

'Deficit irrigation in Mediterranean environment.

What lessons have we learnt from grapevine studies?'

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ABSTRACT

Deficit irrigation techniques, implying that water is supplied at levels below full crop evapotranspiration throughout the growing season or in specific phenological stages, such as regulated deficit irrigation (RDI) or partial root drying (PRD), emerged as potential strategies to increase water savings with marginal decreases of yield and likely positive impact on fruit quality. Understanding the physiological and molecular bases for plant responses to mild to moderate water deficits is of utmost importance to modulate the appropriate balance between vegetative and reproductive development, to improve crop water-use efficiency and to control fruit quality. It is acknowledged that the timing and intensity of the response to soil and atmospheric water deficits, namely in what concerns stomatal control, depends greatly on the genotype. This has profound implications in irrigation management, in particular the timing and amount of irrigation to optimize source-sink relationships and achieve optimal fruit quality in each variety. Mild water deficits also exert direct and/or indirect (via the light environment in the cluster zone) effects on berry development and composition. A current research challenge is determining how the environment, in particular water deficits, regulates genes and proteins of the various metabolic pathways responsible for berry composition and therefore for wine quality.

CLIMATE CHANGE, VINEYARDS AND DEFICIT IRRIGATION

Current projections by the International Panel for Climate Change (IPCC, 2007) predict that water scarcity will increase in the near future in many regions of the globe. Moreover, a large proportion of vineyards are located in regions with seasonal drought (e.g. climate of the Mediterranean type) where soil and atmospheric water deficits, together with high temperatures, exert large constraints in yield and quality. However, with enhanced pressure on water resources, the increasing demand for vineyard irrigation will only be met if there is an improvement in the efficiency of water use. Deficit irrigation techniques, where water is supplied at levels below full crop evapotranspiration (ET_c) throughout the growing season or in specific phenological stages, such as regulated deficit irrigation (RDI) or partial root drying (PRD), emerged as potential strategies to increase water savings with marginal decreases of yield and likely positive impact on fruit quality (Ferreres and Soriano, 2007; Costa et al 2007; Chaves et al 2007; 2010).

Under RDI, plant water status is maintained within pre-defined limits of deficit (with respect to maximum water potential) during certain phases of the seasonal development, normally when fruit growth is least sensitive to water reductions (Kang and Zhang, 2004). The rationale underlying this practice is that optimization of numbers of fruits, fruit size and quality will be achieved by keeping

grapevine vigour in balance with potential production. If water deficit is applied early in the season the effects will be achieved mostly through a reduction of berry cell division (McCarthy et al., 2002); if water deficits are imposed at later stages, then the major effect will be an inhibition of berry growth (Williams and Mathews, 1990).

In PRD, roots are exposed to alternate drying and wetting cycles. Theoretically, roots of the watered side of soil will maintain favorable plant water relations, while dehydration in the other side will induce chemical signaling that will reach the leaves via the transpiration stream, reducing stomatal conductance and/or growth (Santos et al., 2003). This signaling (increased ABA concentration) follows sap flow restoration through the previously dried root system and as a consequence may be transient (less than 24 hours) (Dodd et al 2008). PRD irrigation may also have an impact on root growth, leading to increased root development in the deeper soil layers (Dry et al. 2000; Santos et al 2007). An increase in root hydraulic conductance, putatively resulting from aquaporin stimulation by ABA, and the induction of new secondary roots was also reported in fruit trees subjected to PRD (Kang and Zhang 2004).

In what concerns PRD in grapevine, there are contrasting results in the literature, with several studies reporting no significant differences between PRD and DI (deficit irrigation considered as the control of PRD; where the same amount of water as in PRD is given, but divided by the two sides of the rooting zone), as for example Bravdo et al. (2004) and Gu et al.(2004), whereas others show positive effects (Stoll et al 2000; Chaves et al 2007; 2010 see also Fig 1). These apparent contradictions may be related to differences in the intensity of the chemical signaling under PRD irrigation that seems to be dictated by the type of soil, the prevalent rainfall and evaporative demand in the region, as well as the frequency of switching irrigation from one side of the rootzone to the other (Dry et al 2001; Chaves et al 2007). Genotypic differences in stomatal sensing of water deficits or the delivery of ABA by the rootstock, may also explain different results (Antolin et al., 2006; De la Hera et al., 2007). Drought sensitive varieties may respond better to PRD (Souza et al., 2005a). The type of soil will impact on the extent of soil water redistribution, which in turn will buffer dehydration in the dry rootzone. Bravdo (2005) suggests that hydraulic redistribution from deeper to shallower roots may prevent under field conditions the clear results obtained in potted plants subjected to PRD under split root systems (Davies et al., 2002). Dry (2005) also suggests that PRD may not be successful when soil porosity favors lateral spread of irrigation water or an insufficient volume of irrigation is applied at the time of the switch for restoration of the wet side to field capacity. There is also some evidence that in low vigor vineyards PRD is unable to induce better agronomical output than the conventional deficit irrigation strategy, since the growth inhibition more pronounced in PRD than in DI will decrease source (leaves) to sink ratio below the optimum, resulting in yield losses without any improvement in berry quality (Lopes et al, own results; see Fig 2). Finally, Sadras (2009) in a meta-analysis of a broad range of horticultural crops reported that in general there was no improvement in the irrigation water productivity (yield per unit irrigation water applied) under PRD, as compared to DI.

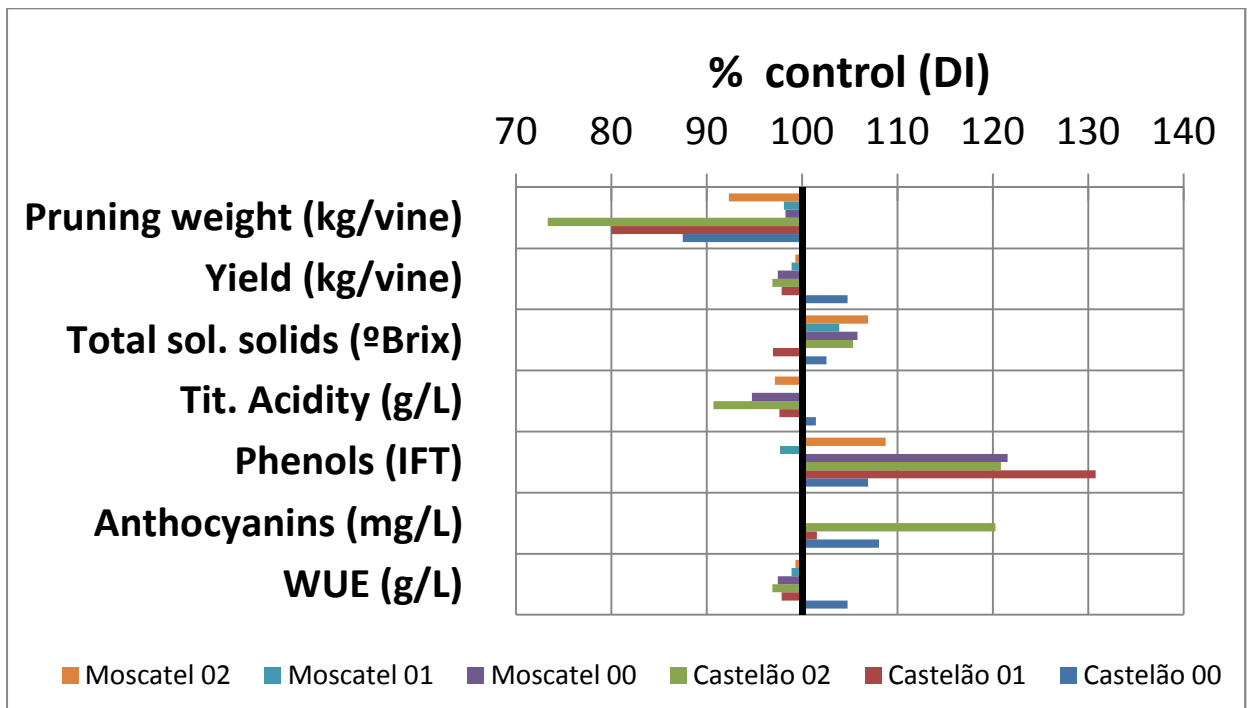


Figure 1: PRD pruning weight, yield, quality parameters and WUE as a function of DI, studied in two varieties, Moscatel and Castelão, during three years, in a sandy soil in Pegões. Central Portugal (redrawn from Chaves et al 2007).

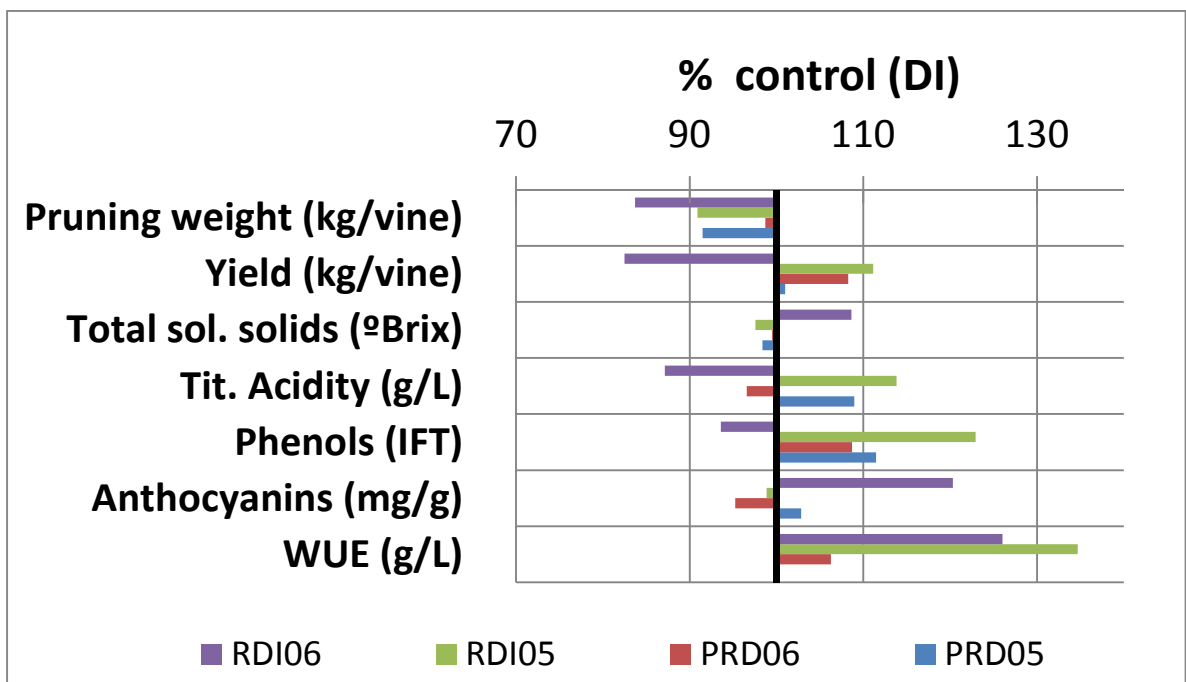


Figure 2: PRD and RDI pruning weight, yield, quality parameters and WUE as a function of DI, studied in the variety Aragonez during two years (2005 and 2006), in a loamy soil in Alentejo. South Portugal (Lopes et al unpub).

PHYSIOLOGICAL BASES FOR PLANT RESPONSES TO MILD TO MODERATE WATER DEFICITS

The use of deficit irrigation strategies rely on observations in several crops subjected to moderate water deficits that yield is not significantly reduced and quality of production may even increase under such conditions. Understanding the physiological and molecular bases for plant responses to mild to

moderate water deficits as it occurs under deficit irrigation is of utmost importance to modulate the appropriate balance between vegetative and reproductive development, to improve crop water-use efficiency and to control fruit quality.

In general, grapevines are well-adapted to semi-arid climate like the Mediterranean, due to the large and deep root system and physiological drought avoidance mechanisms, such as an efficient stomatal control of transpiration and of xylem embolism (Lovisolo et al., 2002), and/or the ability to osmotically adjust (Rodrigues et al., 1993). Under mild to moderate water deficits (WD) stomata closure and growth inhibition are among the early plant responses, restricting water loss and carbon assimilation at the leaf and whole plant levels. The decline in photosynthetic rates generally takes place at lower pre-dawn water potentials than the decline in stomatal conductance, giving rise to a (transient) increase in intrinsic water use efficiency (A/g_s or WUE_i) (Gaudillère et al., 2002; Souza et al., 2005b). This is reflected in a lower water use (WU) and higher WUE by the crop, an important aim of deficit irrigation strategies in vineyards (Chaves et al., 2007). Similarly, stomatal closure at midday, an important adaptation to high VPD in some species of xeric habitats (Maroco et al., 1997), may lead to an increase in WUE_i when photosynthesis is maintained. This has been observed in grapevine (Souza et al. 2003).

When drought is combined with high air temperature and evaporative demand, as for example during sudden heat waves, dramatic reductions in plant carbon assimilation and a partial loss of canopy leaf area may occur (Flexas et al., 2002; Maroco et al., 2002; Chaves et al., 2007). Under such conditions, regulated deficit irrigation must be carefully surveyed in order to prevent negative impacts in grapevine yield and berry and wine quality.

As for the signalling involved in plant response to deficit irrigation a great deal of evidence highlights the importance of ABA as root-sourced signal transported via the xylem and implicated in stomatal regulation of droughted plants (see review by Wilkinson and Davies, 2002). Even so, other compounds like the precursors of ABA (Jiang and Hartung, 2008), low concentration of cytokinins (Hansen and Dorffling, 2003), and changes in mineral composition or pH of the xylem (Jia and Davies, 2007) might also be implicated in the regulation of water use at the leaf level (recently reviewed by Schachtmann and Goodger, 2008). On the other hand, there is no clear picture of the relative importance of hydraulic and chemical signalling on plant response to PRD irrigation. There are studies indicating a marked decrease of g_s in PRD grapevines relative to conventionally-irrigated vines, in spite of comparable shoot water status (Dry and Loveys, 1999; Du et al., 2006), therefore suggesting the involvement of a non-hydraulic signal in stomatal regulation. Several other studies, however, did not find evidence for a more marked stomatal closure in PRD than in DI grapevines (Souza et al., 2003; Rodrigues et al., 2008). The higher water status of PRD plants may be derived from the observed restriction in vegetative growth of PRD plants (Santos et al., 2003 2005; Chaves et al., 2007), leading to lower plant water use and thus more water available in the soil near the root system.

GENOTYPIC DEPENDENT RESPONSES TO WATER DEFICITS IN VITIS VINIFERA

It is acknowledged that the timing and intensity of the response to soil and atmospheric water deficits, namely in what concerns stomatal control, depends greatly on the genotype. This has profound implications in irrigation management, in particular the timing and amount of irrigation to optimize source-sink relationships and achieve optimal fruit quality in each variety (Medrano et al., 2003;

Chaves et al., 2007). *Vitis vinifera* L. is characterized by large genetic variability with several thousands of varieties being cultivated worldwide. However, most of those genotypes remain uncharacterized, which limits their use for breeding, for example to increase WUE or improve berry quality traits.

Genotype related differences in WUE and water stress resistance may arise from constitutive differences in leaf gas-exchange, plant capacity to osmoregulate and plant hydraulics. Photosynthesis, stomatal conductance and WUE_i were shown to vary with grapevine variety (Bota et al., 2001; Schultz 2003; Soar et al., 2006). Still, variation in photosynthetic efficiency seems to be small (Bota et al., 2001), suggesting that genotypic variation in WUE is largely linked to diversity in stomatal conductance, both under well-watered and water deficit conditions (Escalona et al., 1999; Gaudillère et al., 2002; Chaves and Oliveira, 2004). Under drought conditions, stomata seems to keep water flow within safe limits, therefore avoiding xylem embolism (Sperry et al., 2002). Higher stomata sensitivity to water deficits may compensate for higher vulnerability to cavitation under drought (Schultz, 2003).

Leaf morpho-anatomy and related biochemistry (epicuticular wax composition, lipid composition, mesophyll thickness etc) may also play a role in explaining plant adaptation to water stress (Boyer et al., 1997). Differences among *V. vinifera* have been reported in these characteristics (Schultz, 1996).

Grapevine is generally considered a “drought avoiding” species, with an efficient stomatal control over transpiration (Chaves et al., 2007; 2010; Shultz, 2003). However, some genotypes have shown a better control of stomata than others in response to water deficits and accordingly have been classified as isohydric (drought avoiders or “pessimistic”); the others, showing lower control over stomatal aperture under water stress, were considered anisohydric, with an “optimistic” response (Schultz, 2003; Soar et al., 2006). Schultz (2003) considered Grenache to be a nearly isohydric genotype showing a marked regulation of stomatal conductance to decreasing soil water, whereas Syrah exhibited a response closer to an anisohydric type. The same contrasting behavior between Grenache and Syrah in response to atmospheric moisture stress was found by Soar et al. (2006), who attributed the higher sensitivity of stomata in Grenache to the higher concentration of ABA in the xylem sap as compared with Syrah. He provided evidence of a midday increment of the expression of key genes involved in the ABA biosynthetic pathway, significantly higher in the leaves of Grenache than in Syrah. However, contradictory reports appeared in the literature showing that the same variety could behave differently depending on experimental conditions (see the reviews by Lovisolo et al., 2010 and Chaves et al 2010). For example, var. Syrah and Grenache that exhibited an anisohydric and near-isohydric behaviour, respectively, in field experiments (Schultz, 2003; Soar et al., 2006), did not display the same stomatal behaviour when experiments were performed with potted plants.

Bearing in mind the available data, a classification of grapevine varieties as strict iso- or anisohydric may prove inappropriate. It seems plausible that stomatal responses to water deficits in a specific variety will vary according to the particular combination of the rootstock, the climate (VPD and temperature) and the intensity and duration of water deficits.

BERRY GROWTH AND METABOLISM UNDER WATER DEFICITS

Water deficits influence berry development, metabolism and final composition, and its timing and intensity dictate the extent of alterations occurring in wine colour and flavour. In general, mild water deficits were shown to have a positive impact on wine quality in red varieties (Bravdo et al., 1985).

Under this context, deficit irrigation can provide the means to manipulate wine sensory characteristics. However, the effects of deficit irrigation on berry and wine quality will depend on the climatic characteristics during the growing season, the soil type, the grapevine variety and the timing of application (Santos et al., 2003, 2005).

Transcriptional analysis of grape berries from vines subjected to moderate water deficits at the end-ripening stage showed alterations on mRNA expression patterns particularly associated with cell wall, sugar and hormone metabolism (Deluc et al., 2007). The most profound alterations were related to ethylene, auxin and abscisic acid, but an enhancement of the expression of several genes of the phenylpropanoid pathway was also observed.

The impact of water deficit on grape berry proteome was reported by Grimplet et al. (2009). These authors studied the alterations observed in the skin, pulp and seed proteomes of fully ripe berries when comparing water-deficit vines (no irrigation) with well-watered plants (irrigation from pre-véraison to the end of berry maturity) and showed that 7% of pericarp proteins were water-stress responsive. Using such an approach, we are currently studying the proteome dynamics of grapevines of the var. Aragonez (syn. Tempranillo) along berry development using three irrigation strategies. When comparing berries of full irrigated (FI) vines with the ones from deficit irrigated (RDI) and rainfed (NI) vines, several proteins were identified as stress responsive. One such protein was vacuolar invertase (GIN1), which was significantly down-regulated under NI and RDI when compared with FI conditions. These alterations were observed at green stage (pre-véraison) and véraison. Moreover, the peak of expression of this protein that was reported to occur at véraison by others (Deluc et al., 2007) was observed later in RDI than in FI berries. These results suggest that water availability modulates not only the amount, but also the timing of protein expression. It suggests as well that changes taking place very early on during berry development, such as at the green berry stage, may have a profound effect on the final berry maturity (Francisco et al., 'unpubl. res.').

CONCLUSIONS

Deficit irrigation is an efficient strategy to improve WUE and control vigour in grapevine, allowing an optimal grape maturity and therefore a high wine quality. It is now accepted that the efficiency of deficit irrigation (whatever the sub-type) in modulating WUE, growth and grape berry composition is dependent on the variety characteristics (namely its vigour and drought avoiding traits), the type of soil and the prevailing weather (rainfall and temperature). More in-depth and wider studies of varieties in response to environmental stresses are instrumental to the understanding of grapevine adaptation to more arid climates. Further knowledge on berry development, including the timing for the accumulation of various berry components, and their dependence on water availability, is critical for an optimal choice of irrigation strategy. Proteomic and transcriptomic studies are providing new avenues for that understanding. The data already available suggest that water deficits interact with development to alter the expression of genes responsible for some grape berry compounds and metabolite transporters. Although some of those changes seem to be transient it is plausible that they will have an impact on berry maturity and the final wine quality.

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