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Research unit	N°	1334
	Name	UMR AGAP (https://umr-agap.cirad.fr/en)
Title of the PhD	Study of the developmental plasticity of the grapevine fruit to drought	

Abstract

The latest IPCC report (www.ipcc.ch) confirmed that temperature and evaporative demand will continue to increase, raising serious concerns on **water availability** for viticulture in many regions.

Present *Vitis vinifera* cultivars have been empirically selected to fit with various regional climates, and constant progress are made on the understanding of this **acclimatization or adaptation** of grapevine to thermo-hydric factors, especially with regard to the construction of yield and fruit quality.

Process based models that describe the effects of abiotic factors on C assimilation and the allocation of photo-assimilates to organs allow pertinent studies about **phenotypic diversity**. However, accounting for **berry asynchrony and population structure** is still needed for the quantitative assessment of the import of water and photo-assimilate in the developing fruit, in order to decipher the fine molecular and genetic mechanisms of adaptation to water deficit. Actually, until now, the future harvest was considered as a single fruit, which is not pertinent on the kinetic point of view.

Using a panel of 16 genotypes exhibiting contrasted phenotypes, the PhD will study the **2 levels of regulation** of the acclimatization and the adaptation to drought: i) the intrinsic metabolic and transcriptomic **responses of the single berry**, ii) the **role of the synchronicity and heterogeneity** of single berry ripening within the bunch, as a possible site of source-sink feedback.

Funding		
Nature	Source	Available /requested
Functioning costs 2020-2023	ANR AAP CE20 - G ² WAS	Available
PHD scholarship (40 months) 1/1/2020 to 31/12/2023	China Scholarship Council	This application

Doctoral school	GAIA - Biology, Interactions, Plant adaptation (Montpellier, https://www.adum.fr/as/ed/gaia/index.pl)
PhD committee	Member 1: Dr. Z. Dai (CAS, Beijing, China) Member 2: Dr. C. Romieu (INRAE, Montpellier, France) Member 3: Pr. L. Torregrosa (Institut Agro, Montpellier, France) Member 4: Pr. E. Gomes (Bordeaux Uni, Bordeaux, France) Member 5: To be determined

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PhD project description

Scientific and socio-economic issues

For several years now, the evaporative demand has exceeded rainfall in many Mediterranean climatic areas worldwide, **degrading the water balance** (Santillan et al., 2018; Torregrosa et al., 2018). For example, the viticulture drought index has been constantly negative since the 2000s in the region of Montpellier. The IPCC reports (www.ipcc.ch) indicate that these trends will continue, accentuating the **climatic constraints** that the wine industry will have to face in semi-arid zones but also in other regions in Europe (Fig. 1) and abroad (Bois B., 2019).

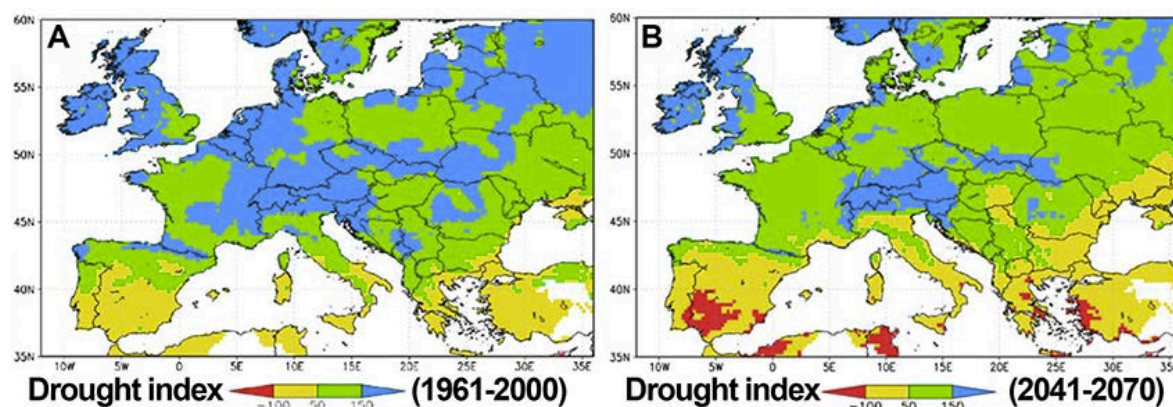


Fig.1 - Simulation of the evolution of the *Viticulture Drought Index* for the next 50 years (Fraga et al., 2013)

Considered a fairly drought-tolerant species (FAO, 2019), vines are generally not irrigated in Europe. The instauration of a progressive and limited water stress during ripening is even considered favourable to the production of quality red wine (Champagnol, 1984; Ojeda et al., 2007; Chaves et al., 2010). However, an excessive **constraint penalizes the yield and quality** of production (Ojeda et al., 2007).

Recent progresses were made on the genetic origin and diversity of the thousands of *V. vinifera* grape varieties grown worldwide (Liang et al., 2019; Riaz et al., 2018), however their phenotypic and **physiological diversity is still poorly documented** (Galet, 2015; Bigard et al., 2018). The thermal needs for the completion of the successive phenological stages are better documented than metabolic specificities (Morales-Castilla et al., 2020), and in this respect, the well-known North-South gradient in wine composition demonstrates the limits of varietal adaptation in terms of fruit quality. In fact, viticulture has adapted to various thermo-hydric conditions through the choice of cultivation routes and the type of wine produced, not only through that of grapevine cultivars.

Despite recent progresses to study the response of vegetative (Coupel-Ledru, 2016) and reproductive (Savoi et al., 2017) organs to water stress, knowledge of the physiological mechanisms involved in acclimatization and adaptation remains too fragmentary to develop **mitigation or selection strategies**. Multifaceted proteomic and transcriptomic responses to stress were recently characterised, principally on leaves or rootstocks (Catacchio et al., 2019; Degu et al., 2019; Liu et al., 2019; Krol et al., 2017; Jiang et al., 2017) but their genetic diversity remains poorly known.

The proposed study will be carried out on a selection of 16 genotypes from a panel of *V. vinifera* genetic diversity (Nicolas et al., 2016). The genotypes, selected from expert background and/or from preliminary data to represent contrasting source-sink ratios, will be confronted to a water stress gradient. We will focus on the consequences of these water and carbon limitations imposed by water deficit on fruit development. This work will be conducted in collaboration with

ecophysiologicalists from UMR LEPSE who will characterize the functioning of the vegetative system under water stress, in the frame of the **French ANR G2WAS program** (2020-2024, Total budget of 3 100 K€). Two levels of regulation of grape acclimatization and adaptation will be explicitly addressed: i) the transcriptomic and intrinsic metabolic response of the single berry and ii) the role of the synchronicity and heterogeneity of ripening of single berries within the bunch.

Providing a better understanding of the direct and indirect effects of water stress on berry development, this study will be decisive to: i) **develop** mitigation strategies, notably through better management of water stress and ii) to develop genetic resources and **diagnostic tools** for the selection of drought-tolerant varieties.

State of the scientific art - Originality of the project

The **G2WAS ANR project** (umr-agap.cirad.fr/research/main-projects/g2was) aims to study the effects of water deficit on vines on intra- and inter-annual scales, by integrating the dynamics of production, storage and use of carbon resources in vegetative and reproductive systems. The final objective is to identify the genomic regions regulating **adaptive mechanisms** at the level of the vegetative and reproductive organs, through a GWAS study of a diversity panel of 279 *V. vinifera* varieties (workpackage WP3).

In order to optimize the experimental conditions (stress level) and most pertinent parameters to analyze on such numerous genotypes, the physiological response of the vine to a growing water deficit will be studied in depth (WP2). In this WP, the PhD will address the response of 16 contrasting, representative genotypes subjected to a gradient of 10 water conditions. This work will be carried out on the M3P Phenodyn platform (www6.montpellier.inrae.fr/lepse_eng/M3P) that is dedicated to the fine characterization of the **plant response to drought**. The use of a similar platform allowed the identification of water stress tolerance QTLs in *Vitis* rootstocks (Marguerit et al., 2012) and, for scions, revealed the genetic diversity of the regulation of night-time transpiration and the links between hydraulic properties and stomatal regulation (Coupel-Ledru et al., 2014; 2016). However, the fruits, which are the strongest sinks for water and photo-assimilates of the vine during drought period, were systematically removed in these studies.

The effects of water stress on grape development and metabolism are diverse. Deluc et al (2009) and Hochberg et al (2015) reported variations in various central metabolic compounds including sucrose, several amino and organic acids, ascorbate and raffinose. Water deficiency can also impact the synthesis of volatile compounds (Bindon et al., 2007; Savoi et al., 2016), accumulation of carotenoids (Deluc et al., 2009) and phenolic compounds (Castellarin et al., 2007a, b; Hochberg et al., 2015).

A **structure-function model** has recently been developed to describe the effects of water deficit on water and sugar flows in grapes (Zhu et al. (2019)). It is based on 2 varieties of *V. vinifera* subjected to 2 water stress levels, and includes 5 modules: (i) canopy architecture; (ii) leaf gas exchange; (iii) water transport; (iv) carbon distribution; and (v) berry growth. This first integrative model paves the way for understanding the relative contributions of **different processes in the growth and ripening of fleshy fruits** and their response to water stress. However, it relies on the critical assumption that the future harvest and the fruit can be assimilated on the kinetic point of view, an oversimplification neglecting the 2-3-week asynchrony between berries, in well-watered conditions. Furthermore, **primary metabolism** within the fruit have not been detailed, whereas the balance between sugars and organic acids is a determining factor of the grape quality. Finally, this work, which was only carried out on 2 varieties, did not take into account inter-annual effects.

We have previously attempted to deconvolute the effects of thermal stress on grape berry phenology and primary metabolism, evidencing subjacent transcriptome regulations (Rienth et al., 2014; 2016), based on **berry sorting at different dates**. Gradually, we have been led to completely reconsider metabolic and hydric flows within the berry, as opposed to the population (Shahood et al., 2019) and to propose new sampling and phenotyping schemes in genetic and transcriptomic studies (Bigard et al., 2019; Savoi et al., in progress). In fact, **phloem unloading** in the fruit is much faster than kinetic approaches of the overall harvest would suggest, as in these last ones, the speed of fruit development and the shift between individuals are obviously summed up. Taking these phenomena into account in genetic studies significantly increases heritabilities for fruit traits under developmental control (growth, sugars and organic acids), which increases the power of QTL identification (Breil et al, in preparation). Malate breakdown appeared as an inducible phenomenon, depending on the balance between photo-assimilate availability, and fruit respiration, as influenced by temperature (Rienth et al., 2016; Romieu et al., 2016). **Single berry approaches** have also enabled the identification of ON/OFF genes, according to phloem activity (Savoi et al., in progress), and put forward the central role of vacuolar sugar/H⁺ antiporters in the stoichiometry between malic acid breakdown and sugar storage (Romieu et al., 2018; Shahood et al., 2019).

We therefore propose to **complement the classical eco-physiological variables** (Zhu et al., 2019) with a precise description of the modifications induced by water stress on the flow of water and C to the fruits. **Transcriptomic analyses** will be done at key developmental stages to identify the **gene networks** recruited during the response to drought of phenotypically distant grapevine genotypes. This transcriptome profiling will facilitate **candidate gene analysis** of the QTLs produced by GWAS in WP3. To take into account inter-annual effects (Guilpart et al., 2014), the effects of a constraint in year N on grape development and composition at N+1 will also be characterised.

Research questions proposed to the applicant

1. What **molecular signals** are mobilized by a water-deficient berry during the different sub-phases of ripening?
2. Is the **desynchronization of the induction of sugar storage** between fruits dependent on the source/sink balance and is it an important form of feedback during water stress?
3. If so, how can the **temporal structure of the population** be taken into account in modelling/prediction of yield and quality at the plant level?
4. Is there a **genetic plasticity in the allocation of photo-assimilates** between vegetative compartments and pericarp in the year of the stress and what are its consequences on the next growing cycle?

Working hypotheses

1. The application of a precise water deficit gradient in the **Phenodyn platform** will produce informative developmental and molecular phenotypes.
2. **Single berry phenotyping** will provide original data on the effects of water deficit on fruit development and associated transcriptomic patterns.
3. The 16 genotypes will exhibit diverse **water use efficiencies**, water and photo-assimilate partitioning patterns between vegetative and reproductive compartments with annual and inter-annual effects.

Material and methods (available and/or to be produced)

Plant material - 40 genotypes from the GWAS panel of 279 genotypes were grown for 2 years (2018 and 2019) in 20 copies/genotype. Within this material, 14 genotypes will be selected according to the following criteria: expert data, genetic diversity and if known: iso/anisohydric behaviour and level of night-time leaf transpiration, vegetative vigour, fruit volume, fruit sugar demand, level of organic acid accumulation, composition of phenolic compounds (anthocyanins). Two microvine lines (Torregrosa et al., 2019) with contrasting phenotypes for organic acid content and berry size were also prepared and characterized under greenhouse conditions without water stress: growth, organic acid content, sugars and cations. The possibility offered by the microvine to infer spatio-temporal development data (Luchaire, 2015) will enable the modulation of the fruit's response to water deficit to be studied in greater detail over a range of source-sink ratios.

Experimental conditions - Ad hoc phenotyping facilities (Phenodyn, www6.montpellier.inra.fr/m3p) allowing to accommodate 16 genotypes x 10 plants have been booked, greenhouse and ecotron spaces are available for pre- and post-stress periods.

Methodologies - Protocols for monitoring single-berry development (Savoi et al., in preparation) and strategies for the constitution of representative fruit samples have been developed (Rienth et al., 2014, 2016). RNAseq data analysis pipelines are routinely used (in 2019, more than 110 RNAseq analyses performed on berries at different stages of development). SouthGreen bioinformatic platform (umr-agap.cirad.fr/l-unit/infrastructure-technical-platforms/software-platforms/platform-south-green-de-bioinformatique) allowing the storage and analysis of massive sequencing data is available to our research unit. Primary metabolite analysis methods are routinely performed in our research groupe as well as in our department (umr-agap.cirad.fr/l-unit/infrastructure-platforms-technical/platforms/phenotyping-biochemical).

Provisional research programme

Prior to the application of water stress, the panel of 16 genotypes will be grown outdoor during winter/spring 2019/2020. In order to mimic the period and intensity of stresses faced by the vine, the plants will be introduced into Phenodyn at the time of fruit softening (beginning of sugar accumulation).

Given the phenological diversity of the panel of 16 genotypes, the entry of the genotypes into the Phenodyn platform will be spread over 1 month. A destructive T0 will be done on each genotype (5 plants/genotype) to estimate the volume and biomass of the vegetative, root and reproductive organs at the time of application of the hydric constraints. The deficit applied will range from 100% ETP to 30% ETP to cover a range of water scenarios from no water stress to very high stress levels (leaf water potential < - 10 MPa).

The growth of single berries will be monitored by rheology (firmness) and imaging (growth increment) from the "herbaceous plateau" stage. Samples from the reproductive stages to be analyzed will be selected to cover the 4 critical sub-stages of berry ripening under water stress: softening and sugar loading at constant volume, start of water import, transition from malate respiration to sugar respiration, max volume and stop of phloem loading. 15 to 30 berries/stage/stress level/genotype will be sampled. On representative stress levels (to be defined according to the eco-physiological parameters collected by colleagues from UMR LEPSE, see below), the variables studied will be: glucose, fructose, malate, tartrate, amino acids, major cations (K, Mg, Ca) and phenolic compounds (anthocyanins).

This will enable the impact of the deficit on the dynamics of growth and phloem discharge and the accumulation of metabolites within individual berries to be studied. The durations of the second growth phase will be compared, between genotypes and conditions, on the basis of image

analysis. The net storage rates of water, sugars, organic acids and K⁺ will be calculated in the synchronous berry, depending on the level of stress applied. By analysing all sampled berries, it will be possible to extrapolate the impact of water stress on the temporal structure of the fruit population.

Transcriptomic analyses will be carried out on 6 of the 16 genotypes selected to maximize the phenotypic response to the water stress in the vegetative system (leaf water potential, limitation of vegetative growth, data acquired by colleagues from UMR LEPSE) and reproductive organs (evolution of fruit growth). The RNAseq data will be aligned with the various transcriptomes and genomes available in 2020, before counting, normalizing and extracting the differentially expressed genes according to stress level, developmental stage and genotype.

After application of the water constraint in year 1, the plants will be grown outdoors for a second growing cycle. This will allow to study the effect of the stress in year 1 on the growth and distribution of photo-assimilates in the fruit the following year. This second phenotyping will be simplified to allow a quantitative assessment of the grapes at the end of phloem discharge, a stage corresponding to the end of the importation of metabolites and solutes into the fruit.

Estimated schedule

Year 1

- > Choice of the panel of 16 genotypes and implementation of the device in Phenodyn
- > T0 and phenotyping of the 160 plants subjected to water deficit during maturation
- > Creation of a fruit sample library for sub-stages of berry ripening
- > Metabolic analyses of individual berries on the 16 genotypes

Year 2

- > RNA extraction for 6 genotypes x 5 stages, NGS, bioinformatics analyses
- > Phenotyping of the 160 plants grown in standard conditions outdoor
- > Creation of a fruit sample library for sub-stages of berry ripening (effects Y > Y+1)
- > Metabolic analyses of individual berries

Year 3

- > Interpretation and integration of data
- > Drafting of papers and thesis report, participation in an international congress
- > Defense of the PhD in Nov/Dec 2023

Cognitive and technical skills requested to the applicant

Background in **plant biology**, in fruit **biochemistry** and/or plant response to abiotic factors

Taste for **experiment in biology**, precise sampling techniques, data **statistical analyses**

Previous experience in **bioinformatics**, i.e. **transcriptome analysis**, gene annotation...

Capacity for **team work** and **autonomy**

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