Adapting plant material to face water stress in vineyards : which physiological targets for an optimal control of plant water status?

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Abstract

Aims : Water scarcity, associated with climate change, is a particular threat to the sustainability of viticulture in present areas of cultivation, usually prone to drought. Breeding grapevine for reduced water use, better water extraction and maintained production (i. e., high water use efficiency) is therefore of major interest.

Methods and results : This requires a comprehensive knowledge of the physiological impacts of drought on yield and quality. Attention should be paid to those mechanisms involved in the regulation of water status in plant tissues, as it is the primary parameter affected by drought. Transpiration rate, which has a major influence on plant water status, should therefore receive special attention in breeding programs. Beyond scions, the role of rootstocks, which have been largely introduced in vineyards, should be investigated further as it determines water extraction capacity and could modify water balance in grafted plants.

Conclusion : Here we review recent advances in the characterization of genetic variability in the control of water use and water status, whether induced by rootstock or scion.

Significance and impact of the study : This review should help scientists in choosing the relevant physiological targets in their research on grapevine tolerance to drought, whether for breeding prospects or new management practices.

Keywords : grapevine, drought, water use, rootstocks, genetics

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Introduction

Vineyards are predominantly located in drought prone areas. They commonly experience moderate soil water deficit, which is favorable to wine quality provided that it remains moderate (Becker and Zimmerman, 1984). Excess of water, by contrast, can reduce color intensity and sugar content of berries and produce unbalanced, flat wine (Matthews *et al.*, 1990; Medrano *et al.*, 2003). Thus, moderate soil water deficit is the best compromise to promote the expression of high enological potential without altering yield. This is usually achieved in most vineyards but global change seriously threatens this fragile equilibrium. Specifically, under the combined influence of high evaporative demand (dry, warm air) and soil water deficit, plant tissues start dehydrating with detrimental impacts on production and berry quality (Jones *et al.*, 2005; Deluc *et al.*, 2009).

To face transient drought or longer-lasting dry climates, irrigation is developing in production areas. However, pressure on agricultural use of water resources is rising. Irrigation of the vineyard often results as very competitive or impossible. To prepare for the future, viticulture should adapt by limiting water use while maintaining yield. Vineyard establishment and management practices, such as lower plantation density, control of water balance through soil surface management, and thinning, can be considered as valuable short-term solutions (Garcia de Cortazar Atauri, 2006; Duchêne *et al.*, 2010; Ripoche *et al.*, 2010). However, these techniques might not always be sufficient to cope with increasingly dryer conditions (Garcia de Cortazar Atauri, 2006). Additional strategies are needed, including the use of suitable plant material. This requires a comprehensive knowledge of the physiological impacts of drought on yield and quality.

In the following, we review the primary consequences of water deficit on grapevine. Specifically, genetic variability in the mechanisms involved in the control of plant water status is examined.

Physiological responses to water deficit

1. Drop in plant water potential as a primary consequence of water deficit

Water potential characterizes water availability from a thermodynamic point of view. Denoted Ψ, it is at the basis of water movements from the soil to the plant organs and ultimately to the atmosphere. Conventionally, free water at sea level has a potential of zero, corresponding to the maximal water availability in a saturated soil. Soil drying results in a
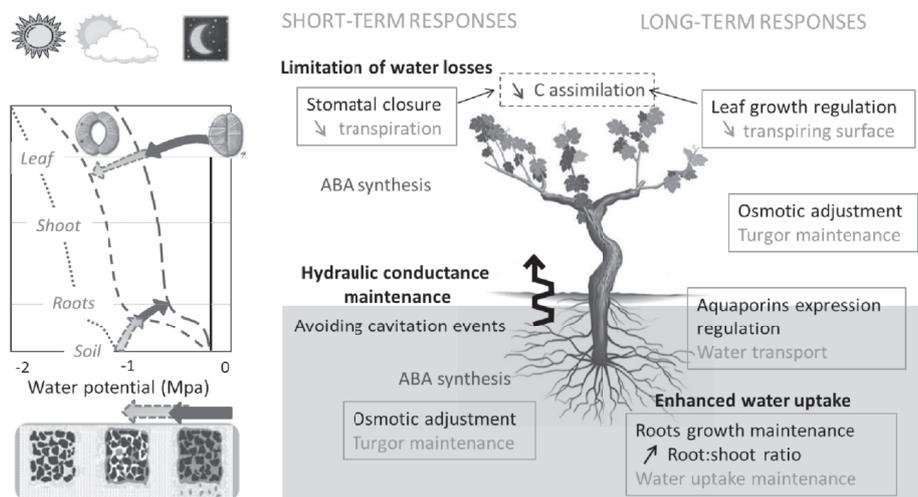

Figure 1. Physiological responses associated with a drop in plant water potential. Simplified representation adapted from Chaves *et al.* (2010) and Marguerit (2010).
The left diagram illustrates the drop of water potential occurring at different intensities depending on the soil water potential (dryer from right to left) and of the evaporative demand (higher from right to left). During the night, water potential equilibrates (vertical line). In the daytime, under high evaporative demand, plant water potentials become more negative (dashed lines) and further decline in dry soil (dotted line). Arrows indicate the influence of the physiological adaptations (limitation of water losses, maintenance of hydraulic conductance and enhanced water uptake) on water potentials, highlighting the favorable (filled, black arrows) and the unfavorable situations (dotted, grey arrows). The right diagram outlines the main physiological adaptations favoring the maintenance of plant water status. The negative consequences of a decrease in leaf water potential on carbon assimilation are also highlighted.

decrease of soil water potential (Ψ becomes more negative as water binds to soil particles and concentrating solutes). Under non transpiring conditions, water potentials in plants equilibrate with the most humid layer explored by the root system (Améglio *et al.*, 1999). As transpiration rate increases in the daytime, plant water potential decreases. This drop in water potential is more severe when hydraulic conductance is limiting water transport on the path from the soil through the plant to the leaves (Figure 1). Because excessive drops in water potential may be disastrous for plants, they have developed diverse adaptations to prevent them.

2. Cavitation threatens hydraulic integrity of xylem conduits

In a transpiring plant, sap water ascends towards the leaves using the non-living, heavily thickened and lignified xylem vessels and tracheids. Water flow follows a gradient of increasingly negative pressure within a continuous water column. Any break in this column would disrupt the whole water flow.

When soil drying combines with high evaporative demand, high tensile strength develops in the xylem, thereby favoring cavitation, which is the apparition of gaseous bubbles (caveats) in the xylem sap due to water evaporation, aggregation of dissolved gases or air entry through pit membranes. Once initiated the bubble then rapidly expands to overrun the vessel (Brodersen *et al.*, 2013). This gaseous embolism may result in the rupture of the water column in the xylem, being a major threat for the plant.

Vessel embolism decreases stem hydraulic conductance, which in turn decreases leaf water potential itself, favoring further embolism. In the absence of stomatal closure or reduction in leaf area, this cycle can result in functionality loss of all the conducting tissue. This results in dramatically amplified effects of water deficit on the drop in leaf water potential along the water path (Brodribb and Cochard, 2009; Zufferey *et al.*, 2011) with catastrophic consequences on plant dehydration and even death (McDowell *et al.*, 2008). Vessel size partly determines plant vulnerability to cavitation, small-diameter conduits being less vulnerable (Tyree, 2003) but less efficient to transport water. Thus, plant adaptation to dry environments depends on a trade-off between efficient conduits and low vulnerability to cavitation. In grapevine, which displays long vessels (a common feature among liana species), vessel sizes are dependent on the cultivar (Chouzouri and Schultz, 2005; Tramontini *et al.*, 2013a), leaving room for genetic variation in drought response.

Threshold water potential for cavitation also varies with species, cultivars and growth conditions. As compared to other species, grapevine has commonly been described as vulnerable to cavitation occurring at high (less negative) water potential threshold (Schultz and Matthews, 1988; McElrone *et al.*, 2012). Up to 70% loss of conductivity has been reported with moderate tensions in stems around -0.75 MPa (Tibbetts & Ewers, 2000). Nevertheless, an efficient control of water losses through stomata often protects grapevine from cavitation (Zufferey *et al.*, 2011).

Recent studies report that transport capacity could be largely restored by the end of the day or during the night, when transpiration rate decreases. This has been assigned to water refilling of embolized xylem vessels. Although mechanistically debated, restoration of water transport capacity has been observed in a number of species, whether in roots (Domec *et al.*, 2006; Lovisolo *et al.*, 2008a), shoots (Zwieniecki and Holbrook, 1998) or leaves (Johnson *et al.*, 2009). Plant capacity to restore hydraulic integrity over night under dry conditions would largely depend on soil exploration by roots (Zufferey *et al.*, 2011). Carbohydrates stored in cells neighboring the conducting vessels, together with aquaporins (e.g. membrane channel proteins facilitating water transport), also appear as possible, important actors of this restoration (Salleo *et al.*, 2009).

3. Limitation of transpiration releases hydraulic tension and saves water

One of the most obvious and immediate effects of water deficit is a reduction in shoot growth (Chaves, 1991), with cell expansion being particularly sensitive to water shortage (Hsiao, 1973). Branches are more sensitive than first order axes (Lebon *et al.*, 2006), and observation of growth cessation at the shoot apices is a powerful tool to early detect incipient water deficit (Pellegrino *et al.*, 2006). Limited vigor under drought results in a decrease of evaporative areas, thereby lowering transpiration and releasing water tension in the xylem. Leaf folding or wilting are other adaptations having similar, although reversible, effects on water saving by increasing boundary layer resistance and reducing intercepted light, hence lowering surface temperature and evaporative demand.

Additionally, plants dynamically modulate the aperture of stomata, those micropores located at the leaf surface that make possible water vapor and CO_2 exchanges. A rapid stomatal closure is generally

observed under water deficit (Damour *et al.*, 2010), which efficiently lowers water flow density. However, this way of saving water has a heavy cost for the plant because stomatal closure unavoidably lowers CO_2 uptake and decreases photosynthesis, although to variable extent depending on species and varieties (Tardieu and Simonneau, 1998). Plants thus face a dilemma, and adaptive strategies are necessary to reach a trade-off ensuring CO_2 uptake while limiting water losses.

Other adaptations may participate in minimizing transpiration rate, including changes in thickness and composition of the waxy cuticle that waterproofs the leaf surface and forces water to leave the plant through stomata. Relation between cuticle components and their efficacy to limit water losses remains to be understood (Riederer and Schreiber, 2001).

4. High root water extraction capacity postpones the negative impact of water deficit

Root development is highly plastic, with typical shifts in the allocation of plant's resources (carbohydrates) towards root growth at the expense of the shoots in dry conditions. This allows the plant to increase soil exploration for water uptake while reducing transpiration (Sharp and Davies, 1985; Cramer *et al.*, 2013). The maintenance of root growth capacities during water deficit, together with some plasticity in root hydraulic architecture under fluctuating conditions, depend on the species and, in grapevine, is variable among rootstocks (Bauerle *et al.*, 2008).

5. Osmotic adjustment helps maintaining water into the cells

Plants evolved in different ways to maintain physiological activity while water potential declines. A major response is osmotic adjustment, which allows the cells to maintain their water content and turgor even when water potential decreases in their vicinity. Osmotic adjustment in a cell consists of trapping or generating solutes to increase their concentration, leading to interactions of water with solutes inside the cell. This decreases the osmotic potential, a component of the total water potential, while turgor, the other component in cells, can be maintained even when a given drop in total water potential is transmitted to the cell from its environment.

This widespread response to water stress occurs in leaves, roots and reproductive organs of many species (Turner and Jones, 1980; Morgan, 1984) and is under genetic control (e.g. Teulat *et al.*, 2001). In grapevine, osmotic adjustment has been evidenced under water deficit in leaves (Rodrigues *et al.*, 1993) and roots (During and Dry, 1995). It might be a major strategy to avoid tissue dehydration and maintain grapevine production in dry conditions (Hare *et al.*, 1998; Patakas and Noitsakis, 1999). The most interesting solutes are those that, besides their role in osmotic adjustment, play a role in nutrient or energy storage, membrane protection or detoxifying activities (Szabados *et al.*, 2011).

6. Primary traits for a drought tolerant grapevine ideotype

Plant responses to drought are plural and involve a range of morphological and physiological adaptations of both aerial and underground organs. The primary features of interest for grapevine encompass a tight control of water losses through stomatal regulation, osmoregulation, together with photosynthesis maintenance to the benefit of berry development and root growth. The tight coupling between photosynthesis and transpiration, which are both controlled by stomata and leaf area, does not make trivial to decrease transpiration without altering photosynthesis. However, the ratio of photosynthesis to transpiration rates varies to some extent with environmental conditions and genotypes (Tomas *et al.*, 2014; Medrano *et al.*, 2015). An adequate control of stomatal aperture allows the plant to take advantage of the environmental conditions by lowering the water cost of gas exchange.

Physiological control of leaf water potential in a drying soil

1. The stomatal control of transpiration

Transpirational water losses, which, in combination with soil drying, are responsible for drawing down water potential in plants, mainly occur through the stomata. Stomata form microscopic pores mainly located on the abaxial (inferior) epidermis of the leaves in grapevine, a species therefore qualified as hypostomatous. A pair of adjacent guard cells controls the pore aperture through rapid modification in cell volume associated with turgor changes. Changes in turgor result either from variations in total water potential driven by soil or air drying (hydraulic response), or from active changes in osmotic potential caused by solute movements (into or out of the guard cells), themselves generated by chemical signals that modify ion transporter activity (biochemical response). Moreover, stomatal density displays a high inter-specific and intra-specific variability, as exemplified for grapevine (Boso *et al.*,

2011). However, variability in stomatal density was not found to explain much of the differences in transpiration rate (Hopper et al., 2014).

Stomatal closure in response to water deficit is controlled by abscisic acid (ABA), a plant hormone having long been recognized as a key player in plant abiotic stress responses (Loveys, 1984; Wilkinson and Davies, 2002; Yamaguchi-Shinozaki and Shinozaki, 2006). ABA biosynthesis, metabolism, and transfer towards guard cells modulate stomatal sensitivity to water deficit (Stoll et al., 2000; Cramer et al., 2007). ABA synthesis in roots was first proposed as the pivot of plant response to drought. Soil drying is sensed by the roots as their water potential decreases, resulting in an increased ABA biosynthesis by this compartment (Simonneau et al., 1998). ABA is then conveyed to the leaves through the xylem vessels (Tardieu and Simonneau, 1998). ABA biosynthesis also occurs in the leaves (Holbrook et al., 2002; Christmann et al., 2005; Christmann et al., 2007; Ikegami et al., 2009) where hydraulic and chemical signals trigger foliar ABA synthesis in response to water deficit (Christmann et al., 2013; Mittler & Blumwald, 2015), although the precise signal transduction still remains to be deciphered. Several key enzymes of the ABA biosynthetic pathway, namely ABA2, AAO3, and NCED3, are expressed in specific areas of vascular tissues in response to water deficit (Endo et al., 2008). Importantly, VvNCED1 coding for 9-cis-epoxycarotenoïd dioxygenase NCED, an enzyme catalyzing the first committed step in ABA biosynthesis, has been identified as decisive for ABA accumulation under water shortage in grapevine (Speirs et al., 2013; Rossdeutsch et al., 2016). Variations of pH between tissues, together with the action of glucosidases or glucosyl esterases, modify the concentration of free ABA reaching the stomata (Nambara and Marion-Poll, 2005). Depletion of ABA may also participate in the regulation of ABA balance. A specific group of enzymes, including the ABA 8'-hydroxylases, regulates ABA degradation to inactive compounds (Speirs et al., 2013). A strong allelic diversity for genes involved in either ABA biosynthesis or degradation could explain genetic variations in ABA accumulation under water deficit (Nambara and Marion-Poll, 2005; Riahi et al., 2013). In grapevine, variability in ABA accumulation has been observed among rootstocks (Peccoux, 2011) as well as scions (Soar et al., 2004).

Additionally to ABA accumulation, stomatal sensitivity to the hormone is also highly variable (Tardieu and Simonneau, 1998; Rossdeutsch et al., 2016). It depends on numerous molecular steps at the guard cell level. Perception of ABA corresponds to binding to the PYR/PYL/RCAR proteins (Brandt et al., 2012). This leads to conformational change in the receptor enabling ABA interaction with PP2Cs phosphatase, which in turn releases SnRK2s kinases. SnRK2s activate transcription factors, ABA-responsive element Binding Factors (ABFs), which results in ABA-responsive gene expression (Klingler et al., 2010; Boneh et al., 2012). This cascade modulates the activity of ion channels in the guard cells, which translates in osmotic and turgor changes, and ultimately regulates stomatal closure (Joshi-Saha et al., 2011). Many other actors involved in those responses have been identified, including variations in internal Ca^{2+} concentration and accumulation of nitrous oxide in guard cells.

How chemical control of stomatal aperture interacts with hydraulics is still a matter of debate. It has recently been proposed that ABA might affect leaf hydraulic conductance through a decrease in water permeability within leaf vascular tissues. ABA would thus promote stomatal closure in a dual way via effects on hydraulics upstream stomata and a direct biochemical effect on the guard cells (Pantin et al., 2013). Variability in the role of ABA on hydraulic conductance remains to be explored as a possible cause of the large diversity of stomatal sensitivities to ABA observed among species and within grapevine cultivars.

2. Isohydric genotypes are able to maintain leaf water potential in drying soils

Soil drying inevitably results in a decrease of water potential in plants including leaves. However, contrasting controls of leaf water potential have been observed across species when submitted to similar soil water deficit conditions (Tardieu and Simonneau, 1998). So-called isohydric species, such as maize, efficiently maintain high leaf water potential in the daytime (Ψ_M) when the soil dries, whereas anisohydric species, such as sunflower, exhibit substantial decrease of Ψ_M (Tardieu et al., 1996). In several species including the overall, roughly isohydric grapevine (Prieto et al., 2010), a variable efficacy to maintain high Ψ_M has been observed across genotypes. Two widespread cultivars, namely Grenache and Syrah, have been consistently described with different responses to soil water deficit. Grenache was shown to be near-isohydric, compared with Syrah, which exhibited more anisohydric behavior (Schultz, 2003; Soar et al., 2006b).

The classical view relates the contrasted (an)isohydric behaviors to the more or less efficient control of transpiration rate by stomatal closure (Buckley, 2005). Stomatal conductance was shown to decrease earlier during the course of a soil drying episode in isohydric species, thus reducing the drop of leaf water potential in the daytime as compared to anisohydric species (Tardieu and Simonneau, 1998). The anisohydric behavior would thus favor photosynthesis maintenance under water deficit. This has been confirmed in grapevine (Lovisolo *et al.*, 2010) where anisohydric cultivars also exhibit higher vigor in conditions of water deficit (Pou *et al.*, 2012), as long as soil drying does not induce any serious decrease of plant water potential. Anisohydric plants might also be more resistant to cavitation than isohydric ones (Schultz, 2003; Alsina *et al.*, 2007) and might easily recover from partial cavitation events, thus exhibiting a higher tolerance to moderate water deficit events. However, beyond a certain threshold in soil drying, the anisohydric behavior might not remain favorable because high levels of dehydration lead to serious damages. This has been exemplified for grapevine cultivars such as Syrah and Chardonnay (Alsina *et al.*, 2007). By contrast, the isohydric cultivar Cabernet-Sauvignon displays a reduced photosynthesis but is preserved against damages such as photoinhibition, which is the alteration of photosynthesis due to high light intensity (Hochberg *et al.*, 2013). Hence, one of these behaviors can be more interesting depending on the water deficit scenario (duration, intensity, combination with evaporative demand). While anisohydric cultivars may be recommended in the case of short periods of moderate water deficit because they sustain production, the isohydric ones appear as more suitable to face long lasting periods of severe drought. Specificities of the climatic scenarios should be considered to define the more advantageous type of cultivar from an agronomic point of view.

3. Reconsidering the origin of the variation in (an)isohydric behaviors

The classical view of (an)isohydry was recently questioned in several studies. It was proposed that changes in hydraulic conductance may contribute, concurrently with stomatal regulation, to the control of Ψ_M under adverse conditions (Franks *et al.*, 2007; Pantin *et al.*, 2013). Additionally, (an)isohydry would not be a genotype-constitutive feature (Lovisolo *et al.*, 2010) but could vary in a same plant following season and development (Poni *et al.*, 1993; Chaves *et al.*, 2010). Some studies concluded to variable ranking of (an)isohydric behaviors between grapevine cultivars, notably Grenache and Syrah (Pou *et al.*, 2012). The genetic origin of (an)isohydry was thus challenged.

Genetic variation in (an)isohydry was extensively studied in grapevine using a mapping population obtained from a cross between Syrah and Grenache (Coupel-Ledru *et al.*, 2014). Significant genetic control of Ψ_M under moderate drought was observed under controlled conditions using potted plants in a phenotyping platform. Several genomic regions (QTLs) were identified as underlying the genetic variation of Ψ_M. Further, the maintenance of Ψ_M under water deficit conditions was not simply controlled by transpiration response to soil drought. Some of the QTLs detected for genetic variation in Ψ_M response to moderate water deficit collocated with QTLs for transpiration response, but others collocated with QTLs detected for plant hydraulic conductance (Coupel-Ledru *et al.*, 2014). Overall, genetic variation of Ψ_M under water deficit conditions correlated with variation in plant hydraulic conductance (Coupel-Ledru, 2015). It was thus proposed that whole plant hydraulic conductance under water deficit might combine with stomatal control of transpiration to determine (an)isohydry. Specifically, variation in (an)isohydry may result from slight deviation in the balance between transpiration rate and hydraulic conductance.

The genetic analysis of the Syrah × Grenache offspring (Coupel-Ledru *et al.*, 2014) also evidenced that transpiration rate and soil-to-leaf hydraulic conductance mostly correlated. This may explain why grapevine can be considered as roughly isohydric by contrast with other species like sunflower where more severe drops in Ψ_M rapidly occur as the soil dries (Tardieu *et al.*, 1996). In grapevine, this balance may be the result of multiple coordination between stomatal response and variation in specific hydraulic conductance in leaves (Pou *et al.*, 2012), petioles (Schultz, 2003) and roots where correlation with expressions of water channel proteins in roots has been evidenced (Vandeleur *et al.*, 2009). Identification of genes specifically associated with QTLs detected for hydraulic conductance and control of Ψ_M but not for transpiration response (and vice versa) would be of particular interest to look for origins of possible imbalance between transpiration and water transport capacity and to progress on the determinism of (an)isohydry.

Rootstocks : the hidden half

While the choice of scion varieties is often regulated by their performance in specific climatic conditions or marketing purposes (van Leeuwen and Seguin, 2006), rootstocks offer more flexible solutions for adapting the grafted plant to drought. A large variability in rootstock response to water deficit has been reported by several authors (Carbonneau, 1985 ; Ollat *et al.*, 2016 ; Zhang *et al.*, 2016), although underlying mechanisms still need to be enlightened. Rootstocks participate in the regulation of plant water balance through their own uptake capacities associated with root growth and water transport (Carbonneau, 1985 ; Bauerle *et al.*, 2008 ; Alsina *et al.*, 2011 ; Peccoux, 2011 ; Zhang *et al.*, 2016) or via their effects on stomatal regulation (Lovisolo *et al.*, 2010 ; Marguerit *et al.*, 2012) and above ground development (Jones, 2012). Water extraction capacities by roots are reported to be variable between rootstocks and genetically controlled (Carbonneau, 1985 ; Soar *et al.*, 2006a ; Marguerit *et al.*, 2012), even though the physiological mechanisms underlying this trait are still unknown. In addition, rootstocks are known to affect scion phenology, vegetative growth, yield and fruit quality (Tandonnet *et al.*, 2010).

1. Root development
to better explore soil water resources

A deep and dense root system favors water uptake to compensate for water losses by transpiration. Grapevine is known for its ability to grow deep roots. Root distribution and root system architecture are more affected by soil type and training system than by rootstock genotype (Smart *et al.*, 2006). In addition, interactions with scion genotypes have a strong effect on root system development (Tandonnet *et al.*, 2010). By contrast, rootstock genotype has more impact on root density expressed as biomass - or root number by volume of soil - (Southey and Archer, 1988 ; Peccoux, 2011), or on the ratio of fine roots to total roots (Van Zyl, 1988). In the vineyard, some highly drought tolerant rootstocks such as 140Ru are more able to grow roots in deep soil layers (Southey and Archer, 1988). Furthermore, the maintenance of root growth under dry conditions as well as the root system plasticity with soil water status may differentiate rootstock genotypes (Bauerle *et al.*, 2008) according to their strategy to cope with drought (Comas *et al.*, 2010). Further investigations of root growth properties for different rootstocks would be profitable for the future.

2. The control of water transport to shoot

The root system contributes in a non-negligible way to the whole plant resistance to water flow (Steudle, 2000). There is a large variability among rootstocks in root vascular anatomy (vessel diameter and length, percentage of conducting tissues ; Pongracz & Beukman, 1970 ; Alsina *et al.*, 2011 ; Peccoux, 2011). These differences can affect root ability to convey water to the canopy (i. e. hydraulic conductance), and root vulnerability to cavitation. Differences between rootstocks for root hydraulic conductance have been reported (de Herralde *et al.*, 2006 ; Peccoux, 2011 ; Tramontini *et al.*, 2013b), but may be more related to whole root system size than individual root properties (Alsina *et al.*, 2011). In addition, drought effect on root hydraulic conductivity may differ between rootstocks. Barrios-Masias *et al.* (2015) observed a lower decrease of root conductivity for the drought tolerant rootstock 110R, in comparison to the drought sensitive 101-14MGt. Differences are related to the development of suberized apoplastic barriers in the root tips at the beginning of the maturation zone. In grapevine, roots together with leaves are more sensitive to embolism than the other plant compartments (Tramontini & Lovisolo, 2016). Besides, it was recently shown that wild *Vitis* species stems differ for their sensitivity to cavitation under water stress and their ability to repair after rehydration, paralleling contrasting responses of root pressure to re-watering associated to osmotic regulation (Knipfer *et al.*, 2015).

Without any doubt, these facts have specific, molecular origins in the context of grafted plants. Transcriptomic analyses in the root tissues of various rootstock-scion combinations submitted to long term water deficit support the involvement of cell wall and osmotic metabolisms in the variability of responses among rootstocks (Peccoux, 2011).

3. Aquaporins as key actors in transmembrane water transport

The ability to drive water from root tips to stomata does not only depend on vascular pathways. Water also follows inter- and intracellular pathways that are under the control of water channel proteins embedded in cell membranes, named aquaporins (Maurel *et al.*, 2015). The genes encoding for such proteins have been identified for grapevine (Fouquet *et al.*, 2008 ; Shelden *et al.*, 2009). Their expression has been reported in different plant compartments, various genotypes and under drought conditions (Galmes *et al.*, 2007 ; Gambetta *et al.*, 2012 ; Rossdeutsch, 2015). Some of these genes are more

expressed in root tips than in more mature suberized zones of the roots where the radial hydraulic conductivity is lower (Gambetta *et al.*, 2013). Differences have been reported among rootstock genotypes for the expression of these genes under well-watered and drought conditions, or for the proportion of conductance under the control of aquaporins (Lovisolo *et al.*, 2008b; Gambetta *et al.*, 2012; Rossdeutsch, 2015). Although the expression of some aquaporin genes like *VvPIP1;1* in roots appears to correlate with hydraulic conductance and plant transpiration (Vandeleur *et al.*, 2009), the situation in a grafted plant is much more complex and scion effects have to be considered as well (Tramontini *et al.*, 2013b; Rossdeutsch, 2015). Rootstocks also present contrasting abilities to produce ABA under drought conditions (Rossdeutsch *et al.*, 2016) and the interactions of chemical and hydraulic signals of soil water status from rootstock to scion should be taken into account. The role of ABA in the control of the expression and activity of aquaporins is now clearly established (Finkelstein, 2013; Grondin *et al.*, 2015).

4. Genetic architecture for transpiration and growth as controlled by rootstock

The genetic architecture for water deficit responses induced by rootstock remains poorly studied (Marguerit, 2010; Marguerit *et al.*, 2012). Specifically, it can be questioned to what extent transpiration, growth and water use efficiency are genetically controlled by the rootstock. This question has been addressed in a 3-year experiment using a pedigree population issued from the cross between *V. vinifera* Cabernet Sauvignon × *V. riparia* Gloire de Montpellier made up of 138 individuals. Transpiration rate, δ^{13}C (a proxy for water use efficiency), transpiration efficiency (ratio of biomass produced to water transpired), water extraction capacity and the response of transpiration to water deficit were characterized. Broad sense heritability was above 0.3 for most traits, although with significant year effects highlighting the strong impact of the environment. Few significant correlations were found between traits. As mentioned above for scions, traits related to genetic variability in rootstock exhibited a polygenic control as revealed by the detection of multiple QTLs. One QTL for water extraction capacity was identified in the three years on linkage group 3, confirming the hypothesis proposed by Carbonneau (1985) and Soar *et al.* (2006a) that this trait was genetically controlled at the rootstock level. A genetic architecture of transpiration plasticity to water deficit was evidenced which was partially independent from the genetic architecture of transpiration rate, suggesting an independent selection process for these two traits. Riparia Gloire de Montpellier, reputed as sensitive to water deficit, early reduced its scion transpiration as the soil was drying. The genetic architectures of δ^{13}C and transpiration efficiency were partially independent, underlining the complexity of selecting plant material for water use efficiency (Condon *et al.*, 2004). Transpiration efficiency appeared to be less influenced by climatic (year) effect and soil water conditions, and could therefore be more easily used for breeding. The QTLs detected in the offspring included genes that have been characterized as potentially involved in water deficit responses (Marguerit *et al.*, 2012). Candidate genes related to hormone (notably ABA) and hydraulic (aquaporins) signaling between the rootstock and the scion are particularly interesting as they play a major role in water deficit responses (Soar *et al.*, 2006a; Vandeleur *et al.*, 2009).

This review and other data collected on rootstocks show that drought tolerance may probably be acquired through different mechanisms (Serra *et al.*, 2014; Rossdeutsch *et al.*, 2016). This diversity should be taken into account to adapt plant material to different situations and levels of water deficit.

Conclusions

Grapevine response to water limitation is complex and involves many physiological mechanisms. Genetic variability has been described for several traits related to these mechanisms and many associated genomic regions have already been identified at the scion and rootstock levels. Better knowledge on the role of favorable alleles in these regions will help designing adequate plant material to deal with the increased risk of drought events in the context of climate change.

References

Alsina, M. M., De Herralde, F., Aranda, X., Save, R. and Biel, C., 2007. Water relations and vulnerability to embolism are not related: experiments with eight grapevine cultivars. *Vitis*, **46**, 1-6.

Alsina, M. M., Smart, D. R., Bauerle, T., de Herralde, F., Biel C., Stockert, C., Negron, C. and Save, R., 2011. Seasonal changes of whole root system conductance

by a drought-tolerant grape root system. *Journal of Experimental Botany*, **62**, 99-109.

Améglio, T., Archer, P., Cohen, M., Valancogne, C., Daudet, F.-A., Dayau, S. and Cruiziat, P., 1999. Significance and limits in the use of predawn leaf water potential for tree irrigation. *Plant and Soil*, **207**, 155-167.

Barrios-Masias, F. H., Knipfer, T. and McElrone, A. J., 2015. Differential responses of grapevine rootstocks to water stress are associated with adjustments in fine root hydraulic physiology and suberization. *Journal of Experimental Botany*, **66**, 6069-6078.

Bauerle, T. L., Smart, D. R., Bauerle, W. L., Stockert, C. and Eissenstat, D. M., 2008. Root foraging in response to heterogeneous soil moisture in two grapevines that differ in potential growth rate. *The New Phytologist*, 179, 857-866.

Becker, N. and Zimmerman, H., 1984. The effect of different amounts of water on grapevines in containers, on shoot maturation, berry development and wine quality. *Bulletin de l'OIV*, **57**, 584-596.

Boneh, U., Biton, I., Zheng, C., Schwartz, A. and Ben-Ari, G., 2012. Characterization of potential ABA receptors in *Vitis vinifera*. *Plant Cell Reports*, **31**, 311-321.

Boso, S., Gago, P., Alonso-Villaverde, V., Santiago, J. L., Mendez, J., Pazos, I. and Martínez, M. C., 2011. Variability at the electron microscopic level in leaves of members of the genus *Vitis*. *Scientia Horticulturae*, **128**, 228-238.

Brandt, B., Brodsky, D. E., Xue, S., Negi, J., Iba, K., Kangasjärvi, J., Ghassemian, M., Stephan, A. B., Hu, H. and Schroeder, J. I., 2012. Reconstitution of abscisic acid activation of SLAC1 anion channel by CPK6 and OST1 kinases and branched ABI1 PP2C phosphatase action. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 10593-10598.

Brodersen, C. R., McElrone, A. J., Choat, B., Lee E. F., Shackel, K. A., and Matthews, M. A., 2013. In vivo visualizations of drought-induced embolism spread in *Vitis vinifera*. *Plant Physiology*, **161**, 1820-1829.

Brodribb, T. J. and Cochard, H., 2009. Hydraulic failure defines the recovery and point of death in water-stressed conifers. *Plant Physiology*, **149**, 575-584.

Buckley, T. N., 2005. The control of stomata by water balance. *The New Phytologist*, **168**, 275-292.

Carbonneau, A., 1985. The early selection of grapevine rootstocks for resistance to drought conditions. *American Journal of Enology and Viticulture*, **36**, 195-198.

Chaves, M. M., 1991. Effects of water deficits on carbon assimilation. *Journal of Experimental Botany*, **42**, 1-16.

Chaves, M. M., Zarrouk, O., Francisco, R., Costa, J. M., Santos, T., Regalado, A. P., Rodrigues, M. L. and Lopes, C. M., 2010. Grapevine under deficit irrigation: hints from physiological and molecular data. *Annals of Botany*, **105**, 661-676.

Chouzouri, A. *and* Schultz, H. R., 2005. Hydraulic anatomy, cavitation susceptibility and gas-exchange of several grapevine cultivars of different geographic origin. *Acta Horticulturae*, **689**, 325-331.

Christmann, A., Hoffmann, T., Teplova, I., Grill, E. *and* Müller, A., 2005. Generation of active pools of abscisic acid revealed by in vivo imaging of water-stressed Arabidopsis. *Plant Physiology*, **137**, 209-219.

Christmann, A., Weiler, E. W., Steudle, E. *and* Grill, E., 2007. A hydraulic signal in root-to-shoot signalling of water shortage. *Plant Journal*, **52**, 167-174.

Christmann, A., Grill, E. *and* Huang, J., 2013. Hydraulic signals in long-distance signaling. *Current Opinion in Plant Biology*, **16**, 293-300.

Comas, L. H., Bauerle, T. L. *and* Eissenstat, D. M., 2010. Root dynamics and function. *Australian Journal of Grape and Wine Research*, **16**, 131-137.

Condon, A. G., Richards, R. A., Rebetzke, G. J. *and* Farquhar, G. D., 2004. Breeding for high water-use efficiency. *Journal of Experimental Botany*, **55**, 2447-2460.

Coupel-Ledru, A., Lebon, É., Christophe, A., Doligez, A., Cabrera-Bosquet, L., Péchier, P., Hamard, P., This, P. *and* Simonneau, T., 2014. Genetic variation in a grapevine progeny (*Vitis vinifera* L. cvs Grenache × Syrah) reveals inconsistencies between maintenance of daytime leaf water potential and response of transpiration rate under drought. *Journal of Experimental Botany*, **65**, 6205-6218.

Coupel-Ledru, A., 2015. Physiological and genetic determinisms of water use in grapevine. PhD Dissertation, Montpellier SupAgro, Montpellier.

Cramer, G. R., Ergül, A., Grimplet, J., Tillett, R. L., Tattersall, E. A., Bohlman, M. C.,… *and* Cushman, J. C., 2007. Water and salinity stress in grapevines: early and late changes in transcript and metabolite profiles. *Functional & Integrative Genomics*, **7**, 111-134.

Cramer, G. R., Van Sluyter, S. C., Hopper, D. W., Pascovici, D., Keighley, T. *and* Haynes, P. A., 2013. Proteomic analysis indicates massive changes in metabolism prior to the inhibition of growth and photosynthesis of grapevine (*Vitis vinifera* L.) in response to water deficit. *BMC Plant Biology*, **13**, 49.

Damour, G., Simonneau, T., Cochard, H. *and* Urban, L., 2010. An overview of models of stomatal conductance at the leaf level. Plant, *Cell and Environment*, **33**, 1419-1438.

de Herralde, F., del Mar Alsina, M., Aranda, X., Save, R. and Biel, C., 2006. Effects of rootstocks and

irrigation regime on hydraulic architecture of *Vitis vinifera* L. cv. Tempranillo. *Journal International des Sciences de la Vigne et du Vin*, x**40**, 133-139.

Deluc, L. G., Quilici, D. R., Decendit, A., Grimplet, J., Wheatley, M. D., Schlauch, K. A., Mérillon, J.-M., Cushman, J. C. and Cramer, G. R., 2009. Water deficit alters differentially metabolic pathways affecting important flavor and quality traits in grape berries of Cabernet Sauvignon and Chardonnay. BMC *Genomics*, **10**, 212.

Domec, J.-C., Scholz, F. G., Bucci, S. J., Meinzer, F. C., Goldstein, G. and Villalobos-Vega, R., 2006. Diurnal and seasonal variation in root xylem embolism in neotropical savanna woody species : impact on stomatal control of plant water status. *Plant, Cell and Environment*, **29**, 26-35.

Duchêne, E., Huard, F., Dumas, V., Schneider, C. and Merdinoglu, D., 2010. The challenge of adapting grapevine varieties to climate change. *Climate Research*, **41**, 193-204.

During, H. and Dry, P. R., 1995. Osmoregulation in water stressed roots : responses of leaf conductance and photosynthesis. *Vitis*, **34**, 15-17.

Endo, A., Sawada, Y., Takahashi, H., Okamoto, M., Ikegami, K., Koiwai, H.,… and Nambara, E., 2008. Drought induction of Arabidopsis 9-cis-epoxycarotenoid dioxygenase occurs in vascular parenchyma cells. *Plant Physiology*, **147**, 1984-1993.

Finkelstein, R., 2013. Abscisic acid synthesis and response. The Arabidopsis Book, 11, e0166.

Fouquet, R., Léon, C., Ollat, N. and Barrieu, F., 2008. Identification of grapevine aquaporins and expression analysis in developing berries. *Plant Cell Reports*, **27**, 1541-1550.

Franks, P. J., Drake, P. L. and Froend, R. H., 2007. Anisohydric but isohydrodynamic : seasonally constant plant water potential gradient explained by a stomatal control mechanism incorporating variable plant hydraulic conductance. *Plant, Cell and Environment*, **30**, 19-30.

Galmés, J., Pou, A., Alsina, M. M., Tomàs, M., Medrano, H. and Flexas, J., 2007. Aquaporin expression in response to different water stress intensities and recovery in Richter-110 (*Vitis* sp.): relationship with ecophysiological status. *Planta*, **226**, 671-681.

Gambetta, G. A., Manuck, C. M., Drucker, S. T., Shaghasi, T., Fort, K., Matthews, M. A., Walker, M. A. and McElrone, A. J., 2012. The relationship between root hydraulics and scion vigour across *Vitis* rootstocks : what role do root aquaporins play? *Journal of Experimental Botany*, **63**, 6445-6455.

Gambetta, G. A., Fei, J., Rost, T. L., Knipfer, T., Matthews, M. A., Shackel, K. A., Walker, M. A. and McElrone, A. J., 2013. Water uptake along the length of grapevine fine roots : developmental anatomy,

tissue-specific aquaporin expression, and pathways of water transport. *Plant Physiology*, **163**, 1254-1265.

Garcia de Cortazar Atauri, I., 2006. Adaptation du modèle STICS à la vigne (*Vitis vinifera* L.) : utilisation dans le cadre d'une étude d'impact du changement climatique à l'échelle de la France. *PhD Dissertation*, Montpellier SupAgro, Montpellier.

Grondin, A., Rodrigues, O., Verdoucq, L., Merlot, S., Leonhardt, N. and Maurel, C., 2015. Aquaporins contribute to ABA-triggered stomatal closure through OST1-mediated phosphorylation. *The Plant Cell,* **27,** 1945-1954.

Hare, P. D., Cress, W. A. and Van Staden, J., 1998. Dissecting the roles of osmolyte accumulation during stress. *Plant, Cell and Environment*, **21**, 535-553.

Hochberg, U., Degu, A., Fait, A. and Rachmilevitch, S., 2013. Near isohydric grapevine cultivar displays higher photosynthetic efficiency and photorespiration rates under drought stress as compared with near anisohydric grapevine cultivar. *Physiologia Plantarum*, **147**, 443-452.

Holbrook, N. M., Shashidhar, V. R., James, R. A. and Munns, R., 2002. Stomatal control in tomato with ABA-deficient roots : response of grafted plants to soil drying. *Journal of Experimental Botany*, **53**, 1503-1514.

Hopper, D. W., Ghan, R. and Cramer, G. R., 2014. A rapid dehydration leaf assay reveals stomatal response differences in grapevine genotypes. *Horticulture Research*, 1, 2.

Hsiao, T. C., 1973. Plant responses to water stress. *Annual Review of Plant Physiology*, **24**, 519-570.

Ikegami, K., Okamoto, M., Seo, M. and Koshiba, T., 2009. Activation of abscisic acid biosynthesis in the leaves of *Arabidopsis thaliana* in response to water deficit. *Journal of Plant Research*, **122**, 235-243.

Johnson, D. M., Woodruff, D. R., McCulloh, K. A. and Meinzer, F. C., 2009. Leaf hydraulic conductance, measured in situ, declines and recovers daily : leaf hydraulics, water potential and stomatal conductance in four temperate and three tropical tree species. *Tree Physiology*, **29**, 879-887.

Jones, G. V., White, M. A., Cooper, O. R. and Storchmann, K., 2005. Climate change and global wine quality. *Climate Change*, **73**, 319-343.

Jones, H. G., 2012. How do rootstocks control shoot water relations? *The New Phytologist*, **194**, 301-303.

Joshi-Saha, A., Valon, C. and Leung, J., 2011. Abscisic acid signal off the STARTing block. *Molecular Plant*, **4**, 562-580.

Klingler, J. P., Batelli, G. and Zhu, J.-K., 2010. ABA receptors : the START of a new paradigm in phytohormone signalling. *Journal of Experimental Botany*, **61**, 3199-3210.

Knipfer, T., Eustis, A., Brodersen, C., Walker, A. M. and McElrone, A. J., 2015. Grapevine species from varied native habitats exhibit differences in embolism formation/repair associated with leaf gas exchange and root pressure. *Plant, Cell and Environment*, **38**, 1503-1513.

Lebon, E., Pellegrino, A., Louarn, G. and Lecoeur, J., 2006. Branch development controls leaf area dynamics in grapevine (*Vitis vinifera*) growing in drying soil. *Annals of Botany*, **98**, 175-185.

Loveys, B. R., 1984. Diurnal changes in water relations and abscisic acid in field-grown *Vitis vinifera* cultivars. III. The influence of xylem-derived abscisic acid on leaf gas exchange. *The New Phytologist*, **98**, 563-573.

Lovisolo, C., Perrone, I., Hartung, W. and Schubert, A., 2008a. An abscisic acid-related reduced transpiration promotes gradual embolism repair when grapevines are rehydrated after drought. *The New Phytologist*, **180**, 642-651.

Lovisolo, C., Tramontini, S., Flexas, J. and Schubert, A., 2008b. Mercurial inhibition of root hydraulic conductance in *Vitis* spp. rootstocks under water stress. *Environmental and Experimental Botany*, **63**, 178-182.

Lovisolo, C., Perrone, I., Carra, A., Ferrandino, A., Flexas, J., Medrano, H. and Schubert, A., 2010. Drought-induced changes in development and function of grapevine (*Vitis* spp.) organs and in their hydraulic and non-hydraulic interactions at the whole-plant level : a physiological and molecular update. *Functional Plant Biology*, **37**, 98-116.

Marguerit, E., 2010. Déterminisme génétique des réponses au déficit hydrique de la transpiration et de la croissance, induites par le porte-greffe, chez la vigne : approche intégrée de génétique quantitative et d'écophysiologie. *PhD Dissertation*, Bordeaux University, Bordeaux.

Marguerit, E., Brendel, O., Lebon, E., Van Leeuwen, C. and Ollat, N., 2012. Rootstock control of scion transpiration and its acclimation to water deficit are controlled by different genes. *The New Phytologist*, 194, 416-429.

Matthews, M. A., Ishii, R., Anderson, M. M. and O'Mahony, M., 1990. Dependence of wine sensory attributes on vine water status. *Journal of the Science of Food and Agriculture*, **51**, 321-335.

Maurel, C., Boursiac, Y., Luu, D.-T., Santoni, V., Shahzad, Z. and Verdoucq, L., 2015. *Aquaporins in plants. Physiological Reviews*, **95**, 1321-1358

McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T.,… and Yepez, E. A., 2008. Mechanisms of plant survival and mortality during drought : why do some plants survive while others succumb to drought? *The New Phytologist*, **178**, 719-739.

McElrone, A. J., Brodersen, C. R., Alsina, M. M., Drayton, W. M., Matthews, M. A., Shackel, K. A., Wada, H., Zufferey V. and Choat, B., 2012. Centrifuge technique consistently overestimates vulnerability to water stress-induced cavitation in grapevines as confirmed with high-resolution computed tomography. *The New Phytologist*, **196**, 661-665.

Medrano, H., Escalona, J. M., Cifre, J., Bota, J. and Flexas, J., 2003. A ten-year study on the physiology of two Spanish grapevine cultivars under field conditions : effects of water availability from leaf photosynthesis to grape yield and quality. Functional Plant Biology, 30, 607-619.

Medrano, H., Tomás, M., Martorell, S., Escalona, J.-M., Pou, A., Fuentes, S., Flexas, J. and Bota, J., 2015. Improving water use efficiency of vineyards in semi-arid regions. *A review. Agronomy for Sustainable Development*, **35**, 499-517.

Mittler, R. and Blumwald, E., 2015. The roles of ROS and ABA in systemic acquired acclimation. *The Plant Cell*, **27**, 64-70.

Morgan, J. M., 1984. Osmoregulation and water stress in higher plants. *Annual Review of Plant Physiology*, **35**, 299-319.

Nambara, E. and Marion-Poll, A., 2005. Abscisic acid biosynthesis and catabolism. Annual Review of Plant Biology, 56, 165-185.

Ollat, N., Touzard, J.-M. and Van Leeuwen, C., 2016. Climate change impacts and adaptations : new challenges for the wine industry. *Journal of Wine Economics*, **11**, 139-149.

Pantin, F., Monnet, F., Jannaud, D., Costa, J. M., Renaud, J., Muller, B., Simonneau, T. and Genty, B., 2013. The dual effect of abscisic acid on stomata. *The New Phytologist*, **197**, 65-72.

Patakas, A. and Noitsakis, B., 1999. Mechanisms involved in diurnal changes of osmotic potential in grapevines under drought conditions. *Journal of Plant Physiology*, **154**, 767-774.

Peccoux, A., 2011. Molecular and physiological characterization of grapevine rootstock adaptation to drought. *PhD Dissertation*, Bordeaux University, Bordeaux.

Pellegrino, A., Gozé, E., Lebon, E. and Wéry, J., 2006. A model-based diagnosis tool to evaluate the water stress experienced by grapevine in field sites. *European Journal of Agronomy*, **25**, 49-59.

Pongracz, D. P. and Beukman, E.F., 1970. Comparative root anatomy of Vitis rootstocks. *Agroplantae*, **2**, 83-94.

Poni, S., Lakso, A. N., Turner, J. R. and Melious, R. E., 1993. The effects of pre- and post-veraison water stress on growth and physiology of potted Pinot Noir grapevines at varying crop levels. *Vitis*, **32**, 207-214.

Pou, A., Medrano, H., Tomàs, M., Martorell, S., Ribas-Carbó, M. and Flexas, J., 2012. Anisohydric behaviour in grapevines results in better performance under moderate water stress and recovery than isohydric behaviour. *Plant and Soil*, **359**, 335-349.

Prieto, J. A., Lebon, E. and Ojeda, H., 2010. Stomatal behavior of different grapevine cultivars in response to soil water status and air water vapor pressure deficit. *Journal International des Sciences de la Vigne et du Vin*, **44**, 9-20.

Riahi, L., Zoghlami, N., Dereeper, A., Laucou, V., Mliki, A. and This, P., 2013. Single nucleotide polymorphism and haplotype diversity of the gene NAC4 in grapevine. *Industrial Crops and Products*, **43**, 718-724.

Riederer, M. and Schreiber, L., 2001. Protecting against water loss : analysis of the barrier properties of plant cuticles. *Journal of Experimental Botany*, **52**, 2023-2032.

Ripoche, A., Celette, F., Cinna, J.-P. and Gary, C., 2010. Design of intercrop management plans to fulfil production and environmental objectives in vineyards. *European Journal of Agronomy*, **32**, 30-39.

Rodrigues, M. L., Chaves, M. M., Wendler, R., David, M. M., Quick, W. P., Leegood, R. C., Stitt, M. and Pereira, J. S., 1993. Osmotic adjustment in water stressed grapevine leaves in relation to carbon assimilation. *Functional Plant Biology*, **20**, 309-321.

Rossdeutsch, L., 2015. Contribution du métabolisme de l'ABA et de la conductivité hydraulique à la réponse de la transpiration en situation de contrainte hydrique chez la Vigne. Variabilité génétique et effets du greffage. *PhD Dissertation*, Bordeaux University, Bordeaux.

Rossdeutsch, L., Edwards, E., Cookson, S. J., Barrieu, F., Gambetta, G. A., Delrot, S. and Ollat, N., 2016. ABA-mediated responses to water deficit separate grapevine genotypes by their genetic background. *BMC Plant Biology*, **16**, 91.

Salleo, S., Trifilo, P., Esposito, S., Nardini, A. and Lo Gullo, M. A., 2009. Starch-to-sugar conversion in wood parenchyma of field-growing *Laurus nobilis* plants : a component of the signal pathway for embolism repair? *Functional Plant Biology*, **36**, 815-825.

Schultz, H. R. and Matthews, M. A., 1988. Resistance to water transport in shoots of *Vitis vinifera* L. Relation to growth at low water potential. *Plant Physiology*, 88, 718-724.

Schultz, H. R., 2003. Differences in hydraulic architecture account for near- isohydric and anisohydric behaviour of two field-grown *Vitis vinifera* L. cultivars during drought. *Plant, Cell and Environment*, **26**, 1393-1405.

Serra, I., Strever, A., Myburgh, P. A. and Deloire, A., 2014. Review : the interaction between rootstocks and cultivars (*Vitis vinifera* L.) to enhance drought tolerance in grapevine. *Australian Journal of Grape and Wine Research*, **20**, 1-14.

Sharp, R. E. and Davies, W. J., 1985. Root growth and water uptake by maize plants in drying soil. *Journal of Experimental Botany*, **36**, 1441-1456.

Shelden, M. C., Howitt, S. M., Kaiser, B. N. and Tyerman, S. D., 2009. Identification and functional characterisation of aquaporins in the grapevine, *Vitis vinifera*. *Functional Plant Biology*, **36**, 1065-1078.

Simonneau, T., Barrieu, P. and Tardieu, F., 1998. Accumulation rate of ABA in detached maize roots correlates with root water potential regardless of age and branching order. *Plant, Cell and Environment*, 21, 1113-1122.

Smart, D.R., Schwass, E., Lakso, A. and Morano., L., 2006. Grapevine rooting patterns : a comprehensive analysis and a review. *American Journal of Enology and Viticulture*, **57**, 89-104.

Soar, C. J., Speirs, J., Maffei, S. M. and Loveys, B. R., 2004. Gradients in stomatal conductance, xylem sap ABA and bulk leaf ABA along canes of *Vitis vinifera* cv. Shiraz : molecular and physiological studies investigating their source. *Functional Plant Biology*, **31**, 659-669.

Soar, C. J., Dry, P. R. and Loveys, B. R., 2006a. Scion photosynthesis and leaf gas exchange in *Vitis vinifera* L. cv. Shiraz : mediation of rootstock effects via xylem sap ABA. *Australian Journal of Grape and Wine Research*, **12**, 82-96.

Soar, C. J., Speirs, J., Maffei, S. M., Penrose, A. B., McCarthy, M. G. and Loveys, B. R., 2006b. Grape vine varieties Shiraz and Grenache differ in their stomatal response to VPD : apparent links with ABA physiology and gene expression in leaf tissue. *Australian Journal of Grape and Wine Research*, **12**, 2-12.

Southey, J. M. and Archer, E., 1988. The effect of rootstock cultivar on grapevine root distribution and density. *In : Van Zyl J. L. (Ed.) The Grapevine Root and its Environment*. Pretoria : Department of Agriculture and Water Supply, pp 57-73.

Speirs, J., Binney, A., Collins, M., Edwards, E. and Loveys, B., 2013. Expression of ABA synthesis and metabolism genes under different irrigation strategies and atmospheric VPDs is associated with stomatal conductance in grapevine (*Vitis vinifera* L. cv Cabernet-Sauvignon). *Journal of Experimental Botany*, **64**, 1907-1916.

Steudle, E., 2000. Water uptake by roots : effects of water deficit. *Journal of Experimental Botany*, **51**, 1531-1542.

Stoll, M., Loveys, B. and Dry, P., 2000. Hormonal changes induced by partial rootzone drying of

irrigated grapevine. *Journal of Experimental Botany, 51*, 1627-1634.

Szabados, L., Kovacs, H., Zilberstein, A. and Bouchereau, A., 2011. Plants in extreme environments : importance of protective compounds in stress tolerance. *Advances in Botanical Research*, **57**, 105-150.

Tandonnet, J.-P., Cookson, S. J., Vivin, P. and Ollat, N., 2010. Scion genotype controls biomass allocation and root development in grafted grapevine. Australian *Journal of Grape and Wine Research*, **16**, 290-300.

Tardieu, F., Lafarge, T. and Simonneau, T., 1996. Stomatal control by fed or endogenous xylem ABA in sunflower: interpretation of correlations between leaf water potential and stomatal conductance in anisohydric species. *Plant, Cell and Environment*, **19**, 75-84.

Tardieu, F. and Simonneau, T., 1998. Variability among species of stomatal control under fluctuating soil water status and evaporative demand : modelling isohydric and anisohydric behaviours. *Journal of Experimental Botany*, **49**, 419-432.

Teulat, B., Borries, C. and This, D., 2001. New QTLs identified for plant water status, water-soluble carbohydrate and osmotic adjustment in a barley population grown in a growth-chamber under two water regimes. *Theoretical and Applied Genetics*, **103**, 161-170.

Tibbetts, T. J. and Ewers, F. W., 2000. Root pressure and specific conductivity in temperate lianas: exotic *Celastrus orbiculatus* (Celastraceae) vs. native *Vitis riparia* (Vitaceae). *American Journal of Botany*, **87**, 1272-1278.

Tomás, M., Medrano, H., Escalona, J. M., Martorell, S., Pou, A., Ribas-Carbó, M. and Flexas, J., 2014. Variability of water use efficiency in grapevines. *Environmental and Experimental Botany*, **103**, 148-157.

Tramontini, S., van Leeuwen, C., Domec, J.-C., Destrac-Irvine, A., Basteau, C., Vitali, M., Mosbach-Schulz, O. and Lovisolo, C., 2013a. Impact of soil texture and water availability on the hydraulic control of plant and grape-berry development. *Plant and Soil*, **368**, 215-230.

Tramontini, S., Vitali, M., Centioni, L., Schubert, A. and Lovisolo, C., 2013b. Rootstock control of scion response to water stress in grapevine. *Environmental and Experimental Botany*, **93**, 20-26.

Tramontini, S. and Lovisolo, C., 2016. Embolism formation and removal in grapevines: a phenomenon affecting hydraulics and transpiration upon water stress. In: Geros H., Chaves M. M., Medrano H. and Delrot S. (Eds.) Grapevine in a Changing Environment : A Molecular and Ecophysiological Perspective. Wiley and Sons, New York, pp 135-147.

Turner, N. C. and Jones, M. M., 1980. Turgor maintenance by osmotic adjustment : a review and evaluation. In: Turner N. C. and Kramer P. J. (Eds.) Adaptation of Plants to Water and High Temperature Stress. Wiley and Sons, New York, pp 87-103.

Tyree, M. T., 2003. Plant hydraulics : the ascent of water. *Nature*, **423**, 923-923.

Vandeleur, R. K., Mayo, G., Shelden, M. C., Gilliham, M., Kaiser, B. N. and Tyerman, S. D., 2009. The role of plasma membrane intrinsic protein aquaporins in water transport through roots : diurnal and drought stress responses reveal different strategies between isohydric and anisohydric cultivars of grapevine. *Plant Physiology*, **149**, 445-460.

van Leeuwen, C. and Seguin, G., 2006. The concept of terroir in viticulture. *Journal of Wine Research*, **17**, 1-10.

van Zyl, J. L., 1988. Response of grapevine roots to soil water regimes and irrigation systems. *In : Van Zyl J. L. (Ed.) The Grapevine Root and its Environment*. Pretoria : Department of Agriculture and Water Supply, pp 30-43.

Wilkinson, S. and Davies, W. J., 2002. ABA-based chemical signalling : the co-ordination of responses to stress in plants. *Plant, Cell and Environment*, **25**, 195-210.

Yamaguchi-Shinozaki, K. and Shinozaki, K., 2006. Transcriptional regulatory networks in cellular responses and tolerance to dehydration and cold stresses. *Annual Review of Plant Biology*, **57**, 781-803.

Zhang, L., Marguerit, E., Rossdeutsch, L., Ollat, N. and Gambetta, G. A., 2016. The influence of grapevine rootstocks on scion growth and drought resistance. *Theoretical and Experimental Plant Physiology*, **28**, 143-157.

Zufferey, V., Cochard, H., Ameglio, T., Spring, J.-L. and Viret, O., 2011. Diurnal cycles of embolism formation and repair in petioles of grapevine (*Vitis vinifera* cv. Chasselas). *Journal of Experimental Botany*, **62**, 3885-3894.

Zwieniecki, M. A. and Holbrook, N. M., 1998. Diurnal variation in xylem hydraulic conductivity in white ash (*Fraxinus americana* L.), red maple (*Acer rubrum* L.) and red spruce (*Picea rubens* Sarg.). *Plant, Cell and Environment*, **21**, 1173-1180.