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Combining ecophysiological models and genetic analysis : a promising way to dissect complex adaptive traits in grapevine

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Abstract

Designing genotypes with acceptable performance under warmer or drier environments is essential for sustainable crop production in view of climate change. However, this objective is not trivial for grapevine since traits targeted for genetic improvement are complex and result from many interactions and trade-off between various physiological and molecular processes that are controlled by many environmental conditions. Integrative tools can help to understand and unravel these Genotype × Environment interactions. Indeed, models integrating physiological processes and their genetic control have been shown to provide a relevant framework for analyzing genetic diversity of complex traits and enhancing progress in plant breeding for various environments. Here we provide an overview of the work conducted by the French LACCAVE research consortium on this topic. Modeling abiotic stress tolerance and fruit quality in grapevine is a challenging issue, but it will provide the first step to design and test *in silico* plants better adapted to future issues of viticulture.

Mots clés : Process-based models, climate change, adaptation, G×E interaction, grapevine

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Introduction

Exploiting genetic diversity or designing new scion varieties and rootstocks with better performance under water stress or high temperature is one of the possible paths to sustain high-quality viticulture in view of future climate change (Duchêne, 2016). However, this breeding challenge is not trivial for perennial fruit crops, including grapevine, since the main traits targeted for genetic improvement (*e.g.* plant growth and tolerance to abiotic stresses, yield, fruit quality) are quantitative and complex, as they result from many interactions and trade-off between various physiological and molecular processes that (i) act at different temporal, spatial and structural scales and (ii) depend on environmental conditions and management strategies.

Ecophysiological process-based models (PBMs) can predict quantitative traits of one genotype in any environment, whereas quantitative trait locus (QTL) models predict the contribution of alleles under a limited number of environments (Tardieu, 2003). Approaches combining both ecophysiological modeling and QTL analyses have been developed recently (Hammer *et al.*, 2006 ; Reymond *et al.*, 2003 ; Yin *et al.*, 1999), essentially in annual crops, to overcome the strong G×E interactions in the control of complex traits in plants and to improve QTL detection power. The method dissects the genotypic variation of a given complex trait into simpler ecophysiological model parameters linked to key underlying processes involved in this trait. Then, co-localization (or absence thereof) between QTLs for the trait and QTLs for model parameters can give new insights into the contribution of processes involved in the trait.

Hence, it may help in the choice of candidate genes, or may give clues about the genomic regions to be combined in an ideotype. This approach is particularly well suited for studying plant adaptive responses to diverse environmental conditions (Prudent *et al.*, 2011). It appears as a valuable tool to help make informed decisions with regard to genotypic adaptation options and ideotype design in the context of climate change (Ramirez-Villegas *et al.*, 2015).

Such an approach combining ecophysiological modeling and genetic analyses is still in infancy in the international grape community (Duchêne *et al.*, 2012 ; Marguerit *et al.*, 2012). We report here some of the pioneering work from the French LACCAVE research consortium on this topic. Models developed for plant drought response and berry sugar accumulation are outlined. These models consist of simple response curves for one trait or are able to simulate more complex physiological processes. Genetic parameters were defined and their variations among genotypes or segregating populations analyzed. The potential use of such models to simulate grapevine ideotype behavior under future climatic conditions is discussed.

Gene-by-gene breeding approach remains elusive for complex traits in grapes

Over the past century, conventional plant breeding has been used successfully to improve several crops. With the recent progress in molecular technologies for genome sequencing and functional genomics, genes have become tangible rather than virtual entities (Hammer *et al.*, 2006). It is widely anticipated that a gene-by-gene approach will improve plant breeding efficiency. Indeed, there have been successes in developing plants that are more resistant to pests or tolerant to herbicides. Those cases involved single-gene transformations where plant phenotypic response scaled directly from the level of molecular action. However, this has not yet been extended to key complex traits where relationships among components and their genetic control involve quantitative multi-gene interactions (Tardieu, 2003).

In grapes, up to now, few physiological functions have been clearly related to known gene sequences, and the tremendous progress in gene discovery has only weakly aided genetic selection (Martinez-Zapater *et al.*, 2010). This results partly from the complexity of most of the traits of interest and their control by multiple interacting genes, which themselves interact with the environment (Bertin *et al.*, 2010). Therefore, QTLs for a given trait usually explain only a low proportion of the observed trait variations (Fanizza *et al.*, 2005). In addition, as most of these QTLs depend on the environment and the genetic background (Chenu *et al.*, 2009 ; Reymond *et al.*, 2004), extensive experiments over several years at different sites or under different environments have to be performed. Although this approach is useful to evaluate QTL stability (Prudent *et al.*, 2011), it is time-consuming and expensive and can be only conducted with few genotypes and traits (Bertin *et al.*, 2010).

To understand and unravel these Genotype × Environment interactions, the use of PBMs has been

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proposed (Hammer *et al.*, 2005; Yin *et al.*, 2004; Yin and Struik, 2016).

Modeling plant responses to future environments is still a challenging issue in grapes

PBMs have been increasingly used in perennial fruit crop research during the last 50 years and are undoubtedly interesting heuristic tools for quantifying plant responses to environmental and management factors within a mathematical framework (Génard *et al.*, 2007; Struik *et al.*, 2005). This framework allows dynamic simulations of the main underlying biophysical processes that determine plant growth and development and fruit quality build-up, as well as characterization of the phenotypic plasticity. Environmental factors are often considered as input model-driving variables, and parameters are used to represent genotype-specific characteristics. Phenotypes or traits of interest are the emergent outcomes of the represented system. As PBMs represent causality between component processes, they can predict plant behavior beyond the environment for which model parameters were estimated. This singular property allows the models to potentially resolve G×E interactions into underlying processes and predict plant performance in any environment. As a result, these models can offer significant advantages in assessing and simulating the effects of climate change as compared to purely statistical or rule-based models derived

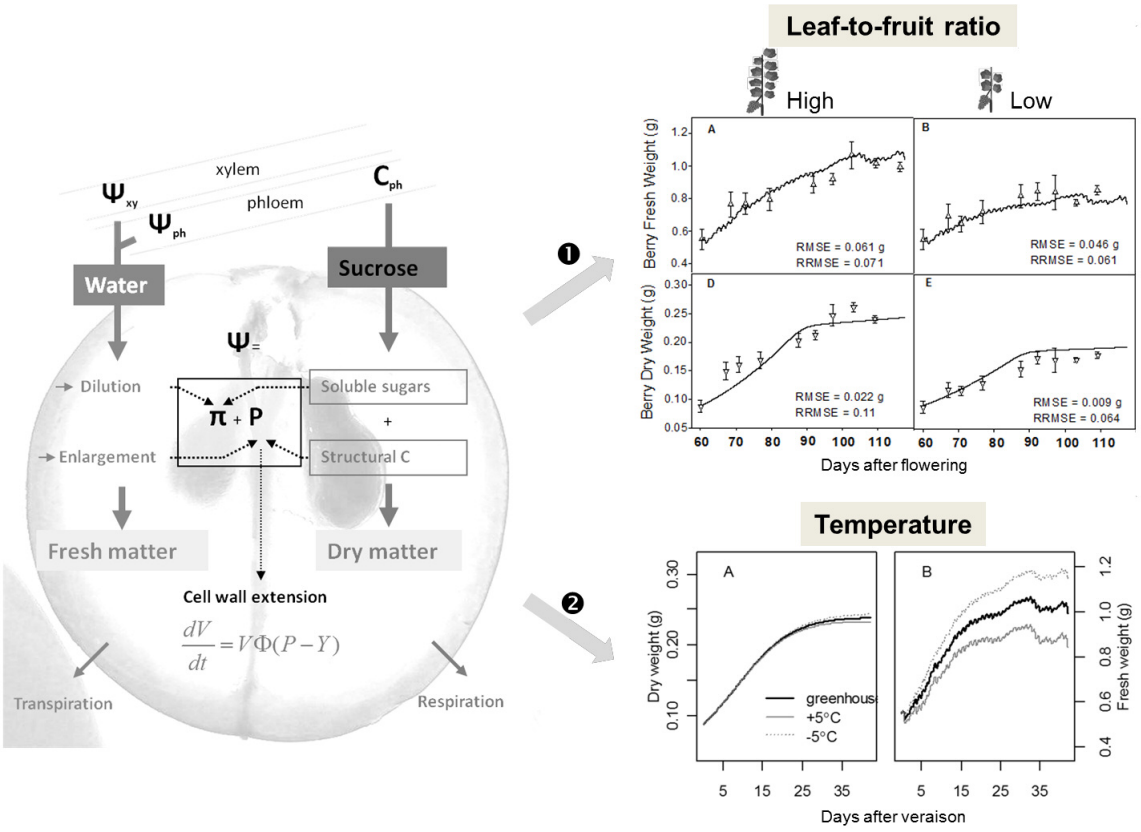


Figure 1 - Modeling the effects of environmental and management practices on dry and fresh mass accumulation in ripening grape berries (adapted from Dai *et al.*, 2008, 2010).
A process-based model was developed to describe the growth of an individual berry on a diurnal basis taking into consideration only fundamental biophysical processes and their response to external conditions. It accurately predicted mean berry fresh and dry mass accumulation in response to different leaf-to-fruit ratios or canopy temperature. Briefly, the model represents a virtual mean berry during the post-veraison developmental stage, which is assumed to behave as a single cell separated by a composite membrane from the parent vine and the outside environment. Water accumulation was calculated through the water balance between xylem and phloem water influx and transpiration water loss, controlled by water potential gradient between the berry and the parent vine. Meanwhile, dry mass accumulation was simulated with the balance between phloem sugar import and respiration carbon depletion. The inputs of the model included initial fresh and dry mass, phloem sugar concentration, xylem water potential, fruit temperature and air humidity.

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from previously collected data, which have no explanatory power (Soussana *et al.*, 2010). However, shortcomings exist. Uncertainty in PBM outputs could be higher than for the empirical approach due to greater model parameters and data inputs to represent the many processes in the system (Challinor *et al.*, 2009). The addition of processes and parameters makes it hard to evaluate error propagation and to understand the different sources of uncertainty and their relative importance. Moreover, applied to similar environmental conditions, different models often provide different results (Rötter *et al.*, 2015). Finally, modelers must keep in mind that whatever the level of complexity of PBMs, it will be impossible to reproduce precisely the biological reality and to identify all the factors for all situations that may influence plant performance (Sinclair and Seligman, 1996).

A large diversity of PBMs exists in grape literature (see for review Dai *et al.*, 2010; Moriondo *et al.*, 2015), developed at different time and spatial scales, ranging from crop models, which aim at simulating the entire plant growth cycle (*e.g.* Bindi *et al.*, 1996; Garcia de Cortazar-Atauri *et al.*, 2006), to functional models, which focus more on specific processes such as phenology (Cola *et al.*, 2014; Garcia de Cortazar-Atauri *et al.*, 2009; Parker *et al.*, 2011, 2013), leaf gas exchanges (Prieto *et al.*, 2012), plant water dynamics (Lebon *et al.*, 2003), or berry growth and quality (Dai *et al.*, 2008; **Figure 1**). The choice of which processes to represent in detail and the level of complexity achieved for a given process is of course conditioned by the understanding of underlying grapevine physiology and the available experimental dataset. It is also governed by research focus and intended model use. Therefore, several key processes are still poorly simulated in current grape PBMs. For instance, modeling the distribution of acquired resources among source and sink organs (in particular to the root system) and its plasticity in relation to external availability is one of the weakest features. It is, however, of great importance in plant growth and yield (Vivin *et al.*, 2002). The perennial nature of grapevine is also rarely considered, and the relevant contribution of resource reserves in simulating the plant growth process is not well represented (Moriondo *et al.*, 2015). An understanding of below-ground processes and nutrient assimilation is widely lacking in most models. Concerning yield and fruit quality, models are mainly restricted so far to berry growth, focusing on dry mass accumulation; forthcoming fruit models must now focus on essential aspects of berry composition such as sweetness, acidity, and secondary metabolites (Dai *et al.*, 2010).

Presently, most PBMs account to some degree for the effects of environmental variables and basic plant management. PBMs typically respond to temperature, plant water status, radiation, and atmospheric CO_2 concentration and therefore can be applied to assess impacts of, and adaptation to, future climate projections (Mosedale *et al.*, 2016). However, to deepen this analysis, it is still necessary to enlarge their ability to capture the effects of climatic variability and extremes (Soussana *et al.*, 2010). For example, PBMs often consider the increasing temperature effects on various processes including phenology, carbon uptake and assimilation, and evapotranspiration; however, heat stress impacts or acclimation feedbacks are not considered explicitly, which can generate biased predictions in the models under analysis. Similarly, water and nutrient stresses are typically captured so far by empirical calibration. It is also known that increased CO_2 concentration can limit water loss through stomata; however, many models lack explicit details about photosynthesis and cannot account for the interaction between water use and production (Rötter *et al.*, 2015). As such, they may overemphasize the effects of future droughts. Finally, progress has been made in testing PBMs with field experiments under a wide range of growing conditions, even effects of CO_2 with FACE experiments (Bindi *et al.*, 2001). However, multi-site, multi-year experiments studying the effects of climate change variability are still scarce.

Process-based models could provide a relevant framework for analyzing genetic diversity and enhancing progress in plant breeding

While current PBMs often prove as valuable in guiding research as in providing quantitative predictions, they still lack the ability to describe all the subtle complexities associated with genotypic differences (Yin and Struik, 2008), and only few models incorporate knowledge derived from genomic studies. To become effective tools for addressing G×E interactions, existing models first have to be improved, both in terms of model structure and input parameters (Bertin *et al.*, 2010). Predicting complex traits in relation to G×E interactions requires the design of mechanistic models that represent as much as possible the underlying physiological processes and generate the phenotype of the plant as an

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emergent consequence of model dynamics (Boote *et al.*, 2001).

A key feature of the models considered is the level of granularity that adequately captures the crucial elements of system dynamics (*i. e.* models should be 'as simple as possible, but not simpler') (Hammer *et al.*, 2006); therefore, much of the fine detail is not required in generating a robust prediction of system behavior (Tardieu, 2010). Secondly, the model equations describing the mechanisms should ideally contain a few genotypic parameters independent of the environment, (i) of which values show a significant range of variation among the studied genotypes and (ii) which have significant influences on model outputs (Bertin *et al.*, 2010), and thus are likely to induce changes in important emergent properties. Model parameters - one set of parameters representing one genotype - must be precisely estimated at low labor cost on a large number of genotypes. They should have a biological meaning, and mutants for parameters should be available to allow the validation of theoretical variations in the models (Bertin *et al.*, 2010). Sensitivity analysis of the model to its parameters can also help in identifying important genotypic parameters and their putative effect under different climates (Quilot *et al.*, 2005). Under these conditions, a robust model provides a dynamic biological framework to analyze component traits. This can generate improved connection to the genetic architecture that controls the trait of interest by identifying model parameters that link more stably to genomic regions than direct phenotypic measures (Tardieu, 2003), as illustrated recently in a tomato sugar model (Prudent *et al.*, 2011).

In grapes, such an approach combining the evaluation of genetic parameters from PBMs and the genetic dissection of the parameters with QTL analyses is scarce. To our knowledge, it has been only successfully applied to quantify the effects of

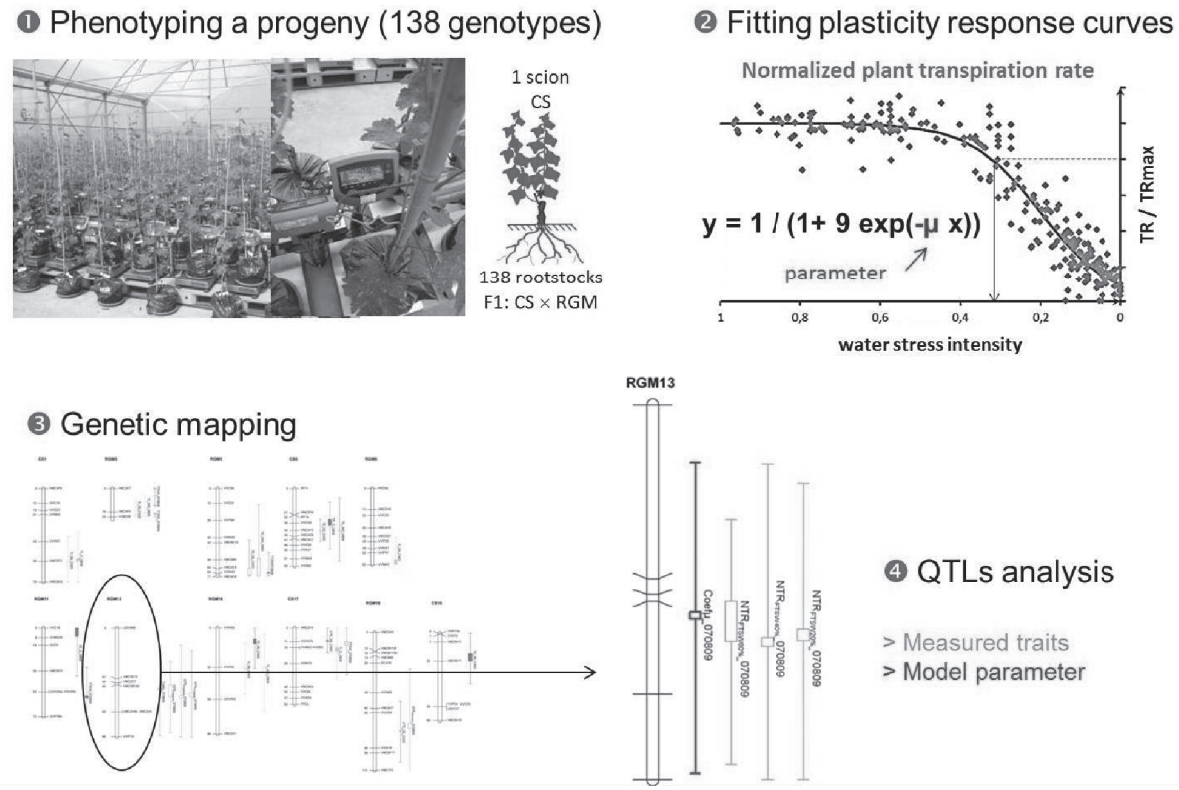


Figure 2 - Diagram of the different steps to identify QTLs of model parameters
(adapted from Marguerit *et al.*, 2012). 1) Experimental set-up to control water deficit intensity with balances and to obtain daily transpiration data of 138 genotypes of the mapping pedigree issued from a cross between *Vitis vinifera* Cabernet-Sauvignon and *Vitis riparia* Gloire de Montpellier, 2) Transpiration response curves to water deficit intensity were fitted for all genotypes and each one was characterized by its μ value. Lower μ values were associated with an earlier downregulation of transpiration (in terms of water stress intensity), 3) QTL identification was carried out and genetic maps with QTL localization could be represented, 4) Comparison of the localization of measured traits and model parameter.

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allelic variations on parameters of phenological models (Duchêne *et al.*, 2012) and to analyze rootstock control of scion transpiration in response to water deficit (Marguerit *et al.*, 2012; **Figure 2**). In both studies, genetic parameters were defined from simple response curves for one trait and their variations among genotypes or *Vitis* segregating populations analyzed. Concerning fruit quality, a PBM predicting post-veraison sugar accumulation in berries was recently developed (Dai *et al.*, 2009) in order (i) to dissect the relative influence of three underlying processes : assimilate supply (S), metabolic transformation of sugars into other compounds (M), and dilution by water uptake (D); and (ii) to estimate the genetic variability of S, M, and D. Model analysis over three growing seasons in the progeny from a Riesling × Gewurztraminer cross showed that a coefficient (k) related to the non-sugar use of carbon imported in berries was different between the individuals of the progeny, explaining part of the variability in sugar (Dai *et al.*, 2016). The QTLs linked with this model parameter need to be determined to identify the underlying gene candidates that control the utilization of imported carbon for the non-sugar compounds in grape berry. The combination of physiological observations with model analysis provides an alternative way to identify gene candidates that are involved in berry quality regulation.

Models integrating physiological processes and their genetic control are a first step to design and test *in silico* plants for future environments

A well-defined objective, which describes the desirable features of concerned traits, is a prerequisite for successful breeding programs, including breeding new genotypes specifically adapted to the future environments projected by climate change models. The objective definition process will need first to assess the potential sustainability of the existing genotypes under the future climatic conditions. The next step will be to search by simulation how to combine genetic information to obtain virtual genotypes best adapted to various climatic scenarios (*i. e.* nearest to ideotypes). This process is usually narrowed into mathematical optimization problems to identify the best combinations of genetic parameters values (Quilot-Turion *et al.*, 2012). The feasibility to create the designed cultivar has to be tested by combining PBMs with genetic controls. This is because a virtual cultivar designed without considering the naturally existing genetic variability may not be created in real breeding procedure. In fact, modelers can screen the best allelic combination of genes controlling a given trait through model simulation under a specific environment. However, producing the identified genotype can be easy or difficult depending on the positions of the considered genes and the distance between them, although breeders have developed strategies to separate closely linked genes (Letort *et al.*, 2008). In addition, it is extremely useful to have an idea of the value of a virtual genotype without having really to build it, especially in the case of pleiotropy when compromises have to be made. Using model parameters to build such genotypes should help to overcome the limitations due to environmental pressure on QTL detection. The exploitation of QTLs in breeding programs is, however, conditioned by their heritability, the level of genetic variations in the populations, the genetic correlations among them, and the number of loci related to the trait.

Many PBMs have been used in various crops to conduct *in silico* simulation by integrating the existing genotypes with projected future environments, yet very few studies concerned grapes (Bindi *et al.*, 1996; Garcia de Cortazar-Atauri, 2006; Fraga *et al.*, 2016). For example, phenology models have been successfully used to test the budbreak, flowering and veraison dates of grapevine cvs. Riesling and Gewurztraminer in the future environment (Duchêne *et al.*, 2010). In this work, the authors also analyzed the genetic variations for the parameters of a temperature-based phenology model among genotypes from the progeny of these two varieties. This allowed the design of virtual genotypes and the testing of their behavior (*i. e.* the calculation of the expected budbreak, flowering and veraison dates), under an IPCC (Intergovernmental panel on climate change) scenario. Doing so can provided clues as to whether existing and virtual genetic variability will be reached to face the extent of predicted climate changes. Similar studies should be developed on more complex adaptive traits in the future.

Conclusions

An approach combining ecophysiological modeling and genetic analyses is original and challenging in grapes in terms of objectives and outcomes. It should provide a promising way of overcoming the uncertainties associated with gene and environment context dependencies that currently impede progress in molecular breeding. Furthermore, it is a first step towards ideotypes for new grapevine cultivars better adapted to future issues of viticulture. A prerequisite is the development of robust PBMs able to describe physiological processes and their responses to

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variations in environmental conditions and to allow physiological feedback features and the integration of information from different organizational levels. In addition, PBMs will have to be tested for a large set of genotypes in order to extend their ability to simulate genetic variations and identify strong genotypic parameters.

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