

HOW CAN GRAPEVINE GENETICS CONTRIBUTE TO THE ADAPTATION TO CLIMATE CHANGE?

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Abstract

Climate change is modifying the environmental conditions in all the vineyards across the world. The expected effects on grape and wine production can be positive in some grape growing regions, but under warmer or dryer conditions the volume and quality of the wines produced can be impaired. Adaptation to new climatic conditions includes changes in the cultivation areas, changes in the vineyard or cellar practices, and use of new rootstock × scion combinations. In this article, we provide an overview of the possible effects of climate change on grapevine physiology and berry quality and we describe the more important traits and the genetic variability that can be used in the adaptation process. We also present the modern techniques that can be used by researchers to identify the links between genomic information and behaviors in the field. Finally, we discuss the existing opportunities in the present grapevine collections and the strategies that can be used by breeders to create new varieties.

Keywords: grapevine, climate change, adaptation, genetic variability

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INTRODUCTION

There is no doubt that climatic conditions have changed all around the world during the past decades, and simulations with different scenarios of greenhouse gas emissions (GHG) show that the observed tendencies will continue during the present century (IPCC, 2013). Agricultural production in general is very responsive to environmental conditions, and destabilization of grape and wine production due to climate change can have not only significant direct impacts on farmers' incomes (Moriondo *et al.*, 2011; Webb *et al.*, 2008) and employment in the wine industry, but also indirect impacts on land use, landscapes, tourism activities and rural life in numerous regions.

Because CO₂ is the elementary molecule at the origin of plant biomass, the expected increase in atmospheric CO₂ concentration can have direct effects on the physiology of the plants. However, the most studied effects of this increase are the possible impacts on climatic conditions. The Intergovernmental Panel on Climate Change (IPCC) forecasts an increase of temperatures across the globe (IPCC, 2013) and changes in precipitations, with more contrasts between wet and dry areas and wet and dry seasons, and more extreme precipitation events (IPCC, 2013). The last IPCC report predicts specific regional changes but does not confirm a general tendency of increased drought risks.

Adaptation of the grape and wine industry to climatic changes can be envisaged by moving cultivation areas (Malheiro *et al.*, 2010) and by changing the profiles of the wines produced. Here, we will consider that a successful adaptation to climate change will be for a present grape growing area to produce the same type of wine, with the same volumes, in the future.

This goal can be achieved by changes in the vineyard or cellar practices (Duchêne *et al.*, 2014b; Keller, 2010) or by local changes in the location of the vineyards using the existing small-scale variability (Bonnefoy *et al.*, 2013). Here, we will focus on how can grapevine genetics help in the adaptation process.

Before describing the genetic variability and how it can be used, an overview of the expected effects of climatic changes on grapevine is necessary.

EXPECTED EFFECTS OF CLIMATE CHANGE

1. A shift in developmental stages

The first effect of climate change is an advance of developmental stages, observed worldwide (Duchêne and Schneider, 2005; Jones and Davis, 2000; Petrie and Sadras, 2008; Ramos *et al.*, 2008). The link between grapevine phenology and temperatures is so close that it has been used, on the one hand, to assess temperatures from the past centuries (Chuine *et al.*, 2004) and, on the other hand, to propose models for predicting developmental stages in the future (Duchêne *et al.*, 2010; Fila *et al.*, 2014; Webb *et al.*, 2007). These models forecast an advance of two to three weeks by 2050 when compared to the last 30 years (Duchêne *et al.*, 2010; Moriondo *et al.*, 2011; Webb *et al.*, 2007). With empirical models, Barnuud *et al.* (2014b) show that the shift in the dates when sugar content reaches 22°Brix will be greater in cool than in warm regions in Australia.

As a consequence of earlier véraison dates, berry ripening will occur earlier in summer, under higher temperatures, and this can have a significant impact on berry quality.

2. Effects on grape and wine quality

High temperatures accelerate the decrease of grape acidity, mainly because of a faster degradation of malic acid (Buttrose *et al.*, 1971; Kliewer, 1971; Sweetman *et al.*, 2014). The comparison between different grape growing regions (Barnuud *et al.*, 2014b) or vintages (Duchêne *et al.*, 2014a; Neethling *et al.*, 2012) confirms this result. Varieties whose berries contain high quantities of tartaric acid should be less sensitive to climate change (Shiraishi, 1995) because the quantity of tartaric acid per berry is stable during berry ripening (DeBolt *et al.*, 2008).

An increase of sugar content in berries or alcohol content in wines during the past decades was frequently reported (Alston *et al.*, 2011; Duchêne and Schneider, 2005; Neethling *et al.*, 2012). Although the role of changes in management techniques can be discussed, early dates of véraison and better ripening conditions have a key role in this increase. Harvesting earlier is not an appropriate solution because grapes would not have the correct phenolic maturity (Pallioti *et al.*, 2013; Sadras and Moran, 2012).

High temperatures also impair the accumulation of anthocyanins in the berries (Kliewer, 1970; Mori *et al.*, 2007; Teixeira *et al.*, 2013), but increasing solar radiation can have opposite effects (Teixeira *et al.*, 2013). There are indirect results showing that increasing temperatures are generally unfavorable to wine quality (Jones *et al.*, 2005; Moriondo *et al.*,

2011; Tonietto and Carbonneau, 2004), but until now, there are no convincing data on the effects of high temperatures on aroma compounds. Bureau *et al.* (2000) studied the effects of light on aroma compounds by comparing bunches exposed to the sun, bunches shaded by leaves and bunches shaded by black cloths. They quantified molecules of the terpenol family that participate in muscat-like aromas. The highest terpenol content was observed in the naturally shaded bunches and the lowest in the artificially shaded bunches. The authors suggested that these differences could be related to a modification of the red/far red radiation ratio and/or to the temperatures recorded around the bunches. This is in agreement with findings from Reynolds and Wardle (1993) showing that cool growing sites were more favorable to terpenol accumulation than warm growing sites.

Climate change is primarily the result of an increase of atmospheric CO₂ concentrations. In Free Air CO₂ Enrichment (FACE) experiments, elevated CO₂ concentrations had little effect on the concentrations of primary metabolites of the berries, *i.e.* sugars and acids (Bindi *et al.*, 2001; Gonçalves *et al.*, 2009). However, Gonçalves *et al.* (2009) showed that elevated CO₂ concentrations can modify the profile of secondary metabolites in wines.

3. Uncertainties about yield

Besides effects on grape quality, climate change can have quantitative effects on grape production. Increasing concentrations of CO₂ and higher radiation levels are expected to increase biomass production (Bindi *et al.*, 2001; Garcia de Cortazar Atauri, 2006; Moutinho-Pereira *et al.*, 2009). However, the expected increase in total biomass might be limited in the future by rainfall distribution and water availability, especially at the end of the growth cycle (Garcia de Cortazar Atauri, 2006). The effects of climate change on fruit biomass, *i.e.* yield, are more difficult to anticipate. Using statistical models, Santos *et al.* (2011) state that climate change should benefit grape yield in the Douro region in Portugal, whereas Lobell *et al.* (2006) in California anticipate a decrease, more pronounced for table grapes than for wine grapes. With mechanistic models, conclusions are very dependent on the regions studied (Garcia de Cortazar Atauri, 2006) and the climatic datasets used (Bindi *et al.*, 1996). The overall tendency in the South of France and Italy is a decrease in yield potential in the future (Bindi *et al.*, 1996; Garcia de Cortazar Atauri, 2006; Moriondo *et al.*, 2011).

The number of flowers determines an upper limit for the final number of berries per plant or per m² (Duchêne *et al.*, 2001). This variable depends, on the one hand, on the number of flowers per inflorescence and, on the other hand, on the number of inflorescences per shoot. Climate change can affect both variables. Indeed, it has been demonstrated that the higher the temperatures around budburst, the lower the number of flowers per inflorescence (Keller *et al.*, 2010; Petrie and Clingeleffer, 2005; Pouget, 1981). Frost damage around budburst can also reduce the number of inflorescences, but Molitor *et al.* (2014) demonstrated that, in Luxembourg, the risk of frost around budburst should decrease in the future.

High temperatures and high light intensity during the floral initiation process can increase the number of inflorescences (Buttrose, 1970), but a water deficit during this period can have strong opposite effects (Buttrose, 1974; Matthews and Anderson, 1989). Water deficits also negatively affect berry weight, especially when applied before véraison (Intrigliolo *et al.*, 2012; Niculcea *et al.*, 2014). In addition to the effect of water deficit, Guilpart *et al.* (2014) showed that nitrogen availability around flowering is also a driver of grape fertility in the following growing season. It is possible that decreasing soil humidity due to climate change can reduce soil nitrogen mineralization and consequently indirectly affect bud fertility.

The role of atmospheric CO₂ concentrations on the number of flowers has not been investigated yet. It is likely to be positive because bud fertility increases with vine vigor (Huglin and Schneider, 1998), which is higher under elevated atmospheric CO₂ concentrations (Bindi *et al.*, 2001).

It is difficult to forecast the consequences of climate change on grape yields because of the numerous yield components and climatic factors, including CO₂ concentrations, that are playing a role. However, the main concern, coming more from expert opinions than from crop modeling (Pieri and Lebon, 2014), is that yields will be limited by water availability, especially in summer.

The frequency of extreme events (heat waves, heavy precipitations) is expected to increase with the global temperature increase (IPCC, 2013). This qualitative information is difficult to integrate in an adaptation approach, but it is necessary to keep it in mind.

Several authors have attempted to predict the evolution of pests and diseases in the future (Bregaglio *et al.*, 2013; Caffarra *et al.*, 2012; Caubel *et al.*, 2014; Pugliese *et al.*, 2010; Salinari *et al.*,

2006). The conclusions depend on the models and scenarios used. The tolerance/resistance of grapevine varieties to pests and diseases will not be discussed here.

HOW TO USE THE GENETIC VARIABILITY?

Evidence of wine making dates back approximately 5000 years (McGovern *et al.*, 1996). Humans have domesticated the wild species *Vitis vinifera sylvestris* to obtain hermaphrodite plants producing numerous large, sweet berries (This *et al.*, 2006). Thanks to the use of molecular markers, the history of grapevine evolution is now well described (Bacilieri *et al.*, 2013; Lacombe *et al.*, 2013). In this respect, 12314 different accessions of *Vitis vinifera* are referenced in the Vitis International Variety Catalogue (<http://www.vivc.de>, February 2016). They are resulting from two main sources of genetic variation: mutations and sexual reproduction.

Grapevine plants are reproduced by vegetative propagation. New features can appear spontaneously in a bud after accidental modifications in the DNA, which is the physical support of genetic information, during the process of cell division. These modifications include mutations at a single base (Single Nucleotide Polymorphism, SNP), insertion or deletion of short DNA fragments, and insertion of transposable elements (large DNA fragments). These natural and spontaneous events do not always have significant effects, but when they do, the new plant can bear interesting traits: white color, muscat-like aroma or erect habit for example. This emergence of genetic variability is still going on and leads to «clonal variation»: within a variety, slightly different plants can be identified and their characteristics transmitted by vegetative propagation. The mutations sometimes affect only some of the cell layers of plant tissues, creating what is called «chimeras» (Pelsy, 2010). Pinot gris (Hocquigny *et al.*, 2004) and Pinot meunier (Franks *et al.*, 2002) are examples of chimeric grapevine genotypes.

The existing clone collections can be explored to detect any phenotypic variation that could be useful in the adaptation to climate change.

The other major source of genetic and phenotypic variation is sexual reproduction. The grapevine genome is highly heterozygous (Adam-Blondon *et al.*, 2004), which means that a cross between two different varieties will produce an infinite number of different offspring. Many famous cultivars such as Cabernet-Sauvignon (Bowers and Meredith, 1997), Chardonnay (Bowers *et al.*, 1999) or Merlot (Boursiquot *et al.*, 2009) are descendants of other

known varieties. The extent of parentage among grapevine cultivars is surprisingly high. Studying the relationship among 2344 unique genotypes of the INRA «Domaine de Vassal» grape germplasm repository with molecular markers, Lacombe *et al.* (2013) identified only 276 genotypes without direct relationship with any other genotype in the collection, but could reveal the complete parentage of 828 cultivars. This indicates that sexual reproduction, due to chance or controlled by man, is a major driver of genetic diversity in cultivated grapevine.

Researchers use different methods to detect the relationships between the genetic information on chromosomes and the features of grapevine plants. The first one, from an historical point of view, is used for all kind of living organisms such as yeasts, plants or animals. The principle is to create genetic variations through sexual reproduction: crossing two parents, chosen for some traits of interest, generates hundreds of individuals. The genetic information of all the individuals of the progeny is revealed by the use of molecular markers. The number of molecular markers can vary from hundreds to thousands with modern techniques (Barba *et al.*, 2014). In parallel, some traits of agronomical or enological interest are measured on the same plants and statistical methods are used to detect the relationships between the presence of some alleles at a precise locus and the trait of interest. When allelic variations in a chromosomal region are correlated with variations of a trait of interest, this region is described as a «Quantitative Trait Locus» or QTL.

QTL detection has been extensively used in grapevine (review by Martinez-Zapater *et al.*, 2010) for traits such as resistance to fungal diseases (Bellin *et al.*, 2009; Blasi *et al.*, 2011), aroma content of berries (Battilana *et al.*, 2009; Duchêne *et al.*, 2009) or the timing of developmental stages (Duchêne *et al.*, 2012b). The availability of the grapevine whole genome sequence (Jaillon *et al.*, 2007) is very useful for identifying the genes involved in the variations of the trait of interest.

Another method is to characterize the genome and a trait of interest for a large population of unrelated grapevine genotypes. The basic idea is the same as for QTL detection: finding associations between DNA information and the values of a trait of interest. This method, named «Genome Wide Association» genetics, has been successfully used for the detection of alleles linked to the aroma (Emanuelli *et al.*, 2010) or anthocyanin content in grapevine berries (Fournier-Level *et al.*, 2009).

Considering the numerous studies providing statistical relationships between allelic and phenotypic variations, there are only few examples of direct causal links between a DNA sequence and a trait of agronomical or enological interest (Battilana *et al.*, 2011; Feechan *et al.*, 2013; Kobayashi *et al.*, 2004; Mejia *et al.*, 2011).

Once a strong link is found between a variation in the DNA and a variation in a trait of interest (even if it is only statistical), breeders can use this knowledge for creating new grapevine varieties. Molecular markers are used to select the plantlets bearing the desired alleles. The number of molecular markers used will depend on the number of traits under selection and the genetic architecture of the trait. For example, for selecting a genotype with a muscat-like aroma (high linalool content), two specific alleles, one from chromosome 5 and one from chromosome 10, are necessary (Duchêne *et al.*, 2012a; Duchêne *et al.*, 2009).

Currently, QTLs and markers related to disease resistance are routinely used in Marker-Assisted Selection (MAS) programs (Eibach *et al.*, 2007; Riaz *et al.*, 2009).

Breeding programs are currently more oriented towards tolerance to disease than adaptation to climate change. There is, however, increasing information on the genetic determinism of traits playing a role in the adaptation to climate change.

GENETIC VARIABILITY FOR THE ADAPTATION TO CLIMATE CHANGE

In addition to changing cultivation zones and training systems, using different or even new genotypes, for both scion and rootstock, is a potentially powerful means of adaptation. Finding scion × rootstock × training system combinations able to produce commercial-quality wine is a reasonable goal in many grape growing areas. It is, however, difficult to guarantee that the volume of production will be the same as today.

1. Phenology

The first intuitive idea is to use clones or varieties ripening later than those presently used. The variability of flowering and véraison time among existing genotypes is well described (Parker *et al.*, 2013), and we have models using climatic data that are able to predict the developmental stages in the future (see Fila *et al.*, 2014 for example). Numerous QTLs for phenology have been identified (Costantini *et al.*, 2008; Duchêne *et al.*, 2012b; Fechter *et al.*,

2014; Grzeskowiak *et al.*, 2013), and this information can be used to test the adaptation of virtual genotypes in different grape growing areas for the future. However, we have shown that it is likely impossible in the future, even with late ripening varieties, to find the same cool ripening conditions that we experience today (Duchêne *et al.*, 2010). Indeed, there is a continuously increasing gap between the «cool ripening period», shifting later and later in fall, and the onset of ripening, shifting towards the warmest period of summer. This analysis does not apply when ripening already starts in present days before the peak of high temperatures in summer. We should pay as much attention to the ability of genotypes to maintain some required characteristics under warm conditions as to phenological stages.

2. Water use

The crop Water Use Efficiency (WUE) is a key parameter of the adaptation to the expected dryer summers in the future. There are many ways to define this parameter (see Flexas *et al.*, 2010 for a review). From a practical point of view, which can be the one of vine growers, it is the amount of water needed to produce one kilogram of mature grapes. There are many studies on the more efficient management techniques to maximize the WUE (Flexas *et al.*, 2010). WUE will also depend on the scions and rootstocks used, as well as on the timing of water availability. WUE can be studied at different scales within a plant (Flexas *et al.*, 2010) and through different physiological processes (Flexas *et al.*, 2010; Tomás *et al.*, 2014).

There are many studies comparing the behaviors of different grapevine genotypes under water restriction, and classifications have been proposed (Bota *et al.*, 2001; Gaudillère *et al.*, 2002; Tomás *et al.*, 2014). The understanding of the genetic determinism of traits relevant for water stress tolerance is, however, still limited, the first difficulty being to choose a relevant trait to study.

Classification under isohydric or anisohydric is one the methods proposed for describing cultivar behavior under water restriction (Schultz, 2003). Isohydric cultivars are characterized by a high capacity to maintain a high leaf water potential during the day, while the leaf water potential of anisohydric cultivars in the same conditions will drop significantly. The genetic basis for this trait was recently studied through a QTL approach on 186 genotypes, progeny from a reciprocal cross between Syrah and Grenache (Coupel-Ledru *et al.*, 2014). The authors identified many QTLs for traits such as

specific transpiration rate, specific hydraulic conductance, and minimal daytime leaf water potential. The percentage of total variations explained by these QTLs was, however, low and the degree of independence of the genetic determinism of these traits was quite unexpected. Finding the best combination of alleles from different loci, leading to the optimal behavior under water restriction in the field, will require further progress in crop modeling (Tardieu, 2003).

There is also a large variability among rootstocks regarding tolerance to water stress, from 110 R (tolerant) to Riparia Gloire de Montpellier (not tolerant) (review by Serra *et al.*, 2014). Marguerit *et al.* (2012) have detected many QTLs related to transpiration rate, $\Delta^{13}\text{C}$ values in leaves, transpiration efficiency, and water extraction capacity by studying the responses of Cabernet-Sauvignon plants grafted on 138 genotypes from a Cabernet-Sauvignon \times *Vitis riparia* cv. Gloire de Montpellier cross. This study showed that scion transpiration rate and its acclimation to water deficit was controlled by the rootstock. Rootstocks can then also be genetically improved for tolerance to water stress by breeding.

3. Berry quality

A high variability in berry sugar content can be found when comparing genotypes on the same date (Duchêne *et al.*, 2012c) or, conversely, on the date when the sugar content reaches a given value

(Costantini *et al.*, 2008). However, these values depend, on the one hand, on the climatic conditions between véraison and harvest and, on the other hand, on the fruit to leaf ratio of the plants. We have shown in progeny from a Riesling \times Gewurztraminer cross that when taking into account the genetic variability for véraison dates and fruit to leaf ratio, the residual genetic variability for sugar metabolism was low (Duchêne *et al.*, 2012c). Nevertheless, classical breeding has already created varieties with low sugar content producing wines with no more than 10-11% alcohol (Escudier, 2009). Possible driving factors can be a high fruit to leaf ratio, late véraison dates or berry physiology. The actual genetic variability for sugar metabolism, and the underlying QTLs, remains to be explored.

Higher temperatures during ripening are responsible for a faster decrease of berry acidity, due to the degradation of malic acid (Sweetman *et al.*, 2014) but tartaric acid concentration in berries is far less sensitive to high temperatures than malic acid concentration (Kliewer, 1971). Indeed, the quantity of tartaric acid per berry is generally constant throughout berry ripening (DeBolt *et al.*, 2008). Grapevine varieties with a high tartaric/malic ratio should be better adapted to warmer climatic conditions. As shown in Figure 1, there is a genetic variability for the tartaric/malic ratio in grapevine genotypes (Duchêne *et al.*, 2014a; Shiraishi, 1995). QTLs for pH and tartaric acid concentration have

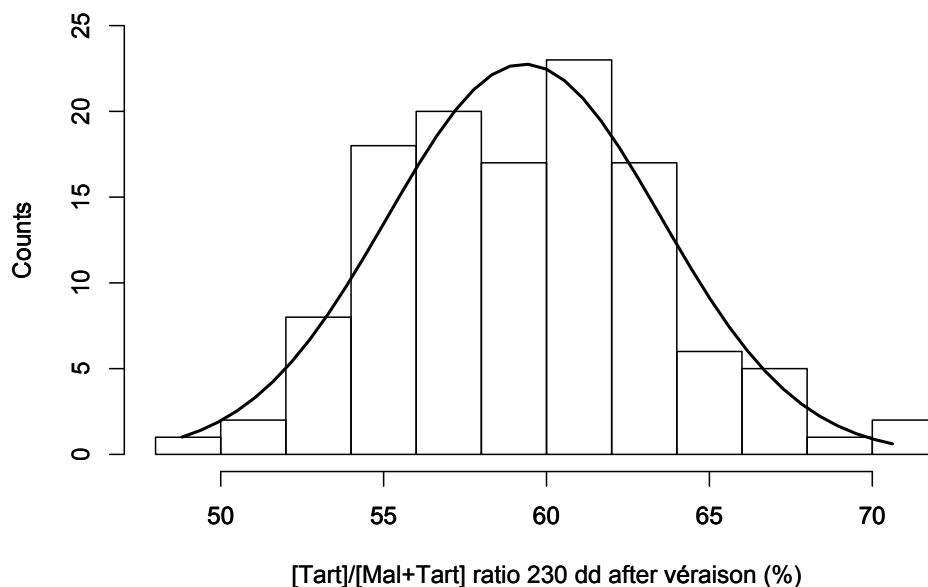


Figure 1 – Variability of the ratio between tartaric acid concentration and the sum of malic and tartaric acid concentrations in progeny from a Riesling \times Gewurztraminer cross (120 genotypes).

Means of data from 2006 to 2009. Organic acid concentrations were measured 230 degree-days (dd) after véraison for each genotype in the INRA experimental vineyard in Bergheim (Duchêne *et al.*, 2014a).

already been detected (Chen *et al.*, 2015; Houel *et al.*, 2015; Viana *et al.*, 2013), which opens the gate for breeding varieties able to keep a correct level of acidity under warmer conditions.

Regarding secondary metabolites, the decrease in anthocyanin content under high temperatures is certainly not equivalent for all the varieties (Barnuud *et al.*, 2014a; Kliewer and Torres, 1972). Understanding the genetic variability behind the profiles of phenolic compounds (Fournier-Level *et al.*, 2009; Huang *et al.*, 2012) can be of great help to breed new varieties whose color would be less affected by high temperatures. Up to now, there is no information on the possible different reactions of aromatic varieties to high temperatures.

CONCLUSION

Climate change will significantly modify the environmental conditions in most, if not all, the vineyards in the world. The impacts on wine production will depend on the region and the type of wine produced, but they will not always be negative: a warmer climate is an assurance to harvest ripe grapes every year and it will offer new opportunities for some currently cool grape growing regions.

The main risks are, on the one hand, a decrease of yields due to water scarcity and, on the other hand, the production of unbalanced wines with high alcohol content and low acidity. The consequences of new climatic conditions on the final concentrations of secondary metabolites (phenolic compounds, aromas) in wines are uneasy to anticipate. For anthocyanins for example, the positive effects of increasing solar radiation can, at least partly, counterbalance the negative effects of increasing temperatures. The possibility to delay harvest dates can also compensate for a lack of anthocyanin synthesis. Because several factors impacting grape anthocyanins will be modified simultaneously, their final concentrations at harvest in future conditions are very difficult to predict. If vine growers are able to better control the sugar content and the acidity of the grapes in the future, they will have more degrees of freedom for choosing the harvest date when the balance between sugars, acidity and aromas or anthocyanins is optimal.

Vineyard management techniques and cellar practices can be modified in the short term. New training systems need to be developed and experimented first, and could be implemented in the middle term.

Adaptation of planting material can take place at several levels. Clone collections already exist and

finding new clones for a given variety with higher acidity or lower sugar content can be achieved quite rapidly. A good point for clonal selection is that new clones can be cultivated without modifications of the regulation rules in the existing grape growing regions, including vineyards under registered designations of origin. The weak point is that the extent of genetic variability found in these collections might be too restricted to meet the challenges. In other words, the existing clonal variability can be useful in the short term, possibly in the middle term, but certainly not in the long term.

The next strategy is to test already existing varieties. Grapevine is already cultivated in warm regions and there are thousands of cultivars available in the genetic resource collections around the world. Except for grape growing regions already at the warm limit of the grape cultivation area, it should be possible to find scion × rootstock combinations able to grow in most of the present grape growing regions. Finding the appropriate combination from both an agronomical and enological point of view is, however, a goal for the middle term. The acceptance of new varieties will be all the more easy as the typicity of wines will be preserved.

In the long term, the ultimate goal is to breed new varieties. This can be necessary if no scion × rootstock combination gives satisfactory agronomical results or if the requirements for wine typicity are not met. Despite increasing knowledge of the genetic determinism of traits related to phenology, water use and berry quality, we are still lacking ideotypes. In other words, the objectives for breeders are not straightforward. Even with efficient breeding techniques, it takes about 10 years between obtaining a seed and releasing a variety, and even longer for this variety to be cultivated on significant surfaces. Certainly for the first time in human history of breeding, the environmental conditions can change between the time varieties are evaluated and the time wine growers use them. There is a need to anticipate the behavior of genotypes in new environmental conditions. This requires not only reliable models for predicting future climatic conditions but also crop models able to integrate allelic variations and responses to environmental data. Using such models, breeders would be able to identify the best combinations of alleles for a given set of climatic conditions before starting a breeding program using all modern techniques for revealing the genetic information in progenies.

Climate change is likely to modify wine production in many parts of the world. As of today, grapevine

genetic diversity allows grapevine cultivation and wine production in a wide range of environmental conditions across the world. In the future, the existing variability can be used, or extended by sexual reproduction, to provide solutions for adapting grapevine production to climate change.

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