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Review of water deficit mediated changes in vine and berry physiology; Consequences for the optimization of irrigation strategies

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ABSTRACT

The increasing risk of water deficit stress due to global warming subjects winegrowers of traditional rain fed viticulture regions to new challenges regarding vine water status assessment and possible drought mitigation strategies, such as irrigation.
This review summarizes the most recent studies on the impact of water deficit stress on vine and berry physiology; it discusses the latest scientific advances regarding hormonal and hydraulic regulation and segmentation and addresses the current debate on iso/an-isohydricity within vine cultivars. Latest literature on irrigation frequency, water stress memory and the impact of abiotic factors such as VPD (Vapor Pressure Deficit), radiation, temperature and canopy architecture on vine physiology and water use, raise important questions on water status assessment and the implementation of irrigation strategies. Practical consequences regarding the effects of vine water regime on vine water regulatory mechanisms are discussed. Recent technical and scientific advances shed new light on how site specific irrigation strategies matching production objectives could improve vineyard water use.

KEYWORDS

irrigation, water deficit, vine physiology, berry quality, vine water status

INTRODUCTION

In a world where fresh water is becoming an increasingly scarce resource with 80% of it used for irrigation of agricultural crops (FAO, 2016), the optimization of water use should be a primary objective for agriculture. This is particularly true regarding viticulture where a tradeoff between yield loss and quality gain can be economically very significant for producers, and highly modulated by water supply. Global warming leads to altered precipitation patterns and to an increasingly negative climatic water balance during the vegetative cycle (Schultz and Stoll, 2010; van Leeuwen and Destrac-Irvine, 2017) which increases the risks of drought periods. For winegrowers, different drought mitigation strategies exists as reviewed by Medrano *et al.* (2015).

Those consist of different agronomic practices such as adaption of planting density, training system, leaf area, the choice of cultivar and rootstock (Ollat *et al.*, 2016; Romero *et al.*, 2018) and eventually the installation of irrigation systems. The latter represent a particularly challenging new commitment for most growers of regions, where vine cultivation has historically been rainfed and vine water status monitoring and management was not necessary.

Traditionally, in many protected wine-producing areas, so called designations of origin, for example the French AOP system, irrigation is restricted to the period from flowering to the 15th of August, which corresponds roughly with the date of véraison. Historically, these rules have been imposed for the sake of wine quality because water supply during late ripening is ostensibly implicated in an increase in berry weight and yield, with a consequent dilution of quality determining compounds. The rationale behind these regulations has however been questioned from a scientific perspective because it remains unclear whether excess soil water supplied during ripening leads to an increase in berry size and thereby alter wine composition (Keller *et al.*, 2016; Keller and Shrestha, 2014). Facing the new challenges imposed by global warming those regulations are being, or have already been relaxed in some designations of origin in several countries including Spain and Italy, allowing winegrowers the opportunity to irrigate. Growers in traditional dry farmed winegrowing regions, where water deficit becomes an increasing problem are thus given new opportunities, with the associated multiple challenges regarding technological questions of irrigation; how much deficit should be imposed during what time and at what frequency and how can it be monitored?

The type of adopted irrigation system has a large impact on the water footprint. It ranges from traditional surface irrigation, still implemented in some wine growing regions (e.g. Mendoza, Argentina) which amongst the most wasteful of techniques, followed by pressurized overhead irrigation and finally drip irrigation, which is perhaps the most used and efficient water delivery system in use today in viticulture. Irrigation scheduling is therefore one of the most important leverages in viticulture to influence water use efficiency, yield and quality of irrigated vineyards.

Here, we provide an overview and discuss recent scientific literature addressing the consequences of water deficit on berry and vine physiology. The review of the most recent and significant literature dealing with water stress memory effects and irrigation frequency, leads to the proposal of new ideas for an adaption of irrigation strategies with the objective of achieving a sustainable water management.

WATER DEFICIT AND VINE PHYSIOLOGY, MORPHOLOGY AND HYDRAULIC REGULATION

Water deficit affects vegetative and generative growth in multiple ways depending on severity and moment in the season when it occurs. The first physiological response to mild water deficit stress is a reduction in shoot growth, primarily affecting lateral/secondary shoots before growth of the main shoot is reduced and stomata opening is regulated (Lebon *et al.*, 2006; Pellegrino *et al.*, 2005). With increasing water deficit, the vine starts closing its stomata (reduction of stomatal conductance, g_s) to limit transpirational water loss, which leads to a reduction in photosynthesis (Keller, 2010). As growth slacking precedes reduction of photosynthesis during increasing water stress, more carbohydrates become available and can be allocated to reproductive sinks such as fruits, and thus favor the synthesis of berry quality determining compounds (flavor compounds, anthocyanins, sugar content) (van Leeuwen *et al.*, 2009). The physiological mechanisms underlying stomatal regulation involve both

hydraulic and hormonal signals (Bonada *et al.*, 2018; Tombesi *et al.*, 2015). Hormonal regulation acts via the accumulation of the drought hormone abscisic acid (ABA) in leaves, impacting directly on the guard cells which close stomata (Coupel-Ledru *et al.*, 2017). Historical studies indicate that ABA synthesis via the isoprenoid pathway occurs mainly in the roots, followed by transport to the leaves, where it acts on stomatal regulation (Simonneau *et al.*, 1998). However, recent scientific literature points out that the majority of ABA is putatively produced inside the leaves and subsequently transported to the roots where it helps to maintain normal root ABA levels and determines root growth and architecture. This is supported by gene expression studies (Christmann *et al.*, 2007; Speirs *et al.*, 2013) and by estimating ABA transport in sap flow in tall trees, where simple physical transport from roots to leaves would take up to 40 days, however stomatal regulation occurs within hours due to stress (McAdam *et al.*, 2016; Sampaio Filho *et al.*, 2018). Thus stomatal regulation is most likely triggered by leaf ABA in combination with other more rapid signals (Christmann *et al.*, 2007). These signals are probably of a hydraulic nature and caused by cavitations (or embolisms) that occur in xylem vessels when atmospheric demand cannot be met by soil water content. This creates a tension inside the xylem so high that gas molecules from water expand and fill xylem vessels or tracheids, which results in the formation of embolisms and thus a decrease in hydraulic conductivity (Knipfer *et al.*, 2016a; Tramontini *et al.*, 2014). Grapevine has been described as both vulnerable (Jacobsen and Pratt, 2012; Zufferey *et al.*, 2011) and relatively resistant to embolism (Brodersen and McElrone, 2013; Choat *et al.*, 2010). In general more distal organs such as petioles are more sensitive to embolism than more basal parts such as stems (Hochberg *et al.*, 2015).

It is a still ongoing debate as to what extent and by what process embolized xylem vessels can be repaired by the plant. Early studies showed that the restoration of xylem conductivity could only be accomplished by positive root pressure; during the night when transpiration is reduced, roots can accumulate solutes in xylem in concentrations exceeding those of the soil thereby drawing water osmotically back inside the xylem (Holbrook and Zwieniecki, 1999; Knipfer *et al.*, 2015). These mechanisms have been questioned by Knipfer *et al.* (2016b) who provided evidence that embolism removal can occur in the absence of root pressure and is driven by vessel-associated tissue (i.e. parenchyma cells and fibers), and that a long-distance signal is not required to trigger this process. These observations would eliminate the necessity of root pressure as a required driving force for embolism.

However, it has been shown that hydraulic experiments on excised organs are prone to artefacts. Using X-ray micro-computed tomography on intact plants Charrier *et al.*, (2016) circumvented such putative artefacts and showed that *V. vinifera* was not able to refill embolized xylem vessels under negative bulk xylem pressure. If root pressure was positive, refilling only occured up to the stem bases but not to the upper, distal stem portion. Those results have not been challenged until today. In fact, more recent work showed that under positive root pressure (i.e. during the winter) embolism via xylem refilling could occurs. This mechanism of embolism repair has been recently demonstrated for tree species (Choat *et al.*, 2019) and has been confirmed on grapevine (S. Delzon, 2019 *pers comm. in ed*).

This hydraulic vulnerability segmentation provides significant protection of the perennial stem, but raises important questions on the validity of water potential measurement to assess vine water status (as discussed in Rienth and Scholasch, in ed).

Empirical field observations from simultaneous sap flow and water potential monitoring confirm the irreversibility of embolism. For instance, in California, winegrowers have observed that following a decline in the ratio of vine transpiration to reference evapotranspiration (T_{crop}/ET_{ref}) after a heat wave, even large irrigations (ie. >20 mm) are not always able to restitute maximum T_{crop}/ET_{ref} ratio. This suggests that heat waves combined with low soil moisture may increased cavitations, leading to a non-reversible loss of vine hydraulic conductivity. Therefore, even after irrigating, the maximum ratio of T_{crop}/ET_{ref} may remain lower throughout the rest of the season.

These findings and observations have practical consequences for irrigation scheduling and water balance calibration both relying on water potential readings. As the season unfolds, more episodes of drought can result in an increasing divergence between water potential readings and

overall plant water status. Furthermore, the consequences of vine hydraulic conductivity decline on vine water deficit and vine transpiration modelling, may be harder to predict in a context of increasing drought. Hence, water potential measurements may become gradually less reliable during a season and therefore of limited value for the calibration of vine water balance models.

In general, grapevines show a somewhat sensitive stomatal regulation in comparison with other plants and are regarded as drought tolerant and as relatively isohydric species. This means that they are able to maintain a constant leaf water potential even when soil water potential is dropping (Galmes *et al.*, 2007). Several studies showed that grape vine cultivars vary in their sensitivity for cavitation and subsequently in their stomatal regulation during increasing water deficit, which has however recently been questioned (Charrier *et al.*, 2018) and is discussed subsequently. Generally, cultivars that show a more drought sensitive stomatal regulation and consequently maintain a constant leaf water potential when soil water potential is decreasing, are regarded as isohydric and considered as "drought avoiders" or "pessimists" since this comportment would conserve remaining water resources in the soil. Such cultivars seem to be better adapted for regions where drought periods are severe and long lasting (Simonneau *et al.*, 2017). Conversely, cultivars that show an an-isohydric or more "optimistic" behavior maintain their stomata open during increasing soil water deficit, thereby decreasing their leaf water potential, hence maintaining high transpiration. The latter behavior is more water "wasting", consequently they can maintain photosynthesis and higher vigor under water deficit than isohydric cultivars. Hence, such cultivars seem more adapted to regions where drought periods are less severe and rather short (Chaves *et al.*, 2010; Schultz, 2003; Soar *et al.*, 2006). However, this concept of a strict classification of cultivars into iso and an-isohydric has been challenged by several research groups. Same cultivars showed often very contradictory even opposed behavior when exposed to water stress such as Cabernet-Sauvignon (Williams and Baeza, 2007), Tempranillo (Antolin *et al.*, 2006; Sebastian *et al.*, 2015) and Syrah (Lovisolo *et al.*, 2010; Schultz, 2003; Soar *et al.*, 2006). Whether an- or isohydricity is genotypically determined as indicated by the identification of several QTLs related to isohydricy (Coupel-Ledru *et al.*, 2017), or whether it is more influenced by abiotic factors in the current, or even more in past seasons (Chaves *et al.*, 2010) and to what extend diversity of scion-rootstock combinations and their interaction with different soils intervene (Lavoie-Lamoureux *et al.*, 2017), is still an ongoing debate (Simonneau *et al.*, 2017). Charrier *et al.* (2018) suggest that a continuum exists amongst *Vitis* species and that there is a transition from anisohydric to isohydric as stress increases. Likewise other authors propose a complete deconstruction of the anisohydric concept across species and advocate for a clear and quantitative definition (Martínez-Vilalta and Garcia-Forner, 2017).

Different soil textures also seem to influence vine water use regulation under water deficit. For example, Tramontini *et al.* (2013) and Tramontini *et al.* (2014) showed that a clay-rich soil can decrease stomatal aperture, the extent of embolism formation, and modulate ABA concentrations in leaves of both iso and anisohydric cultivars.

Morphological adaptations of upper ground tissue triggered by water deficit consist in adaptations that may participate in minimizing transpiration, including a reduction in leaf size and area (Gómez-del-Campo *et al.*, 2002; Hochberg *et al.*, 2017), and changes in thickness and composition of the waxy cuticle that would limit water loss through the leaf surface. The relation between cuticle components and their efficacy to limit water loss remains to be understood (Schreiber and Riederer, 2001). In a very recent transcriptomic study Degu *et al.* (2019) highlight the metabolic strategies of grapevine leaves involved in drought mediation which involves osmotic adjustment as already shown previously (Schultz and Matthews, 1993), an upregulation of stress related genes and pathways such as Proline and GABA (gamma-aminobutiyric acid) metabolism with an incremental contribution of Ca^{+} and sucrose adjustment concomitant with the initiation of leaf shedding.

As regards root growth, it is in general acknowledged that mild water deficit stress increases the root to shoot ratio, because root growth is less sensitive to water deficit than shoot growth and because plants allocate more resources to the organs that acquire the most limiting resource (Ledo *et al.*, 2018; Poorter *et*

al., 2012). A too severe water deficit will cause complete cessation of root growth, because the main driver for root development is soil water (Robbins and Dinneny, 2018).

Root growth in response to water availability is however difficult to assess in field trials (destructive measurement, repeatability, soil heterogeneity) consequently not many studies have been conducted. For example a study from Edwards and Clingeleffer (2013) assessed the effect of different irrigation volumes on dry root mass over a 75 cm soil depth. The authors found that the total root dry weight was highest under well-watered conditions and lowest when least water was supplied. However, the fraction of the total root mass in 25 to 50 cm depth was highest for mild deficit and highest in the topsoil (0-25) under full irrigation. Root architecture can be modified according to the frequency and the volume of irrigation, and irrigation strategy affects the size and distribution of root absorption sites along the soil profile (Bou Nader *et al.*, 2019). As such, Prats-Llinàs *et al.* (2019) found that post-harvest water stress impeded new root formation in the cultivar Chardonnay.

Furthermore, when root mass and root absorption sites are more concentrated near the soil surface, vine water supply is more dependent on changes in soil moisture content occurring immediately below the surface. As soil moisture variations are more abrupt near the surface than at greater soil depth, differences in rooting depth are expected to drive different water deficit profiles (Scholasch, 2018). Root morphological adaptations due to water availability vary with different rootstock types, which has not exhaustively been studied in grapevines. It is however acknowledged that older vines do have deeper and/or more developed root systems which makes them more resistant to drought conditions than younger vines (Bou Nader *et al.*, 2019; Grigg *et al.*, 2018).

Rootstocks that are known to be more drought tolerant such as *Berlandieri-Rupestris* crossings for example 110R, 99R, 1103P or 140Ru, reduce root growth less than *Riparia-Berlandieri* (5BB,SO4), *Riparia-Rupestris* (3309C and 101-14MGT) or *Vinifera-Berlandieri* (41B) crossings when water becomes limiting (Ollat *et al.*, 2016).Yildirim *et al.* (2018) compared 110R with 5BB and 41B and found higher root area, root length, ramification and number of root tips with higher relative water content as well as total carbohydrate and nitrogen in the roots of 110R during drought. In a different study, where Merlot root growth dynamics grafted on either 1103P or 101-14MGt, the drought resistant 1103P exhibited a greater plasticity towards varying water supply and maintained higher root production during summer into deeper soil layers than 101-14MGt (Bauerle *et al.*, 2008). Cabernet-Sauvignon grafted to Ramsey rootstock established under sprinkler irrigation and converted to drip irrigation had significant larger root systems (compared to 100% sprinkler) and coped better with drought after conversion (Soar and Loveys, 2007).

Further morphological adaptation to water deficit regarding petiole hydraulics and xylem vessels were investigated by several research groups. Typically, under a higher irrigation regime, larger vessel diameter and higher hydraulic conductance are observed. For example, Dayer *et al.* (2017) report fewer large-sized vessels with higher vessel density from water stressed vines, as compared to irrigated ones. Similar results are reported by Munitz *et al.* (2018) on a 4 year study with Cabernet-Sauvignon where high water availability during vegetative growth period increased vessel diameter and hydraulic conductivity and caused the vines to be more vulnerable to drought stress late in the season. This is confirmed by data of Hochberg *et al.* (2017) who report that drought-acclimated vines maintained higher gas exchange compared to irrigated controls under water deficit. Vine water requirements can therefore increase in response to increased irrigation. Hence, acclimation of vessel morphology to be more drought resistant could be one of the objectives of a sustainable irrigation strategy seeking to impose early water deficit. However, such strategies should be implemented with caution. If water stress is too severe, it can have negative effects on vine hydraulic functioning in the long term. Severe water stress during previous seasons can lead to decreased water use efficiency induced by a different stomatal response to drought in water stressed vines compared to well-watered vines in the current season (Tombesi *et al.*, 2018). Conversely, irrigation treatment inducing early water deficit for 4 consecutive years led to vines being less vulnerable to end of season water stress in the study of Munitz *et al.* (2018). This highlights that carryover effects exists and can modulate vine water use regulation. Thus, the

consequences of past irrigations should be considered when adopting new irrigation strategies.

Of course other carryover effects exist in plants where fruiting occurs over two consecutive seasons. Those concern reserves such as carbohydrates in the form of starch, present in grapevine perennial tissues and predominates in roots but is present also in trunk and canes (Holzapfel and Smith, 2012; Holzapfel *et al.*, 2010; Pellegrino *et al.*, 2014) and in seasonal organs such as leaves (Dayer *et al.*, 2016). The vegetative and early reproductive development of the vine is almost fully dependent upon its overwinter carbohydrate reserves until flowering (anthesis) (Lebon *et al.*, 2008). As drought periods can hinder replenishment of reserves they can have a negative impact on early reproductive development, influencing the differentiation of flowers in winter buds, their subsequent flowering (flower abscission rate) and inflorescence primordia differentiation in developing winter buds. Winter hardiness and longevity of the vine can also be negatively impacted by low reserves (Li-Mallet *et al.*, 2016; Pellegrino *et al.*, 2014; Rossouw *et al.*, 2017). Rustioni *et al.* (2019) showed that even short periods of late water deficit can have a negative impact on reserve replenishment in a genotype depend matter with Syrah being more sensitive than Cabernet-Sauvignon. In combination with low nitrogen, water deficit stress can aggravate this negative carryover effect on yield, by reducing bud fertility (Guilpart *et al.*, 2014). However in a study of Prats-Llinàs *et al.* (2019) post-harvest water deficit did not influence starch accumulation in perennial organs in Chardonnay.

IMPACT OF WATER DEFICIT ON BERRY PHYSIOLOGY AND COMPOSITION

Grapevine berry development is classically divided into 2 growing phases separated by a lag phase, where growth ceases for several days and the embryo ripens (Conde *et al.*, 2007; Coombe and MccCarthy, 2000; Ollat *et al.*, 2002). During the first green growth phase, berry volume augments due to cellular division and expansion, mainly driven by water import into cell vacuoles principally via the xylem. After the lag phase a short transition phase, which is commonly called véraison and lasts for 24h on a single berry basis. This short transition is characterized by important transcriptomic reprogramming, berry softening, resumption of growth and the beginning of sugar and anthocyanin and is in particular sensible to abiotic stresses (Rienth *et al.*, 2014b; Rienth *et al.*, 2016). During the subsequent second growth phase or ripening, berry growth is only due to cellular expansion driven by apoplastic water and solute import via the phloem. During this phase the berry remains hydraulically connected to the vine (Chatelet *et al.*, 2008a; Chatelet *et al.*, 2008b; Keller *et al.*, 2006), however xylem flow is reversed to evacuate surplus water that enters the berry osmotically by the phloem (Zhang and Keller, 2017). That is why the post-véraison berry becomes more independent and much less sensitive to water potential variations in the soil and vine (Choat *et al.*, 2009; Keller *et al.*, 2006).

Several studies were carried out to investigate the impact of water deficit on berry physiology and quality. The impact of water deficit on berry development is highly dependent on its intensity, the duration of the deficit and the berry developmental stage when it occurs. Early water deficit during the first growth phase has the highest impact on final berry size and consequently yield. It slows down cell expansion in the berry without impacting cell division rate (Ojeda *et al.*, 2001) contrary to still frequently encountered rumors. However, water deficit during early development is still infrequent in most semi-arid regions. Water deficit during the ripening phase is less affecting on final berry size, probably due to a switch from symplastic to apoplastic - osmotically driven sugar unloading, via the phloem (Zhang *et al.*, 2006)

A significant number of experiments showed that moderate water deficit is in general, beneficial for wine quality, particularly for red cultivars where synthesis of quality determining compounds is more complex and costly for the vine (van Leeuwen *et al.*, 2009; Zufferey *et al.*, 2017). Zarrouk*et al.* (2016b) provide a comprehensive compilation of studies published between 2009 and 2016 dealing with water deficit and impact on berry compounds.

Beneficial effects of water deficit can partly be attributed to higher concentration of quality determining compounds due to reduced berry volume but also to an enhanced accumulation of secondary metabolites independently of berry volume (Ojeda *et al.*, 2002). This has been confirmed by several transcriptomic and

proteomic studies where water deficit induced an activation of key enzymes of the phenylpropanoid pathway and its downstream reactions, in particular flavonoid and anthocyanins biosynthesis (Castellarin *et al.*, 2007a; Castellarin *et al.*, 2007b; Cramer *et al.*, 2007; Deluc *et al.*, 2011; Deluc *et al.*, 2009; Savoi *et al.*, 2016). Those positive effects are mainly observed when stress occurs during the second growth phase where synthesis of anthocyanins and of most flavor compounds takes place and the berry is the major carbon sink. Besides an overall increased accumulation of phenylpropanoids (Chorti *et al.*, 2016; Koundouras, 2018) several studies show an alteration in composition of flavonoids and anthocyanins towards tri-hydroxylated anthocyanins (3′,4′,5′-hydroxylated: delphinidin, petunidin, malvidin) (Castellarin *et al.*, 2007a; Cook *et al.*, 2015; Ollé *et al.*, 2011) and some report increased proanthocyanidin concentration and polymerization in grape berry skins (Cáceres-Mella *et al.*, 2017; Kyraleou *et al.*, 2016), whereas others report higher catechin and total polyphenol concentration (Zsófi *et al.*, 2014). Interestingly, the modulation of anthocyanin structure in response to water deficit appears to be highly varietal dependent (Niculcea *et al.*, 2014; Theodorou *et al.*, 2019).

Reported increases in phenolic compounds when water deficit occurs prior to véraison seem to be mainly due to concentration effects (Brillante *et al.*, 2018; Santesteban *et al.*, 2011). Only very few studies report an increase in anthocyanin content on a per berry basis (Koundouras *et al.*, 2009; Ojeda *et al.*, 2002; Ollé *et al.*, 2011). Furthermore, it has recently been shown that water deficit can increase skin break force, skin break energy and skin rigidity of berries of the variety Kékfrankos (Zsófi *et al.*, 2014) or result in greater skin strength at harvest with the variety Cabernet-Sauvignon (Cooley *et al.*, 2017). Latter authors hypothesized that an imposed period of drought prior to véraison induces changes in berry cell wall composition leading to greater mechanical resistance.

The effects of water deficit on flavor and aroma potential are less evident than for phenolic compounds derived from the phenylpropanoid pathway. Depending on the type of aroma precursor, water availability can have various effects as reviewed by Alem *et al.* (2019). Moreover, as for phenylpropanoids it is often difficult to deduce physiological effects of water deficit because most papers present results on a concentration basis without berry weight or volume data, thus concentration effects due to berry volume changes preclude a physiological interpretation. Nevertheless, from a winemaker`s point of view it is important to consider effects on aroma even if they are concentration effects. Most studies dealing with the impact of water deficit on grape aroma compounds yield in very heterogeneous results. Regarding C13-norisoprenoids such as beta-damascenone, beta-ionone, and 1,1,6-trimethyl-1,2-dihydronaphthalene most authors report a positive relation between their concentration and moderate to severe water deficit and consequently an increase of aroma potential, which is particularly true for red varieties such as for Cabernet-Sauvignon (Bindon *et al.*, 2007; Brillante *et al.*, 2018; Koundouras *et al.*, 2009), Merlot (Song *et al.*, 2012) or Tempranillo (Talaverano *et al.*, 2017). In the latter study C6 compounds (hexanal, trans-2-hexenal, and 1-hexanol) and phenol volatiles, ethyl esters and lactones were also increased under water deficit. This is however not confirmed in a study on Merlot, where free C6 compounds decreased under water deficit (Song *et al.*, 2012).

Regarding monoterpenes such as limonene, linalool, ±-terpineol and geranyl acetone several authors suggest that light to moderate water stress increase their concentration (Brillante *et al.*, 2018) but as well their biosynthesis as indicated by transcriptomic studies, where moderate water deficit triggered terpenoid synthase expression in Chardonnay and Cabernet-Sauvignon (Deluc *et al.*, 2011; Savoi *et al.*, 2016). One of the few examples of aroma compounds where concentration in the berry is positively correlated with water availability (Geffroy *et al.*, 2014) is the recently discovered sesquiterpene Rotundone (Wood *et al.*, 2008), associated with peppery flavor in different red cultivars such as Syrah and Duras (Geffroy *et al.*, 2018).

Another important group of aroma compounds in some white wine varieties such as Sauvignon Blanc, Petite Arvine, Colombard and Alvarino are volatile thiols such as 4-mercapto-4-methylpentan-2-one (4MMP), 4-mercapto-4-methylpentan-2-ol (4MMPOH) and the 3-mercaptohexan-1-ol (3MH) present as cysteinylated precursors in the berry (Fretz *et al.*, 2005; Tominaga *et al.*, 2000). It has been shown that only mild water stress can be

beneficial for the production of their precursors and that severe water stress (predawn leaf water potential reaching -1.0MPa) is negative for their synthesis (Peyrot des Gachons *et al.*, 2005). However nitrogen availability is very important for the production of volatile thiols of grapes as shown by Helwi *et al.* (2015) and Helwi *et al.* (2016). As nitrogen absorption can be limited under water deficit (Celette and Gary, 2013) this putatively impedes thiol production and further, reduces aroma potential.

Often water stress effects are indirect and result from higher sun exposure due to a less dense canopy owed to reduced vegetative growth. Traditional examples are Carotenoids and their breakdown products, such as for example the C13-Norisporenoid 1,1,6-trimethyl-1,2-dihydronaphthalene, responsible for the petrol flavor in Riesling and highly correlated with sun exposure (Kwasniewski *et al.*, 2010; Schüttler *et al.*, 2015) but also augmented under water deficit in Cabernet-Sauvignon (Koundouras *et al.*, 2009).

Other UV/temperature degradable compounds and indirectly reduced by water deficit are methoxypyrazines (Šuklje *et al.*, 2012) hence the inverse correlation is often observed. Excessive growth due to high water availability leads to increase of methoxypyrazine as reported by Brillante *et al.* (2018) and Harris *et al.* (2012) where high levels of methoxypyrazines were observed in years of high-water availability. It is still not fully understood whether methoxypyrazines are synthesized in the berries or only in the leaves with subsequent transport to the berries where they are degraded, therefore it is difficult to explain the mechanisms involved in their synthesis and transport as a response to environmental conditions (Lei *et al.*, 2018).

New results suggests that prolonged drought between irrigations may provide other benifits. Cooley *et al.* (2017) reported a higher level of berry skin resistance to mechanical deformation when drought is imposed between 2 irrigations. Authors hypothesized that a period of drought imposed prior to véraison induces changes in berry cell wall composition leading to greater mechanical resistance. Furthermore, Cooley *et al.* (2017) observed that berry skin compositional changes induced by prolonged drought also led to an easier color extraction into red wine, which is desirable for winemakers.

Recent findings regarding potassium (K^+) channels involved in K^+ transport from the phloem cell cytosol to the berry apoplast during berry K^+ loading suggests that higher irrigation regimes could promote higher potassium content in the berry (Nieves-Cordones *et al.* 2018), which in in turn favors potassium tartrate precipitation thereby lowering total acidity of wines. This would represent a further drawback in view of global warming and the consequently accelerated degradation of malic acid (Rienth *et al.*, 2016) leading to low acidities in wines (Mira de Orduna, 2010).

IMPACT OF ENVIRONMENTAL FACTORS AND VINEYARD 3D-ARCHITECTURE ON WATER DEFICIT AND TRANSPIRATION RATE AT CANOPY AND FRUIT-ZONE LEVEL

Under semi-arid conditions, during the classical irrigation period (May-September) VPD increases from a minimum value early morning to reach a peak after solar noon. In Spain, Balbontín (2012) reported daily variations from minimum values ranging between 0.5–1.5 kPa to maximum afternoon values of 4.5–5.5 kPa. In Napa valley, California similar values are reported with maximum afternoon values reaching 6.5 kPa (Scholasch *et al.*, 2009). These high VPD conditions can reduce vineyard g_s, thus reducing carbon assimilation even when available soil moisture is not restricted (Soar *et al.*, 2006). However, reduction in g_s due to high VPD values does not necessarily reduce transpiration rate to the same extent. In fact, for a given level of water supply, higher VPD values tend to increase vine transpiration rate (Scholasch *et al.*, 2009) when canopy size, conductance and level of solar radiations remain constant,

Under well-watered conditions and controlled air humidity, Edwards *et al.* (2011) reported a 3 fold increase in vine transpiration, despite a slight reduction in stomatal conductance while air temperature was increased by 10° C. Using sap flow measurements in commercial vineyards, Bonada *et al.* (2018) reported that increased VPD in heated vines led to higher transpiration rates.

At the berry level, results from Rebucci *et al.* (1997), showed that higher VPD values increased sugar concentration but not sugar

content per berry. This is confirmed by several studies demonstrating that, even as the berry becomes more hydraulically independent of the vine post-véraison, as described earlier, water movement can occur in response to VPD through the skin which can lead to volumes changes (Becker *et al.*, 2012).

SOLAR RADIATION AND TRANSPIRATION RATE EFFECT OF ROW ORIENTATION ON VINE WATER USE

Water requirement for vines is directly proportional to intercepted solar radiation and total canopy transpiration is a function of intercepted radiation, canopy conductance and VPD at the leaf-air interface (Williams and Ayars, 2005). Vineyards with equal dimensions but different row orientations have different patterns of intercepted radiation (Louarn *et al.*, 2008; Prieto *et al.*, 2012).

To describe canopy properties, the fraction of photosynthetically active radiation (PAR) absorbed by the plant and the sum of absorbed PAR over time are commonly measured parameters. For hedgerow crops with heterogeneous canopies those parameters are linked to canopy transpiration and are useful for modelling gas exchange in the soil-plant-atmosphere continuum (Annandale *et al.*, 2004). Due to their 3D structure, vineyards have a complex light interception unlike herbaceous crops with homogenous canopies and continuous ground cover thus PAR is not constant throughout the day in hedgerow crops (Campos *et al.*, 2017). Because of its three-dimensional characteristics the architecture of the canopy has a strong influence on the partitioning between sunlit and shadowed sections. Studying vineyards with vertical shoot positioned (VSP) trellises, Campos *et al.* (2017) demonstrated that under clear sky, once canopy has reached its final size, E-W row orientations yield the lowest PAR absorption. Consequently, a greater water demand can be expected from vineyards with NS and NE-SW row orientation compared to EW.

EFFECT OF HYDRAULIC STRUCTURE, LIGHT AND TEMPERATURE ON TRANSPIRATION REGULATION

In vineyards, the gradient between organ and air temperature increases with higher solar irradiance and decreases with higher wind speed (Bergqvist *et al.*, 2001). Other factors that determine organ temperature are characteristics of surface conductance to water vapor diffusion and overall crop architecture (Saudreau *et al.*, 2011). The amount of intercepted radiation could also be used to model the difference between canopy and ambient temperature. As transpiration cools leaves, leaf temperature increases when transpiration is reduced. In water stressed situations, stomata close and cooling decreases. Consequently, the difference between leaf and air temperature increases under water stress depending on air temperature and wind speed (Sepulcre-Cantó *et al.*, 2006; Tuzet *et al.*, 2003).

In the study of Dayer *et al.* (2017), previously described, under well-watered conditions, shaded leaves exhibited a higher (petiole hydraulic conductivity) $K_{petiole}$ than the sun leaves at the end of the season, which was partially explained by a higher number of vessels per petiole. These results suggest that not only plant water status, but also light environment affect leaf and petiole hydraulics and thus leaf cooling ability. The effect of light and water stress on vine temperature variations should therefore be considered simultaneously.

Studying hedgerow crops, Trentacoste *et al.* (2015), report that West (W) sides of North–South (N-S) hedgerows experience higher canopy temperatures in the afternoon than do East (E) sides in the morning for the same solar irradiance. In vineyards with N–S row orientation, under high irradiance, VPD and air temperature, Greer and Weedon (2012) have measured lower leaf temperatures than air temperatures (between 1–4 °C differences) on E compared to the W sides during the warmest hours of day (i.e. 11 am –3 pm solar time). The E side has a greater heat dissipative capacity, likely due to a higher transpiration rate. Hence, regardless of irrigation or soil moisture regime, variations in canopy exposure to light modulates the vine transpiration hourly profile which in turn affects hourly profile of organ temperatures (Prieto *et al.*, 2013).

Various approaches seeking to assess vine water stress via canopy and atmospheric temperatures are under evaluation (Alfieri *et al.*, 2018; Prueger *et al.*, 2018). Their already promising results reveal however, that more efforts are needed to address fundamental questions on how to measure vine canopy temperature and how to

account for vineyard leaf area architecture (trellising, pruning practices, for example) via airborne thermal sensors to derive an index of vine water status.

Zhu *et al.* (2018) developed a 3D model simulating transpiration, including the effect of water deficit on gas-exchange and leaf temperature without considering how shoot hydraulic structure affects leaf-scale gas-exchange rates. However, the problem of decreasing vessel functioning due to formation of gas emboli throughout, is not considered in such models even if the effects and timing of vessel transitions from functionality to post-functionality are important aspects of plant hydraulic functioning as reviewed by Jacobsen *et al.* (2018).

To incorporate the effect of hydraulic structure on simulated whole grapevine transpiration, recent works have tested a 3D functional-structural plant model, postulating that intra-canopy variability for both leaf water potential and leaf temperature are the main drivers for the prediction of transpiration rates (Albasha *et al.*, 2019). Authors concluded that both hydraulic structure and energy balance simulations were required for a precise prediction of plant-scale gas-exchange rates under soil water deficit. Interestingly, results indicate that even if intra-canopy variability of leaf temperature is considered, changes in shoot hydraulic structure have by far the largest effect on simulated transpiration rates for grapevine.

Different groups have addressed the effects of light, and temperature on transpiration regulation at the fruit level.. Spayd *et al.* (2002) reported that E-exposed fruits were warmer early in the day and remained close to ambient air temperature throughout the afternoon. The W-exposed fruit remained near ambient temperature before midday and increased sharply afterwards. These examples illustrate the dependency of vineyard architectural features on the regulation of leaf and berry temperature. Several studies with different cultivars, showed that berry temperature increases when water stress increases and that this sensitivity to high temperatures is genotype dependent (Carvalho *et al.*, 2016; Theodorou *et al.*, 2019; Zarrouk *et al.*, 2016a). As shown by several studies, berry temperature is of crucial importance for the synthesis and degradation of quality determining compounds. As such Gaiotti *et al.* (2018) emphasize the beneficial effects of cool nights on anthocyanins accumulation. Similar results were obtained by transcriptomic heat stress studies that showed that high temperature is unfavorable for anthocyanin synthesis (Lecourieux *et al.*, 2017; Rienth *et al.*, 2014b; Rienth *et al.*, 2016). Interestingly such effects are most pronounced during the short (24h lasting) véraison phase, where the berry seems to be most vulnerable to abiotic stresses (Rienth *et al.*, 2014b). The effects of high day and/or night temperature on grape flavonoids at different scales have been recently reviewed by Gouot *et al.* (2018), who also concluded that most critical experimental parameters are phenological stages, followed by day/night temperature regimes.

Since there is an interaction between irrigation regime and berry temperature which affects quality, irrigation strategies should take berry developmental stages into account and avoid stress inducing situations around véraison. This means that irrigation schemes need to be adapted according to precocity of different cultivars and sites.

POSSIBLE STRATEGIES TO OPTIMIZE WATER USE EFFICIENCY, QUALITY AND YIELD

1. Deficit irrigation and partial rootzone drying (PRD)

Water use efficiency (WUE) can be defined on different levels. At leaf level , WUE can be defined as the ratio between the net carbon gain by photosynthesis and stomatal conductance (intrinsic water use efficiency) or the ratio between carbon gain and transpired water (instantaneousWUE) On a crop level water use efficiency of productivity can be calculated by relating total produced biomass or yield to water lost by transpiration.

Within cultivated *Vitis vinifera* species a certain genetic variability of WUE seems to exist. However as for iso/anisohydry this appears to be governed to a wide extent by environmental conditions as well as by rootstock-scion combinations. WUE can therefore be influenced to a certain extent by agronomic measures and cultivation practices such as cover crop, trellising systems, planting density, soil and canopy management and irrigation (see review from Medrano *et al.* (2015)

In general, increasing water deficit, increases WUE, entails berry quality gains (see previous sections) but has negative impact on yields as a function of drought severity. There is thus a tradeoff between yield losses and quality gains, which needs to be optimized according to the commercial strategy of the producer. Physiological background behind an improved WUE by water deficit are mainly due to an enhanced guard cell signal transduction decreasing transpiration water loss and an optimized stomatal control that improves the photosynthesis to transpiration ratio. The mechanisms involved in the plant response to RDI (Reduced Deficit Irrigation)-induced water stress include **morphological traits,** e.g., increased root to shoot ratio and improved nutrient uptake and recovery; **physiological traits**, e.g., stomatal closure, decreased leaf respiration, and maintained photosynthesis; and **biochemical traits**, e.g., increased signaling molecules and enhanced antioxidation enzymatic activity" (Chai *et al.*, 2015)

Different deficit irrigation strategies have thus emerged and can be divided into: 1) growth stage-based regulated deficit irrigation (DI), (2) partial root-zone irrigation or drying (PRD) and (3) subsurface dripper irrigation. The latter has been mainly used in nursery systems historically. It is currently the focus of some practical research such as (European project OFIVO, E.Serrano, pers.comm. https://www.reseaurural.fr/sites/default/files/documents/fichiers/2018-12/20181210_pei_tableau_GO_selectionnes.pdf. Comparing surface with subsurface drip irrigation systems for 2 years with Cabernet-Sauvignon grafted on 140 Ru Pisciotta *et al.* (2018) observed that subsurface drip resulted in greater WUE, that the position of trickle line with respect to the trunk can have a different effect on yield. As quoted by the authors, subsurface dripper irrigation practices still deserve further investigation and will not be discussed subsequently.

The general concept of deficit irrigation is that less water is applied than lost by evapotranspiration (ET). The main differences between DI and PR is that DI applied a water deficit over time and PRD over space (Chai *et al.*, 2015).

DI is based on the principle that plant sensitivity to water stress (yield, berry composition) is not constant during all the phenological stages. As discussed in previous sections, early water deficit is more effective on berry size reduction, whereas later deficit promotes secondary metabolism, and impacts on berry volume to a lesser extent. DI seeks to maintain the soil and plant water status in a narrow range to avoid either excessive reduction of water application which can result in severe losses of yield and quality and/or excessive irrigation that would suppresses the advantages of using DI strategies.

PRD consists in wetting and drying approximately half of the root system cycles of 8–14 days depending on the soil type and requires a double irrigation line controlled by different valves that allows irrigation of one half of the root system leaving the other half drying. The wet side delivers enough water to the plant to avoid water stress, while the drying half is linked to the reduction of g_s PRD is based on the knowledge that roots produce hormonal and hydraulic signals (as discussed previously) that reduce g_s and thereby improves WUE (Gil *et al.*, 2018; Stoll *et al.*, 2000; Tombesi *et al.*, 2018)

Many studies compare physiological and qualitative effects of PRD and RD and several excellent reviews summarize the most important results (Chaves *et al.*, 2010; Jovanovic and Stikic, 2018), and conclude that the effects are very similar between both strategies as shown by the meta-analysis of Sadras (2009). Recent deficit irrigation studies of Monastrell grafted on five different rootstocks (140Ru, 1103P, 110R, 161-49 and 41B) in the semiarid winegrowing region of D.O. Bullas, South Eastern Spain highlighted important differences in the rootstock specific response to different deficit irrigation practices (Romero *et al.*, 2018). In the latter study PRD increased the yield and/or berry quality attributes, especially in low (161-49C, 110R) and in the high vigor rootstocks (140Ru, 1103 P), but not in the medium vigor rootstock 41B. Furthermore, PRD did produce a beneficial increase in the nutraceutical potential for practically all rootstocks. PRD on 161-49C grafted vines resulted in lowest WUE/yield but highest berry quality, while PRI vines grafted on 110R had enhanced long-term yield, WUE/yield, and amino acid and resveratrol contents, with similar berry quality. According to this study, both 161-49C and 110R seem good options to achieve a compromise between long-term yield-quality-efficiency.

2. Towards a site-specific deficit irrigation strategy?

A site-specific irrigation should aim to take into consideration all biotic and abiotic factors likely to interfere with vine water status variations such as rootstock-scion combination, soil texture, climate specificities and vine phenological stages, local quality of water, trellis system and canopy architecture.

Due to operational constraints, irrigation scheduling is mostly part of a weekly routine for winegrowers in non-dry farmed regions. Therefore, the timing of irrigation does not necessarily match specific water requirements of a vineyard in a specific situation. As discussed in previous sections of this review, concomitant influences of environmental parameters, vineyard architecture, plant material, soil, and irrigation water on vine water requirements and tolerance to drought, are difficult to predict which makes an optimal irrigation hard to schedule.

The availability of suitable irrigation water presents a primary operational constraint in many dry regions. In semi-arid areas exposed to water scarcity, re-using wastewater is an attractive practice to promote water and cost savings. However, water quality, mainly in regards of a too high salt concentration, inducing salt stress, can have detrimental effects on overall vineyard performance (Costa et al., 2016; Laurenson et al., 2012), more specifically on vine transpiration (Pereira et al., 2015) and can negatively affect yield and berry composition and consequently final wine quality (Miras-Avalos and Intrigliolo, 2017). Using moderately saline water for deficit irrigation, Degaris *et al.* (2016) reported an effect on ion partitioning (Cl^-, Na^+, and K^+) in grapevines berries.

Those examples illustrate, that irrigation strategy needs to integrate many specificities related to vineyard intrinsic properties (soil texture, plant material, for example) but also management constraints (water salinity, vineyard architecture and trellising, summer pruning operations and cover crop management).

To evaluate an irrigation strategy, its effects need to be assessed regularly by considering the tradeoff between a reduction in yield and a gain in quality and not simply relative to its effect on seasonal vine water stress.

The degree of imposed vine water deficit by varying irrigation frequency changes, typically over three periods dependent upon the phenological stage. Reports from numerous irrigation trials generally distinguish a first period going from bud break to bloom or fruit set, a second period until bunch closure, lag phase or véraison and a third period until harvest (Ojeda, 2007).

The modulation of vine water deficit during different periods can show contrasted results due to site-specific interactions with the irrigation strategy. As for example, shown by Munitz *et al.* (2017) in a 4 year trial with Merlot, reducing water supply to create a water deficit stress during late berry development did not negatively impact yield or berry quality. Latter authors concluded that applying higher irrigation from flowering to bunch closure and lower irrigation from bunch closure to harvest has the potential to generate the best balance between vegetative growth, a high yield and an improved wine quality. Reducing or eliminating irrigation during the second and the third period, Zúñiga *et al.* (2018) reported significant effects on yield components, via a reduction of berry volume. Intrigliolo *et al.* (2016) found that post-véraison irrigation resulted in a 26-30% yield increase compared to rain fed vineyards that experienced a post véraison water deficit.

Timing and thresholds for a desired vine water deficit level before triggering irrigation vary thus, according to production objectives defined by growers. However, there is still a tradeoff between quantity and quality. More quality focused winegrowers may tolerate a higher level of stress and lower yields than others where quantitative parameters are more important for economic success. The following section proposes a few concepts that can be helpful to define critical points, considering effects on fruit production and site-specific properties.

3. Recent scientific advances regarding irrigation intervals

High frequency irrigation implies the application of small amounts of water resulting in limited superficial water bulbs. Sebastian *et al.* (2015) report that differences between irrigation frequencies promoted changes in water status that resulted in relevant agronomic differences. In a heavy clay soil, the higher irrigation frequency (every 2 days) led to an efficiency loss

under low water availability conditions. Authors highlight how different irrigation frequencies can affect vineyard performance to achieve practical tradeoffs between the agronomic response, production objectives and operational costs.

Selles *et al.* (2004), observed that less frequent irrigations in a clay loamy soil led to an increased yield and pruning weight. In their study less frequent irrigation resulted in a better distribution of water throughout the soil and mainly the development of a larger root system. Bowen *et al.* (2011) and Bowen *et al.* (2012) compared in a 4-year study the effect of 1- and 3-day irrigation intervals in a loamy sandy soil for Cabernet-Sauvignon, Merlot and Syrah. They observed no effects on pruning weight but found improved yields while maintaining quality with less frequent irrigations.

Bonada *et al.* (2018) measured vine transpiration with sap flow in an experiment combining two temperature (ambient and heated) and two water regimes. A "wet" treatment consisted in weekly irrigations as opposed to a the "dry" treatment where irrigation was only triggered when basal primary leaves showed defoliation symptoms or yellowing.

They observed a decline in sap flow following irrigations under the wet treatment. Furthermore, while warming increased sap flow, seasonal sap flow in wet and heated vines was reduced through the season to a similar level to that in dry treatments. Their results confirm that under warmer conditions, increased sap flow in wet vines is observed only during the irrigation period. In fact, after 2 years, the wet treatment showed a reduced water use over the whole season, probably because higher transpiration rate post irrigation lead to faster depletion of soil water, which over the season, lead to a lower water use after irrigation.

In a regional project distributed over 3 wine growing regions in California, Scholasch (2018) reported the consequences of stretching irrigation intervals based on vine transpiration and vineyard performance. The latter study indicated that under short irrigation intervals, (between 5 to 25 irrigations/season) seasonal water deficit can be more severe even if a similar or a higher total amount of water is applied over the season compared to large irrigation intervals (between 0 and 5 irrigations/season).

For practical application, this would mean that smaller volumes and smaller intervals between irrigations can induce more brutal variations of water use leading to short periods of severe water stress between two irrigations. This creates favorable conditions to cavitation, with consequences on water potential measurements (Rienth and Scholasch, in ed). From a vineyard management standpoint, heavy variations of water stress are consequently more difficult to control than more gradual variations observed following larger irrigations. Maximum interval length between two irrigations is determined by assessment of plant feedback.

Some promising irrigation strategies to improve vineyard water use efficiency consist of applying a large irrigation after a period of moderate drought to fully relieve vine water stress. The goal of applying the largest possible water amount that the root reservoir can hold is to reach the maximum potential vine transpiration level (determined by $K_{cb,max}$) and postpone the next irrigation as long as possible. In between two irrigations, drought periods of varying intensities are imposed according to production objectives. Water deficit variations between two large irrigations are more gradual compared to what is observed between irrigations of smaller volumes (Cooley *et al.*, 2017; Linares Torres *et al.*, 2018; Scholasch, 2018). Those strategies tend to promote water and energy saving and are currently being evaluated by water agencies and energy conservation agencies (project MWD-ICP program (Scholasch, 2015); project EPIC-CEC).

Site specific interactions between vineyard practices and fruit ripening conditions are hard to predict. As pointed out in previous sections, complex interactions exist between irrigation strategies and other vineyard practices such as cluster thinning (Talaverano *et al.*, 2017) canopy manipulation (Brillante *et al.*, 2018), Nitrogen application (Guilpart *et al.*, 2014) and diverse abiotic factors.

Therefore, to fine tune a site-specific irrigation strategy, direct measurements of plant and fruit parameters are needed to account for specific interactions between water deficit and fruit composition. In this context, monitoring berry volume variations and sugar accumulation in response to irrigation could provide critical information to better assess vineyard response to water deficit in combination with other factors.

This is even more important considering that fruit composition respond differently to water stress for different varieties, as shown for Cabernet-Sauvignon vs Shiraz (Hochberg *et al*, 2015) or for Greece's autochthonous varieties Agiorgitiko and Xinomavro (Theodorou *et al.*, 2019) or Italian grape cultivars Montepulciano and Sangiovese (Palliotti *et al.*, 2014). Those results illustrate how changes in secondary metabolism in response to water stress are specific to each cultivar, therefore irrigation threshold and frequency could be defined according to the unique varietal specific response of fruit composition to water stress.

CONCLUSION

In order to increase the efficiency of water use, a main recommendation to growers using or planning to use irrigation, would be to stop applying only leaf-based water assessments as a sole tool for monitoring irrigation strategies, but to assess the success of their agronomic strategies by incorporating berry ripening profiles and vine physiological knowledge. Cultivar and other site-specific characteristics need to be considered to optimize irrigation strategies according to production goals.

In a more comprehensive approach, heterogeneous data obtained by aerial, atmosphere-, plant- and fruit-based methods could be integrated to leverage synergies to optimize irrigation strategies. The current development of AI (artificial intelligence) algorithms will provide a tool to utilize such complex data sets as it is currently being tested within a few existing pilot projects.

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