

Adaptation to soil and climate through the choice of plant material

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Abstract

The choice of rootstock, scion variety, and training system best suited to the local soil and climate are key elements of economically sustainable wine production. The choice of the rootstock/scion variety best adapted to the characteristics of the soil is essential but, by changing climatic conditions, the ongoing climate change disrupts the fine-tuned local equilibrium. Higher temperatures are causing shifts in developmental stages, with increasing fears of spring frost damages on the one hand and ripening during the warmest periods in summer on the other. The expected increase in water demand and longer and more frequent drought events are also major concerns. Genetic control of the phenotypes, through genomic information but also epigenetic control of gene expression, offers a lot of opportunities to adapt the plant material for the future. For complex traits, genomic selection is also a promising method for predicting phenotypes. However, ecophysiological modeling is needed to better anticipate the phenotypes in unexplored climatic conditions. Genetic approaches applied on parameters of ecophysiological models rather than raw observed data are more than ever the basis for finding, or building, the ideal varieties of the future.

Introduction

The production of quality wine in economically viable quantities is the result of a delicate balance between productivity and grape composition. The optimal composition of the grapes depends on the profile of the desired wine and must respond to balances between sugar content, acidity, phenolic composition, and aromas and aroma precursors. This complexity is at the origin of the richness and diversity of the wines produced in France and in the world. Over the centuries, each vineyard has managed to find a balance between its natural environment, the plants, the vine management techniques, and winemaking. These ideal combinations are the reflection of what men considered to correspond best to their tastes, taking into account the constraints and advantages of the environment and the technical means at their disposal. The choice of plant material, the grape varieties, occupies a central place in the "typicity" claimed by the vineyards, whether or not they have an appellation. Climate change will generate imbalances in the environment-plant-people balances slowly developed over time in each vineyard. Can we anticipate these effects and imagine the genotypes that will allow vine-growers to continue to create wealth?

Materials and methods

Many genetic traits, concerning both rootstock and scion, are involved in adaptation to soil and climate. The purpose here is not to review all of them but to focus on those which will be critical for adaptation to climate change, for which genetic variability exists, and finally for which tools for simulating varietal behavior in the future are available.

Results and discussion

Phenology is a pivotal key to the adaptation of varieties to a region, or to a terroir, characterized by climatic parameters. Budburst dates should be early enough to allow for a long cycle, but late enough to avoid spring frosts. The ripening period, which begins at veraison, must take place in climatic conditions that allow sugar levels compatible with the type of wine desired and non-aggressive acidities to be reached. However, it is recognized that temperatures that are too high, although favorable to the parameters mentioned, are not



conducive to the expression of aromas and the accumulation of anthocyanins. Throughout the world, varieties are adapted in such a way that the ripening period conducive to the production of quality wines occurs as late as possible in the fall. For a given variety, the increase in temperatures leads to a double penalty, with a shift in the ripening period towards mid-summer, and for a given calendar date, higher temperatures (Fig. 1). Imagining genotypes that would ripen in cool conditions in the future is possible on the one hand thanks to tools for modeling the stages according to the temperatures, but also by the knowledge of the genetic determinants of these characterize clonal variability within a variety and to explore the extent to which this will compensate for the expected stage advances. The diversity of earliness existing among species of the genus *Vitis* is also an important source of variability that will likely need to be mobilized given the magnitude of the expected changes.

Modeling budburst dates as a function of temperature is less accurate than modeling flowering or veraison dates, but simulations, and unfortunately reality, show an increased risk of spring frosts in the future in some regions (Sgubin et al., 2018). An avoidance strategy, by choosing later budbreak genotypes, is the first to be implemented. Since, to our knowledge, no difference in frost sensitivity at a strictly equal stage has been demonstrated to date, the ability of genotypes to produce secondary shoots may be a parameter allowing some resilience to a frost event in the absence of avoidance.

Once the pitfall of the production of fertile shoots has been overcome, the productivity of the current year will depend, apart from damage from pests or pathogens, essentially on the water supply. This will condition the size of the berries. Water supply, but also nitrogen, will determine the number of inflorescences per shoot the following year (Guilpart et al., 2014). Genetic variability for the response to water availability and demand, both for rootstocks and for scions, is the subject of a large number of works (Brault et al., 2021; Dayer et al., 2020) that cannot be summarized here. Genetic variability for the response to nitrogen is to be explored.

One of the main challenges ahead is controlling the sugar content of the grapes, and therefore the alcohol content of the wines. The accumulation of sugars in grapes strongly depends on environmental factors such as temperature, incident radiation, and soil water availability. These factors, which vary according to the period in which maturation takes place, have very marked effects, often outweighing the effects of genetic variability (Suter et al., 2021). The effect of management methods, in particular the leaf-fruit ratio, also overlaps with the effects of environmental factors. While it is undeniable that there is genetic variability for sugar levels at harvest (Frioni et al., 2020), which may result from the factors mentioned above, it is nevertheless possible to take into account both veraison dates and the leaf-fruit ratio to identify genetic factors governing the assimilation of sugars (Gomès et al., 2021). More accurate approaches, using berry-by-berry sampling or volume monitoring, make it possible to capture the date on which phloem unloading stops and allow for better characterization of the differences between genotypes (Bigard et al., 2018).

Acidity is a major trait of grape berry quality driving the sensory properties of wines, their chemical and microbiological stability, and their aging potential. Grape acidity can be assessed by titratable acidity or pH. pH is determined by the content of organic acids, mainly malic acid and tartaric acid but also by cations, mainly potassium, that partially neutralizes the organic acids.

The genotypes used, both for scion and rootstock varieties, play a major role in the final acidity of wines. Phenology is a confusing factor when trying to compare genotypes. Comparing acidity parameters for different genotypes, even after the same number of days after véraison, can be biased because malic acid degradation depends on temperatures during ripening (Duchêne et al., 2014).

The concentration of tartaric acid in berries is much less sensitive to high temperatures than the concentration of malic acid. Indeed, the quantity of tartaric acid per berry is generally considered constant throughout berry ripening. Grapevine varieties with a high tartaric to malic acid ratio should be better adapted to warmer climatic conditions (Ramos & Martínez de Toda, 2021). There is a genetic variability for the tartaric to malic acid ratio in grapevine genotypes (Bigard et al., 2018; Duchêne et al., 2014) and modeling can help in predicting the effects of the genetic variability in the future (Fig. 2). Quantitative trait loci (QTL) in the grapevine genome driving tartaric acid concentration are already known (Duchene et al., 2020) which opens the gate for breeding varieties able to maintain a correct level of acidity in the warm conditions of the future. The links between genetic variations in [Mal], [Tart], or [Mal]/[Tart] and genetic variations of pH are rarely described because [K+] is often overlooked. Duchene et al. (2020) showed that malic acid concentrations, or the malic to tartaric acid ratios, were driven by strong QTLs on chromosomes 6 and 8, but were not associated with variations in pH. These pH variations were explained by QTLs for the potassium-to-tartaric acid ratio, on chromosomes 10, 11, and 13.



[K+] in grape juices also depends on the rootstock used, which could induce variations of pH between 3.76 and 4.27 in 'Shiraz' grapes (Kodur et al., 2013). Genetic variations for [K+] in leaves in hybrids from a rootstocks cross (Gong et al., 2014) open the possibility of breeding rootstocks for K+ accumulation in scions.

Phenolic compounds are key components of wines: anthocyanins for berry color and condensed tannins for wine structure and astringency. The decrease in anthocyanin content under high temperatures is well-documented (Lecourieux et al., 2017). High temperatures do not reduce the concentrations of all anthocyanins with the same intensity: di-hydroxylated anthocyanins are more affected than tri-hydroxylated anthocyanins, malvidin-3-O-glucoside less than delphinidin-3-O-glucoside (Lecourieux et al., 2017). A locus on chromosome 2 is responsible for berry color (Fournier-Level et al., 2009) and, within colored varieties, genetic polymorphisms in the same genomic region are associated with continuous variations of anthocyanin concentrations (Fournier-Level et al., 2009). Data from Lecourieux et al. (2017) suggest that the effects of high temperatures are all the more significant as the number of methyl groups is lower. In parallel, Fournier-Level et al. (2011) detected a link between genetic variations on chromosomes 1 and 2 with the levels of anthocyanin methylation in a Syrah x Grenache progeny. They were able to associate two SNPs in a gene coding for an O-methyltransferase with the level of methylation. These results indicate that molecular markers can be used for breeding varieties with a high capacity to maintain their coloration under high temperatures.

The effects of temperatures on aromas and aromas precursors are well documented but genetic variations in the magnitude of responses remain to be explored.



Date

Figure 1. Simulations of maximum temperatures during the ripening period for two virtual extreme genotypes and two climatic datasets (Gomès et al., 2021).

The arrows represent the ripening periods, i.e., 35 days starting at 50% véraison, for two virtual genotypes: the earliest and the latest that should be found in an infinite progeny from a Riesling x Gewurztraminer cross. Two climatic datasets are used: historical data from 1976 to 2006 and simulated data (A1B scenario) for Colmar (48°04'46.3"N 7°21'26.0"E).

Conclusion

Climate change is disturbing fragile balances resulting from centuries of adaptation. The choice of the plant material is a key factor that generates the typicity and the reputation, as well as the markets, of the current wine production. Keeping the same profile of wines, but also shifting of wine profile, will require an adaptation of the plant material. The existing genetic variability among clones or varieties is a powerful source of adaptation but the magnitude of the challenge will certainly require exploring the diversity among species and breeding new cultivars with desired characteristics. Knowledge of the genetic determinism of traits for adaptation is continuously increasing, and coupled with ecophysiological modeling, provides an unprecedented tool for building the genotypes of the future. At the same time, a better understanding of epigenetic regulations opens new perspectives for the control of gene expression and plant phenotypes.



Colmar, RCP8.5



Figure 2. Simulations of expected pH 30 days after véraison in the future for two real genotypes from the progeny of a cross between Riesling and Gewurztraminer. For both of them, the sum of tartaric and malic acid in green berries is 220 mmol/l but the tartaric/malic ratio is 0.87 for 205E and 0.44 for 4078G.

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