranean (Van Zeist, 1980), reaching the Iberian Peninsula (Hidalgo, 1990). However, paleobotanical identification of seeds and pollen in the Iberian Peninsula suggests the use of grapes by native populations before the Greek and Phoenician colonization. Moreover, excavations at a Neolithic village near Paris showed the use of *V. vinifera* subsp. *sylvestris* 44 000 years BC (Sefc et al., 2003) suggesting the possibility of several independent domestication events.

The existence of large morphological diversity among Eurasian grapevine cultivars led Negrul (1938, cited in Levadoux, 1956) to distinguish three morphological groups: *Proles orientalis*, cultivated in the South Caspian Sea and the Middle East, showing large bunches and berries (generally used as table grapes), *Proles occidentalis*, cultivated in Western Mediterranean regions and characterized by compact bunches and small grapes (generally used as wine grapes), and *Proles pontica*, cultivated around the Black Sea basin and showing intermediate characteristics between the two previous *Proles* (Negrul, 1938, cited in Levadoux, 1956). This morphological diversification could suggest the existence of genetic contributions from local populations of *V. vinifera* subsp. *sylvestris* to every regional cultivar genetic pools, as well as different selective pressures. In fact, the study of nucleotide diversity at the chloroplast and nuclear genomes support the genetic contribution of Western *V. vinifera* subsp. *sylvestris* populations to local grapevine cultivars in Western Eurasia (Arroyo-Garcia et al., 2006; Cunha, 2009; Myles et al., 2011). This complex history of domestication and dissemination of grapevine genotypes along the Mediterranean area, the natural hybridization among cultivars and between them and wild plants, and the accumulation of somatic genetic variations are responsible for the current morphological and genetic diversity detected in grapevine. Over those positive factors it is worthwhile to mention factors that have reduced genetic diversity, including the bottlenecks generated by the impact of pests and diseases introduced from North America throughout the nineteenth century, like powdery mildew (*Erysiphe necator*) introduced in 1845, phylloxera (*Daktulosphaira vitifoliae*) in 1863 and downy mildew (*Plasmopara viticola*) in 1878 (Töpfer et al., 2011). Those pathogens and pests also contributed to drastically reduce the genetic diversity of natural populations of *V. vinifera* subsp. *sylvestris*.

Currently, viticulture covers circa eight million hectares and in 2011 more than 67 million tons of berries were produced worldwide (http://www.fao.org). Nevertheless, most wine producing countries have chosen a small number of varieties to cover the largest proportion of their vineyard area, leading to the marginal cultivation or even the extinction of a vast number of traditional and local varieties. This situation is dangerously shrinking the genetic pool and increasing the crop vulnerability to challenges such as climate changes and new pests and diseases. Fortunately, there are large grapevine genetic collections trying to keep as many as possible of those neglected genotypes, and the current worldwide interest for high-quality diverse and traditional wines is reviving the interest in using traditional cultivars to create products of excellence in a sustainable agriculture.

15.3 Grapevine responses and adaptation to stressful conditions

Some of the previous chapters of this book have already dealt with adaptations to stressful conditions. Most varieties are well adjusted to a multiplicity of climates, tastes and uses that range from table grapes, dried grapes (raisins), grapes processed into non-alcoholic juice, wines and distilled alcohols. Nonetheless, the present scenario of global climate change, together with the increasing worldwide demand for high-quality wines and the need of a sustainable agriculture, make it essential to understand the adaptive power underlying the grapevine genetic diversity and the environmental limitations of the most popular varieties. It is relevant to characterize the performance of diverse *Vitis* species in general and *V. vinifera* cultivars in their response to the main environmental challenges. This step is essential for a proper management of the grapevine germplasm to cope with stress.

15.3.1 Temperature stress

Temperature is a major factor influencing most grapevine developmental and physiological processes. Therefore temperature is widely considered a foremost influencing factor of grapevine production and quality and worldwide wine production is severely limited by temperature stresses (Web et al., 2011). See also Chapters 7, 10 and 11, which focus on grapevine response to low and high temperatures.

High temperatures

Heat accumulation is essential for a normal reproductive development and fruit ripening. Nevertheless, excessive heat has negative consequences on grapevine performance for viticulture. At first, high temperatures impact on grapevine physiology and growth. In many wine producing regions, midday air temperature can surpass 40 °C in the summer, which can impair vine growth (Liu et al., 2012).

Leaves of the varieties Razegui and Muscat Italia grown under high temperatures had a folded cuticle and cell wall on the adaxial epidermis layer, with greater cell wall thicknesses than plants grown under moderate temperatures. Chloroplasts were more globular under heat stress, with disorganized thylakoids and reduced thickness of grana stacking. These characteristics lead to reduced carbon metabolism and an early onset of senescence in heat-stressed plants (Ben Salem-Fnayou et al., 2011).

The most critical effect of high temperatures in viticulture is related to alteration of berry ripening and composition, restricting the optimal areas for wine grapes production, whose requirements are stricter than for table grapes, raisins or juice production. Together with the activation of thermotolerant responses, characteristic high-temperature effects on berry composition include the reduction of anthocyanins content, a hastened total acidity and malate content fall, and a concentration of sugars (Mira de Orduña, 2010; Carbonell-Bejerano et al., 2013). In fact, heat increase in the last decades is already hastening grapevine phenology in diverse winemaking areas and, consequently, berry ripening takes place now in a warmer season, intensifying this problem (Mira de Orduña, 2010). In general, grape berries from mild climate regions have higher acidity and high temperatures are reported as decreasing the concentration of berry organic acids (Dai et al., 2011). Tartaric and malic acids are the main organic acids present in grape berries (Conde et al., 2007) and although a high genotypic variation is reported, berries of table grapes have a lower organic acid concentration than those of wine grapes (Liu et al., 2006). Independently of temperature conditions, *V. vinifera* cultivars and *Vitis* hybrids can present a huge range of characteristic concentrations of tartrate in ripe berries, ranging from single to more than fivefold. Diversity in malate levels is even higher, ranging from single to almost twentyfold (Liu et al., 2006).

Sugar concentration at maturity is one of the most important traits in grapevine berries. Moreover, in wine making cultivars sugar concentration defines the wine alcohol degree and is reported as temperature dependent. Taken at equivalent ripening degree, grapevine genotypes present a high variability in sugar concentration, in the glucose to fructose ratio and in the presence/absence of sucrose (Liu et al., 2006). However, genotypic variability in response to temperature is lower for sugar concentration than that reported for organic acids content (Dai et al., 2011) except for very high post-veraison temperatures, which can inhibit photosynthetic carbon fixation and then impair berry sugar loading (Costa et al., 2012).

Most studies reporting the effect of temperature on grape berry phenolic compounds focus on the flavonoid anthocyanins class due to its paramount contribution to wine characteristics and quality. Anthocyanins can range from high concentrations in red and black berries cultivars to absent in white cultivars, a variation due to polymorphisms in the colour locus, where several VvMybA transcription factor genes are located (Kobayashi et al., 2004; Mitani et al., 2009). Cabernet Sauvignon, Merlot, Syrah and Monastrell are *V. vinifera* varieties reported as responding to high environmental temperature by lowering anthocyanins concentration. This decrease is explained by an inhibition of anthocyanin synthesis (Ortega-Regules et al., 2006) but the hypothesis that high temperatures could increase anthocyanin degradation was proved in Cabernet Sauvignon through an elegant *ex planta* experimental setup using ^{13}C-phenylalanine (Mori et al., 2007). So far no further reports on anthocyanins degradation after high temperatures are available – neither for *in planta* analysis nor for other grapevine genotypes. Warming temperatures apparently can decouple the ratio between anthocyanins and sugar in berries of Syrah (syn. Shiraz) and Cabernet Franc (Sadras and Moran, 2012), with consequences for wine making by altering the anthocyanin:alcohol ratio. The effects of high temperatures on the anthocyanins:sugar ratio are also reported for mature Merlot (Spayd et al., 2002) and Aqui Queen (*V. labrusca* × *V. vinifera*) (Yamane et al., 2006) grapes. In field conditions the effect of high temperature and solar radiation are mostly exerted concomitantly. However, at least when anthocyanins concentration is considered, a separate effect could be assigned in Merlot grapevine, berry skin temperature being more directly related with anthocyanins content than radiation (Spayd et al., 2002; Ortega-Regules et al., 2006).

Cold

Due to the high economic value of grapevine and the demand for its products, there have been attempts to cultivate grapevine in areas far from its original growing region, and with different climates. As reported in Chapter 11, one of the main limiting environmental conditions for grapevine growth is low temperature. However, when cooled gradually, *V. vinifera* cultivars can tolerate sustained winter temperatures as low as –15 °C without injury, whereas wild North American and Asian species can tolerate exotherms of –35 to –40 °C (Fennell, 2004). When the acclimation process is not enough, serious injury to buds and roots can occur, even in tolerant species, leading to partial or complete loss of production the following year. Furthermore, early spring frosts can injure floral primordia and decrease yields (Fennell, 2004).

15.3.2 H UV radiation

As part of the predicted changes in the climate of European viticulture regions, changes in solar radiation, namely increases in the levels of UV-B, are expected to have an impact on grapevine production (Schultz, 2000; see also Chapters 7 and 10 in this book).

Exposure to UV-B amounts higher than those usually found in nature is likely to lead to tissue necrosis and to induce the expression of stress response genes. Several studies have reported damage to DNA, proteins and membranes and the inhibition of protein synthesis and photosynthetic reactions (Jansen et al., 1998). Photosynthetic activity of leaves of Tempranillo is also impaired by short-term exposure to high UV-B, which is probably related to stomatal factors. Long-time exposure to high UV-B will ultimately lead to acclimation through the accumulation of UV-B-absorbing compounds (Martinez-Luscher et al., 2013). Transcriptomic responses to UV-B in Malbec leaves evidenced the activation of UV-absorbing and antioxidant compounds biosynthesis together with other defence systems (Pontin et al., 2010).

ABA is involved in the UV-B tolerance of grape leaves, acting downstream in the signalling pathway, enhancing the ability of epidermal tissues to filter out UV-B. ABA leads to the increase of antioxidant enzymes and the sterol-structural defence in the variety Malbec (Berli et al., 2010). This response is dependent on the presence of high levels of UV-B irradiation.

In the southern hemisphere the levels of UV radiation are even higher than in the northern hemisphere. In New Zealand, Sauvignon Blanc berries exposed to ambient UV, UV-transmitting or UV-devoid radiation showed burn spots and changes in flavonoid accumulation, particularly under UV-transmitting conditions (Shinkle et al., 2010). It is worth noting that in Europe, the rise in ultraviolet UV-B radiation due to thinning of the stratospheric ozone layer may have a direct impact on berry secondary metabolites, namely anthocyanins (Schultz, 2000). In the red variety Malbec, UV-B caused an increase in berry anthocyanins and flavonols concentration, certainly related to the decrease in fresh weight observed in the same experimental conditions (Berli et al., 2011). Effects of UV on skin stilbenes and volatile compounds accumulation paralleling those on anthocyanins have also been described in Malbec grapes (Berli et al., 2008; Gil et al., 2013).

15.3.3 Drought

As discussed elsewhere in this book, particularly in Chapter 3, water scarcity is one of the major environmental limitations that viticulture will face in the near future, mostly in traditional viticulture areas. About two-thirds of the main viticulture regions of the world have low annual precipitation and are subjected to seasonal droughts that coincide with the grapevine growing season (e.g. Mediterranean climate areas) (Flexas et al., 2010). *V. vinifera* is considered as a drought-tolerant plant because it is able to recover from this stress and, indeed, moderate water stress during berry ripening is regarded as beneficial for the final quality of wines (Chaves et al., 2007; Grimplet et al., 2007; Lovisolo et al., 2010). Nevertheless, water stress decreases fruit yield by reducing the number of berries per cluster when vines are exposed to drought around flowering or fruit set or by decreased berry weight when exposed to post-veraison drought (Hardie and Considine, 1976; Matthews and Anderson, 1989; Ollé et al., 2011). Drought affects grape quality but also vegetative vigour, impairing the growth of lateral branches and thus posing a threat to plant production in coming years (Pellegrino et al., 2005). Leaf area was reduced by water deficit in Syrah and Grenache plants, mainly as a result of reduced shoot branching (Lebon et al., 2006).

Grapevine is well adapted to the Mediterranean climate and tends to exercise fairly tight control over stomatal aperture, being generally considered as a 'drought avoiding' plant species (Costa et al., 2012). There is a large variation in the behaviour of *V. vinifera* cultivars under water stress and, in spite of general drought tolerance, two differential drought responses are observed in grapevine and, accordingly, genotypes can be classified as isohydric or anisohydric (Chaves et al., 2010; Lovisolo et al., 2010). Cultivars defined as isohydric regulate stomatal conductance efficiently in response to water availability and are considered more water stress tolerant than anisohydric cultivars, which show a poor regulation of their hydraulic physiology (Schultz, 2003; Soar et al., 2006; Vandeleur et al., 2009). The classification as iso- or anisohydric is not simply a genotypic characteristic of a variety, because it can change with the water regime. Nevertheless, extensive attempts have been made at classification of varieties, and some consensus can be achieved for most (for a review see Chaves et al., 2010).

The genotypic influence on the strategies developed by each variety to avert drought stress is high. A comparative study between the cultivars Grenache and Chardonnay was undertaken to determine to what extent the cell-to-cell pathway and aquaporins affect changes to root hydraulic conductance in response to the time of day and water stress. In fact, these cultivars showed contrasting responses to water stress and rewatering (Vandeleur et al., 2009).

It is well documented that the variation of berry growth, sugar and phenolic content, as well as ABA concentration, is affected by abiotic stress conditions, including water stress (Matthews and Nuzzo, 2007; Deluc et al., 2011; Zarrouk et al., 2012). Berry growth is apparently less sensitive to water deficits than other shoot organs. Nevertheless, water deficits inhibit berry growth (Dai et al., 2011), mainly at the mesocarp level, so that the seed and skin mass account more significantly to berry weight (Greenspan et al., 1994; Roby and Matthews, 2004). It is commonly assumed that water deficits increase the concentrations of skin proanthocyanidins and anthocyanins in a cultivar-dependent pattern. In Cabernet Sauvignon (red-skinned cultivar) water deficit increased phenylpropanoid metabolism with an increment in anthocyanins accumulation and also in ABA, carotenoid, proline and sugar, while in the white variety Chardonnay, which does not produce anthocyanins in the berry skin, water stress did not alter significantly sugar, proline or ABA concentrations (Deluc et al., 2009; Cramer, 2010). Cabernet Sauvignon behaviour during the ripening phase was confirmed by Castellarin et al. (2007), where water deficit applied before veraison augmented sugar accumulation while the increase in anthocyanins content occurred when water stress was applied either before or post-veraison. A variety-dependent response was shown in the red cultivar Shiraz, to which water deficit applied at post-veraison gave rise to a reduction in berry yield, weight and sugar concentration and an increase in phenolic compounds content, except for anthocyanins (Petrie et al., 2004).

In field-grown Aragonez (syn. Tempranillo) under deficit irrigation in parallel with a non-irrigated regime, during two successive seasons the main compounds affected by water availability were proanthocyanidins and flavonols, which increased with irrigation. In both years, the concentrations of anthocyanins at full maturation were higher in the berries under irrigation regimes but no differences in sugar accumulation were observed between treatments (Zarrouk et al., 2012).

15.3.4 Salinity

V. vinifera is considered moderately sensitive to salt stress (see Chapters 12 and 14). Nonetheless, salinization of soil is a characteristic consequence of irrigation in arid environments, which can lead to reduced vine growth and fruit yield (Keller, 2010). Both ion exclusion ability of roots and rootstock-depending vigour appear important for salt stress tolerance (Walker et al., 2002, 2004). In fact, the root system must take up nutrient ions and water while keeping out the toxic Na^+ and Cl^- ions. As a whole, growth and fruit yield reduction by NaCl in grapevine mainly results from limitation of water transport together with Cl^- and Na^+ accumulation in aerial parts. In the present book (Chapter 12), the role of several metabolic rearrangements that grapevine recurs to in response to salt stress, from amino acid metabolic pathways to specific carbohydrates such as polyols and trehalose, is explored.

15.3.5 Copper toxicity

Grapevine genotypes are generally tolerant to heavy metals in soil (Gimmler et al., 1998; Yang et al., 2011). In that way, *V. vinifera* can adapt to copper exposure by the metal exclusion capacity of their roots, which, however, involves restriction of water transport, correlating with moderation in metabolic activity, net photosynthesis and growth and with the appearance of toxicity symptoms in grapevine cells (Romeu-Moreno and Mas, 1999; Toselli et al., 2009; Juang et al., 2012). Systematic accumulation of copper in the soil of vineyards resulting from the use of Cu-based fungicides has been reported and may become stressful for young vines (Wightwick et al., 2008; Komarek et al., 2010). As reported in Chapter 12, the sequestration of Cu in the vacuole of grape cells constitutes a mechanism for toxic avoidance and several transporters belonging to the Ctr family may account for its distribution within the cell (Martins et al., 2012, 2014a, 2014b, 2014c).

15.3.6 Nutritional deficit stress, iron and magnesium deficiency-induced chlorosis

Under insufficient supply of nutrient ions, cellular metabolism is disturbed and thus vine growth is slowed down. Despite iron being the fourth most abundant element on the Earth's crust, it is extremely insoluble in calcareous soils with high pH (Staiger, 2002), which are the most prevalent soils in many viticultural regions (Keller, 2010). Inhibition of iron uptake by bicarbonate is the cause of lime-induced chlorosis in grapevine (Nikolic et al., 2000). In vines, most Fe accumulates in molecules of the photosynthetic apparatus in chloroplasts and its deficiency, in addition to the typical intervein chlorosis symptoms, causes decreased photosynthesis, leaf size and fruit set, limiting vine growth and yield (Bavaresco et al., 2005a, 2005b; Bertamini and Nedunchezhian, 2005). In contrast to iron chlorosis susceptible genotypes like *V. riparia*, genotypes including *V. vinifera* and *V. berlandieri*, which have evolved in calcareous conditions, can acidify the external medium by excreting organic acids, which improves Fe solubilization and uptake (Brancadoro et al., 1995; Jiménez et al., 2006; Ksouri et al., 2007).

Magnesium is part of chlorophyll molecules and in addition participates as a co-factor in multiple enzymatic reactions and activating protein transporters. Its deficiency in grapevine also generates chlorosis symptoms together with declined growth and yield (Keller, 2010).

15.4 Breeding strategies to manage with stress

15.4.1 Breeding strategies in grapevine

Interest in grapevine breeding was initially triggered by the need to introduce resistance to the Phylloxera plague and the fungal pathogens that were devastating European viticulture in the last part of the nineteenth century (Bouquet, 2011).

However, the solutions provided by the use of Phylloxera-resistant rootstocks and sulfur and copper applications for fungal infections slowed down or completely stopped further breeding. One hundred years later, we are witnessing a renewed interest in grapevine breeding promoted by an increased concern on the environmental impact of fungicides, which could be reduced by the use of pathogen-resistant cultivars (Töpfer et al., 2011), as well as the evidence that a climate change is threatening grape production in classical viticulture areas (Duchene et al., 2012). Fortunately, this renewed interest in grapevine breeding is now supported by the availability of new sets of molecular tools and approaches deriving from the grapevine genome sequence (Jaillon et al., 2007; Velasco et al., 2007) and resequencing programmes (Myles et al., 2010; Da Silva et al., 2013; Venturini et al., 2013; Di Genova et al., 2014). These studies are not only identifying SNPs but also genomic reorganizations and genes that are not shared between all genotypes and could be related to phenotypic differences. Consequently, available molecular tools for genotyping and genotypic selection are growing exponentially (Lijavetzky et al., 2007; Myles et al., 2011; Wang et al., 2012). Thus, limitations for efficient breeding are being reduced to the intrinsic limitations of grapevine biology and time-consuming phenotypic selection.

Taking advantage of the high heterozygosity of grapevine genomes, grapevine breeding programmes are generally based on hybridization and phenotypic selection in F_1. Furthermore, the wide use of phylloxera-tolerant or resistant rootstocks provides the opportunity to perform independent rootstock or cultivar genetic improvement depending on the goals. Backcrosses are not frequently used and in any case would never yield back the original progenitor genotype (Alleweldt and Possingham, 1988). For similar reasons self-crossing is generally avoided because it may result in a large number of plants with deleterious phenotypes or reduced vigour due to inbreeding depression. The outcomes of these classical breeding programmes are always new genotypes, either rootstocks or cultivars, and therefore these procedures are not useful in the genetic improvement of well-known elite cultivars used in wine production.

Tolerance to abiotic stress has not been a major breeding priority for grapevine cultivars till recent times and few cultivars have been selected with this goal (Possingham, 1995; Webb et al., 2011). However, biotic stresses that affect the root system are more frequently considered in the genetic improvement of rootstocks. In general, the effects of salinity and mineral stresses are higher on the rootstock. High- and low-temperature stresses have more direct effects on the scions, whereas tolerance to water stress requires a combination of tolerant traits in both rootstock and scion. Selection for tolerance to abiotic stress has additional difficulties. Any given stress will have a different impact on plant production depending on the intensity, duration and plant developmental stage. Therefore the selection of tolerant plants will have to be performed under the environmental conditions to which the plants will have to be adapted. Moreover, given the interseasonal variations, selections need to be repeated during several years to develop locally adapted cultivars. Considering these constraints, the opportunities to improve the efficiency of breeding for abiotic stress tolerance traits will depend on a deep understanding of the phenotypic traits and the development of suitable screening methods or phenotyping platforms facilitating for selection (White et al., 2012). Understanding the genetic determination of tolerance traits could also help, in some cases, to develop molecular markers for the genotypic selection of tolerance traits. Unfortunately, current information on genetic control of stress responses is limited to a few reports discovering QTLs involved in the control of tolerance to iron deficiency in calcareous soil (Bert et al., 2013), in the response to magnesium deficit (Mandl et al., 2006) and in rootstock-dependent scion transpiration related to water stress (Marguerit et al., 2012). Thus, further efforts are required in the quantitative genetic analysis of segregating populations and in genetic association studies of genotypes core collections for traits related to abiotic stress tolerance in order to optimize the potential of breeding programmes for these traits in grapevine.

Strategies for the genetic improvement of elite cultivars

Many grapevine wine cultivars have been under vegetative propagation for centuries within viticulture regions and their wines have specific features recognized and strongly appreciated by consumers. In addition, the protected designations of origin (DOP) in different European regions determined the cultivars that can be grown or are recommended in each DOP. Because cultivars are unique highly heterozygous genotypes (Alleweldt and Possingham, 1988), the only possibilities for their genetic improvement rely on the use of somatic variation, either spontaneous or induced by mutagenic treatments (Khawale et al., 2007; Torregrosa et al., 2011) or genetic engineering (Vivier and Pretorius, 2002; Reustle and Buchholz, 2009).

Most widely grown wine cultivars have been taken through processes of clonal selection to identify lines or clones with good sanitary status (in terms of virus infections) as well as specific production and quality features (Torregrosa et al., 2011). The identification of qualitative variations affecting the quality of the berries has also allowed the development of new derived varieties such as berry skin colour variants for many elite cultivars (i.e. Pinot Noir, Pinot Blanc, Pinot Gris, etc.) (Torregrosa et al., 2011) or Muscat variants (i.e. Chardonnay Musqué, Gewürztraminer, Chasselas Musqué, etc.) (Emanuelli et al., 2010). Characterization of mutations responsible for different somatic variant phenotypes indicates that most of them are caused by dominant gain of function mutations (Boss and Thomas, 2002; Emanuelli et al., 2010; Fernandez et al., 2010, 2013), which suggests that new unexpected molecular functions providing improved tolerance to abiotic stress could also appear. In fact, local selections within specific table grape cultivars aimed to improve production and quality traits found clones better adapted to the local climatic and productive conditions, in consequence of the variation in traits such as the length of the vegetative/reproductive cycles

(Scott et al., 2000; Costenaro-Da-Silva et al., 2010) or in cluster size and compactness (Fanizza et al., 2003). However, so far field selection of tolerance to abiotic stress has not been reported in somatic variants, probably due to the lack of efficient screening and selection procedures. Moreover, *in vitro* culture selection schemes that were initially developed to select tolerant rootstocks, cultivars or clones for tolerance to specific abiotic stresses such as salinity (Skene and Barlass, 1988; Hamrouni et al., 2008) or chlorosis (Bavaresco et al., 1993b; Tangolar et al., 2008) have not reported new tolerant genotypes. Hopefully, understanding the genetic and molecular basis of relevant somatic variation will provide new clonal selection strategies for the improvement of abiotic stress tolerance in elite wine grape cultivars.

Regarding grapevine genetic transformation, the first protocols were developed in the 1990s (Kikkert et al., 1996; Scorza et al., 1996; Franks et al., 1998) and several updated approaches have been available since then (see Vidal et al., 2010, for a recent review). Few publications report the generation of transgenic grapevine plants with improved stress tolerance. Constitutive expression of a cold-inducible transcription factor (*DREB1b*) from *Arabidopsis thaliana* in the cultivar Centennial Seedless slightly improved the freezing tolerance of transgenic seedlings by increasing their freezing point and reducing electrolyte leakage (Jin et al., 2009). Similarly, cisgenic overexpression of *VvCBF4* in the grapevine cv. Freedom improved freezing survival and reduced freezing-induced electrolyte leakage in non-cold-acclimated vines (Tillett et al., 2012). Also, the expression of a ferritin gene from *Medicago sativa* in transgenic rootstock Richter 110 only conferred a moderate effect in the protection against the oxidative damage generated by different biotic and abiotic stresses (Kós et al., 2008). The use of genetic engineering for the improvement of abiotic stress tolerance in specific cultivars encounters major limitations. These are related to both the difficulties in generating useful stress tolerance traits in grapevine and in the implementation and acceptance of the technology. As mentioned above, plant stress responses take place through complex and interacting pathways triggered by signalling networks that are mostly unknown in grapevine. Even if they were readily known, they are difficult to modify with single- or oligo-gene strategies in such a way that the modification would not alter berry yield and quality. Thus, further work is required to understand grapevine stress responses and to identify genes and gene variants responsible for genetic variation in abiotic stress responses. Even if appropriate genes were known and their phenotypic effects clearly proof in pilot experiments, development of transgenic elite varieties would still need to solve additional problems. Among them we can identify: (i) consumer acceptance of transgenic or cisgenic grape varieties (see Töpfer et al., 2011, for a relevant discussion); (ii) labelling issues concerning grapes and derived wines; (iii) names given to the genetically modified elite cultivars (quite important for wine consumers used to link cultivars to wines) and (iv) environmental biosafety of transgenic grapevine crops. A pilot study by Harst et al. (2009) reported the existence of pollen flow up to 150 m of distance from an experimental plot of transgenic vines. Given the existence of endangered wild populations of grapevine in many wine producing European countries, the possibility of gene flow will have to be considered. Thus genetic engineering strategies are still far from being applied in the improvement of abiotic stress tolerance of elite cultivars.

15.4.2 Available genetic variation within the genus *Vitis* for classical breeding in stress tolerance

Although cultivated grapevine is mainly restricted to a reduced number of cultivars, there are a vast number of different varieties available in governmental or private germplasm collections, estimated at over 5000 (This et al., 2006; Reisch et al., 2012). Considered together, these cultivars involve a large genetic diversity pool that could be searched for adaptation to a wide range of environments and tolerance to different stress conditions. This search should also include natural populations and conserved accessions belonging to *V. vinifera* subsp. *sylvestris* (Cambrolle et al., 2013) as well as naturalized *V. vinifera* genotypes adapted to stressing environments that could bear relevant allelic variants (Milla-Tapia et al., 2013). In addition, American and Asian *Vitis* species may also be major sources of stress tolerance loci and alleles (Alleweldt and Possingham, 1988) although their use in breeding programmes could require additional hybridization and selection steps to avoid undesirable fruit features. In the following paragraphs, examples of genetic diversity in *V. vinifera* and in other species of the genus *Vitis* resulting in tolerance variation to most common abiotic stress agents facing viticulture are presented. Some of these already characterized examples of grapevine genetic sources of abiotic stress tolerance are mentioned in Table 15.1.

15.4.3 Stress dependent on ambient temperature

World areas of grape production are limited by the temperature requirements throughout the grapevine biological cycle. Nevertheless, breeders can take advantage of *Vitis* genetic diversity to extend this range of distribution as well as for a better adaptation to temperature conditions in each region. *V. vinifera* genotypes are generally adapted to temperate and subtropical regions because, even though moderate winter cold is necessary for a uniform budbreak, frosty winters and springs produce freezing of buds and vegetative organs, restricting their distribution in extremely cold latitudes or altitudes. Within this frost susceptibility, there are still differences among varieties. Mediterranean wine varieties like Carignan, Malvasia or Vranac are completely susceptible whereas varieties from north-west Europe including the Pinot group, Traminer, Riesling, Cabernet Sauvignon or Chardonnay show some degree of tolerance, similarly to Muscat Hamburg or Chasselas Doré table grape cultivars (Cindric and Korac, 1990; Zunic et al., 1990; Wolf and Cook, 1994; Lisek, 2012).

Table 15.1 Summary of grapevine genetic sources of tolerance to different abiotic stressing factors available for breeding.

Stressing factor	Tolerance	Genetic sources of tolerance	
		Sort of genotype	**Genotype**
Cold	Cold hardiness	Wine cultivars	Traminer, Riesling, Cabernet Sauvignon, Chardonnay
		Table grape cultivars	Muscat Hamburg, Chasselas Doré
		Other species	*V. amurensis, V. labrusca, V. aestivalis*
Heat	Heat-resistant ripening cycle	Wine cultivars	Nebbiolo, Monastrell, Cinsault, Agiorgitiko, Carignane, Tarrango, Taminga
Water deficit	Water-use efficient scion	Wine cultivars	Escursach, Sangiovese, Callet, Malvasia, Grenache
		Table grape cultivars	Cardinal, Kahli Kerkennah
	Water-deficit tolerant rootstock	Other species and hybrids	*V. berlandieri* × *V. rupestris* hybrids (Richter 110, Paulsen 1103, Ruggeri 140), *V. cinerea* hybrids, *V. yeshanesis* × *V. riparia* hybrids, *V. californica, V. champinii, V. doaniana, V. longii, V. girdiana, V. arizonica*
Saline soil	Chloride excluder rootstock	Other species and hybrids	*V. arizonica, V. girdiana, V. rupestris* hybrids (Ruggeri 140, St George, Schwarzmann, Paulsen 1103), Ramsey hybrid (synonym of Salt Creek, originated from *V. champinii*)
Heavy metals in soil	Acidic soil tolerant cultivar	*V. labrusca* hybrids	Concord, Catawba
	Acidic soil tolerant rootstock	Interspecific hybrids	*V. berlandieri* × *V. rupestris* hybrids (Paulsen 1103, Ruggeri 140, Richter 110, Richter 99, SO4), Kober 5BB (*V. berlandieri* × *V. riparia*) and other hybrid rootstocks (Gravesac, IAC 766, USVIT 8-7)
	Cu resistant	*V. vinifera* subsp. *sylvestris*	*V. vinifera* subsp. *sylvestris* populations from Cu-contaminated soils
Mg deficiency in acidic soil	Mg deficiency tolerant rootstock	Interspecific hybrids	*V. berlandieri* × *V. rupestris* hybrids (Richter 110, Paulsen 1103), Couderc 3309 (*V. riparia* × *V. rupestris*), Börner (*V. riparia* × *V. cinerea*) and other complex hybrids (Sirius, Couderc 1616)
Iron deficiency in alkaline soil	Alkaline soil tolerant rootstock	*V. vinifera*	Cabernet Sauvignon, Khamri and other cultivars
		Other species	*V. berlandieri, V. cinerea, V. champinii, V. califórnica, V. berlandieri* hybrids (Georgikon 28, Fercal, Ruggeri 140, 41B)

Other *Vitis* species originated from areas with lower winter temperatures show stronger cold hardiness, which indicates that they carry genetic determinants for freezing and chilling tolerance that could be exploited by breeders. In fact, those species are able to transmit chilling tolerance to interspecific hybrids useful for wine production (Cindric and Korac, 1990; Wolf and Cook, 1994; Lisek, 2012). Eastern Asian species like *V. amurensis* are successfully used in breeding programmes for cold or freezing tolerance (Alleweldt and Possingham, 1988; Cindric and Korac, 1990; Keller, 2010). Species like *V. labrusca* or *V. aestivalis* also show greater cold hardiness than *V. vinifera* (Wolf and Cook, 1994). Although the genetic causes of cold hardiness in *Vitis* species are still unknown, differences in gene expression and in the composition of cerebrosides, membrane sphingolipids that may be elicited by cold in plants, have been found to correlate with differential tolerance to this stress between *Vitis* species and cultivars (Kawaguchi et al., 2000; Xin et al., 2013).

Low temperatures before flowering time can also be stressing for ovule and pollen development and viability, and therefore can have negative effects on seed and fruit set, as reported in Chapter 9. Low-temperature incidence on flowering success is genotype dependent, with Chardonnay being more susceptible than Syrah and Cabernet Sauvignon more than Sylvaner and Zinfandel (Ewart and Kliewer, 1977; Ebadi et al., 1995a, 1995b, 1996). On the other hand, extreme heat has also been reported to induce flower and developing fruitlet abscission and ovule sterility, depending on the cultivar (Buttrose and Hale, 1973; Kliewer, 1977; Greer and Weston, 2010). Thus, the rate of fruit set and fruit yield in a given climatic condition could be improved by breeding or clonal selection screenings.

Strict requirements should be combined on the grape composition at ripeness to allow for a high-quality wine production. Heat stress restricts the optimal areas for wine grape production as it inhibits vine growth, hastens grapevine phenology and alters fruit composition. Thus, considering the present scenario of global warming, adaptive strategies of viticulture in wine grape growing areas are necessary to keep producing high-quality wines there (Webb et al., 2011). Nowadays, grapevine genetic diversity already aims to adapt viticulture to temperature in each wine production area, although not always in the optimum way (Jones et al., 2005). A plausible strategy to follow in cool regions once they become warmer is to substitute cultivars to those that require higher amounts of temperature during the growing season to reach maturity, and are used at present in warmer regions, such as Nebbiolo, Monastrell, Cinsault, Agiorgitiko or Carignane (Jones, 2006; van Leeuwen et al., 2008). In the same way, cultivars that require less amounts of temperature to reach maturity, like Muller-Thurgau, Gewurztraminer, Pinot Noir, Chardonnay or Chasselas (Jones, 2006; van Leeuwen et al., 2008), could adapt in the future to higher latitudes and altitudes where the growth of grapes for quality wine production had not been achieved before. Additional effort is required to identify genotypes able to adapt to regions in the limit of warmest temperatures that still allow keeping quality wine production in regions with raising temperatures. In these cases, available varietal variation should be searched for adaptable genotypes, for instance performing anthocyanins accumulation independently of high temperatures, organic acid metabolization not affected by heat or exhibiting a phenology insensitive to temperature. In this manner, Merlot phenology and berry composition performs as being more susceptible to climate than Cabernet Sauvignon in the Bordeaux area (Jones and Davis, 2000). Similarly, harvest time of late ripening cultivars has been shown to be less affected by climate warming in Greece (Koufos et al., 2014). There are a few examples of bred *V. vinifera* cultivars performing better in warmer climates and actually Tarrango and Taminga are bred varieties from crosses between Touriga Nacional and Gewurztraminer, which have been grown in Australia in the last century and retain higher acidity. Other bred cultivars like Tyrian, Cienna and Rubienne obtained by Australian CSIRO show enhanced phenolic and colour attributes (Possingham, 1995; Webb et al., 2011). Since the berry molecular processes altered by temperature as well as the underlying genetic control are not fully understood, marker-assisted selection is not possible when breeding for the referred purpose. Another alternative to minimize the effects of high temperatures on berry composition is to select for genotypes with a phenology that positions berry ripening within the range of most favourable temperatures to achieve the optimum berry composition. QTLs determining phenological traits have been identified in a Riesling × Gewurztraminer progeny and in table grape segregating progenies (Costantini et al., 2008; Duchene et al., 2012), which could provide variations to help breeders achieve this aim.

15.4.4 Water stress

Although water stress can be avoided by irrigation, it is desirable to minimize these practices in agriculture due to sustainability reasons. As water stress results from the interaction of roots, which absorb water and sense water availability, with aerial parts, which control stomatal closure and transpiration, both rootstock and scion genotypes determine the performance of the vine under drought and, consequently, the optimum timing and amount of irrigation required for quality fruit production. Grenache cultivar defined as isohydric and considered more water stress tolerant than anisohydric cultivars (Schultz, 2003; Soar et al., 2006; Vandeleur et al., 2009) could be more suitable for viticulture in semi-arid regions. However, it has recently been reported that Chardonnay with an anisohydric behaviour performs a better water recovery after moderate water stress than Grenache or Syrah, considered as isohydric and near isohydric, respectively (Pou et al., 2012). Varieties with a high water use efficiency are also interesting genotypes to face drought, such as the Balearic cultivar Escursach, which shows low water consumption together with relatively high carbon assimilation under water stress (Bota et al., 2001), or the Italian Sangiovese, reported as water efficient under drought despite the anisohydric response of its leaf water potential (Poni et al., 2007; Palliotti et al., 2009). Potted plants of Mediterranean cultivars like Callet, Malvasia and Grenache showed higher and more stable water-use efficiency under drought than other cultivars like Cabernet Sauvignon, Tempranillo or Richter 110. This has been considered as indicative of their adaption to water stress in semi-arid environments (Tomás et al., 2012). Although stomatal conductance is considered to depend on water transport by aquaporins as well as on ABA levels controlling stomatal closure (Soar et al., 2006; Vandeleur et al., 2009), genetic loci determining water stress tolerance have not been identified and genetic markers of drought tolerance in scions are not available to breeders. Identification of genetic markers for water-use efficiency would also help to breed genotypes as scions for a sustainable viticulture under drought. Further genetic determinants of water stress tolerance could be related to cuticle composition, leaf anatomy or vessel size, which could provide tolerance as well (Chouzouri and Schultz, 2005; Moutinho Pereira et al., 2007). In that way, leaf lipid content has been reported to increase during water stress in Cardinal and Kahli Kerkennah drought-tolerant table grape cultivars but not in Guelb Sardouk and Superior Seedless sensitive cultivars (Toumi et al., 2008).

Vine scion genotypes are usually grafted on different rootstock genotypes, which have an influence on scion vigour, gas exchange and water-use efficiency and thus on its tolerance to water stress and agronomic features under drought (McCarthy et al., 1997; Padgett-Johnson et al., 2000; Stevens et al., 2008). Wild North American species like *V. californica*, *V. champinii*, *V. doaniana*, *V. longii*, *V. girdiana* and *V. arizonica*, most of which are originally from habitats with low soil water, have been reported as good genetic reservoirs for rootstocks conferring drought tolerance to grafted *V. vinifera* scions (Padgett-Johnson et al., 2003). Drought-resistant Chinese species and *V. yeshanesis* × *V. riparia* hybrids were also reported (Yuejin et al., 2004). In fact, drought-tolerant phylloxera-resistant rootstock interspecific hybrids that have been selected from breeding programmes and widely used rootstocks for adaption to water-deficient soils include *V. berlandieri* × *V. rupestris* hybrids like Richter 110, Paulsen 1103 or Ruggeri 140 (Ezzahouani and Williams, 1995; Walker and Clingeleffer, 2009). Drought-tolerant bred hybrid genotypes have been produced from *V. cinerea* as well (Pavlousek, 2011). Although the physiological mechanisms are not fully understood, variation in drought stress tolerance conferred by rootstocks is thought to rely mainly on the root surface area, the penetration capacity of the root system and the root system hydraulic conductivity (Alsina et al., 2011; Gambetta et al., 2012). Identification of genetic loci controlling these traits would aid future breeding of drought-resistant rootstock. Currently, several QTLs for Cabernet Sauvignon scion acclimatization of transpiration to water deficit have been identified from a Cabernet Sauvignon × *V. riparia* cv. Gloire de Montpellier cross progeny used as rootstock (Marguerit et al., 2012). Finally, it is also important to consider scion–rootstock interactions because scion genotypes also determine rootstock vigour (Tandonnet et al., 2009) and thus water-deficit tolerance.

15.4.5 Saline stress

Selection of suitable rootstock genotypes is indicated as the most effective way to adapt viticulture to saline soils. Hybrid rootstocks selected for phylloxera and nematode resistance such as Ruggeri 140, St George (from *V. rupestris*) and Schwarzmann (*V. riparia* × *V. rupestris*) have been shown to be strong chloride excluders, which results in the prevention of yield reduction by moderate saline stress and prevents severe damage under high salinity (Tregeagle et al., 2006; Fort and Walker, 2011). Ramsey hybrid (synonym of Salt Creek that was originated from *V. champinii*) and Paulsen 1103 have been designed as salt-tolerant rootstocks for the production of high-quality dried grapes with Sultana grafted as scion (Walker et al., 2007). Although typically less salt stress tolerant, there is also variation within *V. vinifera* cultivars. For instance, varieties maintained for viticulture in semi-arid regions retain a higher degree of tolerance (Sivritepe and Eris, 1999; Cavagnaro et al., 2006).

Screening the genus *Vitis* for genotypes with roots excluding NaCl salt ions should identify rootstocks better adapted to saline soils. In that regard, American *V. arizonica* and *V. girdiana* have been proposed to exclude salt with greater efficiency than the most salt-tolerant commercial rootstocks (Fort and Walker, 2011). Additionally, the identification of genetic loci controlling this trait could improve the selection of saline stress tolerance in breeding programmes aimed at finding rootstock genotypes combining multiple tolerance and resistance. Indeed, a single locus derived from *V. berlandieri* could explain the inheritance of Cl^- accumulation in a (*V. berlandieri* × Sultana) × Biancone progeny (Sykes, 1987). However, complex gene control rather than a single locus seems to underlie the Cl^- excluding capacity of roots derived from other genetic sources given the continuous variation in Cl^- accumulation observed in a cross progeny of Ruggeri 140, a good Cl^- excluder, and K 51-40 (*V. champinii* × *V. riparia* cv. Gloire de Montpellier), a poor Cl^- excluder (Gong et al., 2011). Complex and transgressive segregation of Cl^- accumulation under saline watering also resulted from a Ramsey × Sultana cross (Sykes, 1985). Although less decisive than a rootstock genotype, the performance of the viticulture under salt stress could also be optimized by selection on the scion genotype. For instance, it has been shown that Chardonnay accumulate less Cl^- than Syrah when grafted on strong or weak Cl^- excluder rootstocks (Tregeagle et al., 2006) and fruit yield on saline soil also varies with scion genotype (Zhang et al., 2002).

15.4.6 Heavy metal toxicity stress

Concerning copper toxicity due to accumulation in soils as a result from the use of Cu-based fungicides, genetic diversity within the genus *Vitis* should also imply variation in the tolerance to Cu stress and, in fact, a higher tolerance has been observed in a *V. vinifera* subsp. *sylvestris* population from a heavy metal contaminated soil when compared to reports in *V. vinifera* (Cambrolle et al., 2013). This kind of genotype could be useful for rootstock improvement against Cu stress.

The toxicity of heavy metals is intensified in acidic soils, which in addition cause nutrient deficit symptoms in vines because of Mg, Ca or P deficiencies (Delas, 1984). Grapevine genotypes that have been proved to perform well when rooted in low pH soils are the *V. labrusca* hybrid cultivars Concord and Catawba, as well as the USVIT 8-7 rootstock and Ruggeri 140, Richter 110, Richter 99 or SO4 *V. berlandieri* × *V. rupestris* rootstocks (Conradie, 1983; Himelrick, 1991). Aluminium could also become stressing for grapevine growth in acid soils. Differences in growth inhibition and Al accumulation in roots have been identified among grapevine rootstock genotypes grown in Al supplied soil, which identified Kober 5BB (*V. berlandieri* × *V. riparia*), Paulsen 1103, Gravesac [Couderc 161- 49 (*V. berlandieri* × *V. riparia*) × Couderc 3309 (*V. riparia* × *V. rupestris*)] and IAC 766 [Millardet et Grasset 106-8 (*V. riparia* × (*V. cordifolia* × *V. rupestris*)) × *V. caribaea* de Candolle] as Al-resistant genotypes (Cançado et al., 2009).

15.4.7 Nutritional deficit stress, iron and magnesium deficiency-induced chlorosis

Lime-induced chlorosis is a major stressing factor to challenge in calcareous soils. Although soil treatment strategies like the use of synthetic chelates or fertilizers can be applied, the selection of suitable rootstock genotypes is an efficient measure to avoid calcareous soil-related stress because rootstock strongly contribute to the lime-induced chlorosis response (Bert et al., 2013). Most phylloxera-resistant American species as well as *V. riparia* and *V. rupestris* bred rootstocks are not well adapted to calcareous soils and in the presence of bicarbonate, vines grafted on them show iron-deficiency chlorosis (Bavaresco et al., 1993a; Sabir et al., 2010). Thus, other grapevine genetic resources should be searched for tolerance to this deficiency. In that concern, *V. berlandieri*, *V. cinerea*, *V. champinii* and *V. californica* have been shown as more tolerant than other wild *Vitis* species (Bavaresco et al., 1994, 1995). In spite of *V. vinifera* cultivars like Cabernet Sauvignon being very well adapted to calcareous soils and having also been used in rootstock breeding to introduce the adaptation to such soils, frequently rootstocks used on calcareous soils are hybrids of *V. berlandieri*, like Georgikon 28, Fercal, Ruggeri 140 or 41B, to allow the presence of Phylloxera resistance and other stress tolerances within the same genotype (Bavaresco et al., 1991, 1993a; Nikolic et al., 2000; Sabir et al., 2010). In that manner, Fercal is a bred hybrid [(*V. berlandieri* × Colombard) × (Cabernet Sauvignon × *V. berlandieri*)] generated at the end of the past century that is valuable as a good lime-induced chlorosis-resistant rootstock (Pouget, 1980; Sabir et al., 2010). There is also intraspecific variation in lime-induced chlorosis tolerance and, for instance, the cultivar Khamri is more tolerant than other Tunisian *V. vinifera* cultivars, correlating with its higher root acidification capacity (Ksouri et al., 2006, 2007). Thus genotypes like Khamri would be suitable as calcareous soil tolerance donors in breeding programmes. A QTL with a major effect on resistance to lime-induced iron deficiency has been identified in linkage group 13 from a Cabernet Sauvignon (tolerant) × *V. riparia* cv. Gloire de Montpellier (sensitive) progeny used as rootstock to graft Cabernet Sauvignon as scion on to them (Bert et al., 2013). This QTL could aid in the selection of suitable rootstocks in breeding programmes aimed at the identification of lime-induced chlorosis-tolerant genotypes. However, it is worth noting that this QTL was detected in the sensitive parent and thus it is not the major locus responsible for the tolerance observed in Cabernet Sauvignon. Other smaller QTLs were also identified and none of them was coincident with QTLs identified from cuttings of the same progeny in the absence of grafting, indicating a complexity of interactions and genetic control regulating this response. Indeed, scion genotypes as well as the grafting process itself also influences the level of chlorosis symptoms developed by vines grown on calcareous soils (Bavaresco and Lovisolo, 2000; Bert et al., 2013). Thus, scion genotype as well as scion–rootstock combinations could be optimized against this source of stress.

Mg starvation is frequent in acidic soils and sometimes due to potassium fertilization practices because in some genotypes frequently used as rootstocks, including *V. berlandieri* hybrids like SO4, Ramsey or Fercal, there is competition between Mg and K uptake (Lupton, 1985; Kocsis and Walker, 2003). In contrast, rootstock genotypes that have been shown to display low symptoms of Mg deficiency are Richter 110, Paulsen 1103, Couderc 3309, Couderc 1616 (a complex hybrid from *V. riparia*) and Börner (*V. riparia* × *V. cinerea*) (Kocsis and Walker, 2003).

A major QTL explaining more than 50% of the variation in Mg content and deficiency symptoms was identified in linkage group 11 from vines of a Welschriesling (cultivar with low Mg uptake) × Sirius (complex interspecific hybrid without Mg-deficiency symptoms) progeny (Mandl et al., 2006). This QTL relied on the variation of Sirius alleles and it could be used for assisted selection of Mg-deficiency tolerance in rootstock breeding programmes using Sirius as parent. Nevertheless, the effect of this QTL should be confirmed using these genotypes as rootstocks for grafting before its application in rootstock breeding. It could also be interesting to test whether this locus in linkage group 11 plays any role in other Mg-deficiency tolerant genotypes used as rootstocks for its use with marker-assisted selection purposes.

15.5 Conclusions

In summary, the genetic diversity of *V. vinifera* cultivars provides a valuable reservoir to search for genotypes with higher tolerance to specific abiotic stresses and better adaptation capacity to given environments. Furthermore, other *Vitis* species can be used as additional sources of genetic variation, conferring tolerance to different stressing abiotic conditions for rootstocks or cultivar breeding purposes. Breeders should be willing to search for genotypes adapted to specific conditions rather than universal cultivars adapted to any condition, which indicates the need of local breeding for adaptation to specific environmental conditions. The difficulties of efficiently selecting abiotic stress-tolerant genotypes suitable for quality fruit and wine production will be reduced as further advances in molecular genetics knowledge and screening methods optimize the selection processes.

Acknowledgements

Pablo Carbonell-Bejerano and José Martínez-Zapater's research was funded by project BIO2011-026229 and the Spanish Ministry of Economy and Competitiveness; Foundation for Science and Technology funds PestOE/AGR/UI0240/2011 (CBAA/SA and LC), PTDC/AGR-PRO/118081/2010 (JEED) and the post-doc grant SFRH/BPD/85767/2012 (LC). José Dias was also funded by the Portuguese Ministry of Agriculture and the Sea (PRODER – 2.2.3.1. – PA 18621) and Institute of Grapevine and Wine. Research was also funded by INNOVINE from the EU FP7 (Pablo Carbonell-Bejerano, José Martínez-Zapater, Luisa de Carvalho and Sara Amâncio) and is integrated in the COST (European Cooperation in Science and Technology) Action FA1106 'Quality fruit'.

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Grapevine in a Changing Environment: A Molecular and Ecophysiological Perspective, First Edition. Edited by Hernâni Gerós, Maria Manuela Chaves, Hipólito Medrano Gil and Serge Delrot.
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