

Deficit Irrigation in Mediterranean Vineyards - a Tool to Increase Water Use Efficiency and to Control Grapevine and Berry Growth

J.M. Costa^{1,2}, C.M. Lopes¹, M.L. Rodrigues¹, T.P. Santos¹, R. Francisco², O. Zarrouk², A. Regalado² and M.M. Chaves²

¹ CBAA, Instituto Superior de Agronomia, Tapada da Ajuda, Lisboa, Portugal

² LEM-ITQB, Oeiras, Portugal

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Abstract

Water is increasingly scarce in Mediterranean Europe and irrigated agriculture is one of the largest and most inefficient users of this natural resource. Ecological topics such as the “water foot print” have become more relevant for the academy, consumers, governments and food industry. The wine sector needs solutions to improve its economical and environmental sustainability. Agronomical solutions, such as deficit irrigation (water supply below full crop evapotranspiration) have emerged as a tool for more efficient water use in irrigated viticulture and with likely positive effects on berry quality. Improving our understanding on the physiological and molecular basis of grapevine responses to water stress is an important task for research on irrigated viticulture. Better knowledge of the different genotypic responses (e.g., leaf gas exchange) to water stress can help to optimize crop/soil management and improve yield as well as berry quality traits under unfavourable climate conditions. Mild water deficits have direct and/or indirect (via the light environment in the cluster zone) effects on berry growth and composition. Another important challenge is to determine how soil water deficit regulate genes and proteins of the various metabolic pathways influencing berry composition and consequently wine quality.

WATER SCARCITY, CLIMATE CHANGE AND WATER FOOT PRINT

The majority of the grape acreage around the world is located in Mediterranean type climates, characterized by dry summers and mild winters (Table 1). Mediterranean Europe faces a situation of scarce water resources as a consequence of dry and hot summers, increasing consumption and mismanagement in both intensive agricultural and industrial activities (Carvalho, 2000; Tin, 2008; Collins et al., 2009). The climate change scenarios projected for the regions will exacerbate these impacts, with more frequent and extreme high temperature and drought events in many parts of Mediterranean Europe (IPPC, 2008). This may force a shift of production to cooler areas, the use of new cultivars/rootstocks better adapted to warmer and dryer conditions or changes in crop/soil management (Shultz and Stoll, 2010; Hunter et al., 2010; Lopes et al., 2011).

Meanwhile consumers, retailers, politicians and the industry (agricultural included) have started to realise the need to use inputs like water in a more sustainable way (Chapagain and Orr, 2008; Cominelli et al., 2009; Clothier et al., 2010; Stefanelli et al., 2010). Therefore, concepts such as water and carbon footprint and their assessment are receiving increased attention. In basic terms, the footprint indicates the energy (carbon) or water used, related to both direct and indirect use by the consumer or producer. The water footprint is a consumption-based indicator of water use that looks at both direct and indirect water use of a consumer or producer (Hoekstra and Chapagain, 2008). It is calculated by the volume of fresh water used to produce the product, measured over the various steps of the production chain (Hoekstra, 2010). An increasing number of companies around the world recognise that reducing water foot print should be part of the corporate environmental strategy (Hoekstra, 2010; Clothier et al., 2010). A corporate water footprint strategy includes various aims and activities. Businesses can reduce their operational water footprint by decreasing water consumption in their own operations and by reducing water pollution to zero (Hoekstra et al., 2009). Likewise, the International

Organization for Standardization (ISO) has been working on a protocol for estimating water foot prints (Clothier et al., 2010).

Assessment of the agricultural water footprint is important to define and evaluate correct water policy decisions, which are becoming increasingly complex in dry areas like the South Mediterranean Europe (Aldaya et al., 2010). 85% of the water foot print of humanity relates to food products consumption (Hoekstra, 2010). For wine, literature indicates a water foot print of 120 liters per glass (120 ml) (Cominelli et al., 2009; Water Foot Print Network, 2010). This is an average value that needs to be properly assessed because it depends on the environmental context. Important questions such as how water intensive is wine production and to what extent does it relate to water depletion and/or pollution in a specific region still need to be answered.

MORE EFFICIENT WATER USE IN MEDITERRANEAN VITICULTURE (DEFICIT IRRIGATION)

The species *Vitis vinifera* is apparently well adapted to the Mediterranean climate. Several traits explain such behaviour such as a large and deep root system, efficient stomatal control of transpiration and of xylem embolism and ability to adjust osmotically (Patakas and Noitsakis, 1999; Lovisollo et al., 2002). However, in non irrigated vineyards or where irrigation is not feasible at all, the combination of dry air conditions, high air temperature and high evaporative demand during the summer, limits grapevine yield and berry (and wine) quality (Escalona et al., 1999; Costa et al., 2007; Chaves et al., 2007, 2010). A pronounced decrease in carbon assimilation may occur due to severe reduction in photosynthesis at supra-optimal leaf temperatures combined with water deficits and to a partial loss of canopy leaf area (Flexas et al., 2002; Maroco et al., 2002; Chaves et al., 2007, 2010; Hunter et al., 2010).

The use of irrigation in the south European Mediterranean viticulture is recent, mainly due to prior legislative restrictions. Irrigation emerged as a means to prevent excessive canopy temperature and maintain/improve quality in wine production. In more extreme cases it guarantees plant survival and profitability. Deficit irrigation (DI) involves the supply of water below full crop evapotranspiration (ET_c) homogeneously along the growing season. Alternatively, water can be supplied at specific phenological stages as it happens with regulated deficit irrigation (RDI). RDI creates water deficits during specific periods of the season to save water while minimizing or eliminating negative impacts on crop revenue (Goldhamer et al., 2006). If water deficit is imposed early in the season, the effects will be obtained mostly by a reduction of vegetative growth and berry cell division (McCarthy et al., 2002). If imposed after veraison may enhance anthocyanin accumulation (Dry et al., 2001). In vineyards growing in south Portugal, pruning weight and yield were shown to increase under deficit irrigation as compared to non irrigated but rain-fed vines, while the brix degree was not affected (Figs. 1 and 2). However, the effects of deficit irrigation can vary according to the growing conditions (climate and soil, potted vs soil grown plants) (Bravdo, 2005; Dry et al., 2001; Chaves et al., 2007) and the genotypes (rootstock and cultivar) (De la Hera et al., 2007; Fereres and Soriano, 2007; Chaves et al., 2007, 2010). If not properly managed, deficit irrigation may promote excessive vegetative growth compared to non-irrigated vines, with negative effect on berry pigmentation and sugar content and a decrease in wine quality (Bravdo et al., 1985; Dokoozlian and Kliewer, 1996).

Another strategy involves the alternate watering to each side of the plant root system and is called Partial Root Drying (PRD). Theoretically, watered roots will guarantee favourable water relations, while dehydrated roots will induce the synthesis of hormones, namely abscisic acid (ABA) giving rise to a chemical signal that enables the adjustment of stomata aperture to soil water content. Concerning PRD, literature show contrasting results on grapevine performance. On one hand, no significant differences were observed by Bravdo et al. (2004) between PRD and DI (deficit irrigation taken as control of PRD receiving identical amount of water as PRD, but divided by the two sides of the rooting zone). Also, in low vigour vineyards in Portugal with the cultivar 'Tempranillo'

(Fig. 2), PRD showed no improved agronomical performance in comparison to the conventional DI (Lopes et al., 2011). On the other hand, other reports, however, showed positive effects of PRD (Stoll et al., 2000; Chaves et al., 2007 and Fig. 1).

RESPONSES TO WATER DEFICITS DEPEND ON THE GENOTYPE

The Role of Stomata

Efficient stomatal control of water loss by transpiration is crucial for adaptation of grapevine plants to semi-arid climates. *Vitis vinifera* is known as a drought-avoiding species. Stomatal closure and growth inhibition are among the earliest plant responses to mild to moderate water deficits reducing transpiration and photosynthesis at both leaf and whole plant levels. The reduction of photosynthesis generally occurs at lower pre-dawn water potentials than the reduction of stomatal conductance to water vapour (gs). As a result, there is a (transient) increase in the intrinsic water use efficiency (A/gs or WUEi) (Gaudillère et al., 2002) with consequently lower water use and higher crop WUE, which is basically the aim of deficit irrigation in vineyards (Medrano et al., 2003; Chaves et al., 2007; Costa et al., 2007).

Vitis vinifera has large genetic variability, with a large percentage of genotypes remaining uncharacterized, which limits breeding for higher WUE and/or berry quality (Chaves et al., 2010). Variation in leaf gas exchange characteristics can justify genotype related differences in WUE. Leaf photosynthesis, stomatal conductance and intrinsic water use efficiency were shown to depend on the cultivar (Bota et al., 2001; Schultz, 2003; Soar et al., 2006; Flexas et al., 2009; Chaves et al., 2010). The fact that photosynthetic efficiency shows a small variation among genotypes (Bota et al., 2001) suggests that the variation observed in WUE may largely depend on differences in stomatal conductance under well-watered and dry conditions (Escalona et al., 1999; Gaudillère et al., 2002; Chaves et al., 2010).

Water flow in plants is kept within safe limits to avoid xylem embolism under water stress conditions (Sperry et al., 2002). A higher sensitivity of stomata to water deficits may compensate for larger vulnerability to cavitation under soil drought conditions (Schultz, 2003). Although grapevine is generally efficient in reducing transpiration under water deficit (Schultz, 2003; Chaves et al., 2010), certain genotypes have better stomatal regulation than others in response to drought and were classified as isohydric (drought avoiders or “pessimistic”). Other genotypes in turn, show lower control over stomatal aperture under water stress and were named anisohydric (“optimistic”) (Schultz, 2003; Soar et al., 2006). However, contradictory results for the same cultivar are reported in literature, which may be related to different experimental conditions (Lovisolò et al., 2010; Chaves et al., 2010). For example, the cultivars ‘Syrah’ and ‘Grenache’ had respectively an anisohydric and near-isohydric behaviour in field conditions (Schultz, 2003; Soar et al., 2006) but stomatal behaviour was different if plants were grown in pots (Chouzouri and Schultz, 2005). Therefore, a strict classification of cultivars into two single categories (iso- or anisohydric) seems inappropriate. It is more plausible to consider that stomatal responses to water deficits of a specific cultivar will vary according to the combination of different aspects related to the plant (e.g., rootstock), the surrounding environment (climate - VPD and temperature - and intensity and duration of the water deficit).

Water Stress Monitoring and Plant Selection Based on Stomatal Behaviour

An essential component of irrigation strategies is the effective monitorization of plant water status. This is particularly the case of deficit irrigation to avoid any irrigation water mismanagement that would decrease yield and/or berry quality. There are multiple ways to monitor plant water status: sap-flow measurements, leaf water potential, morphometric sensing of the stem, leaf gas exchange or detection of xylem cavitations (Jones, 2004; Cifre et al., 2005). Although accurate, leaf gas exchange is time consuming and expensive for practical usage.

Leaf/canopy temperature has been used already for long time as an indicator of water stress. In grapevine for example, Grimes and Williams (1990) showed the use of canopy temperature to calculate the stress index (CWSI) and found that they were highly correlated with yield of the table grapevine 'Thompson Seedless'. More recently, thermal imaging has been tested to monitor water stress in grapevine (Jones et al., 2002; Grant et al., 2006; Möller et al., 2007; Costa et al., 2010). The principle behind the technique is that leaf temperature depends on leaf transpiration (stomatal conductance \times VPD) and consequent evaporative cooling due to phase change from liquid to vapour. The most common application of leaf temperature measurement for plant physiologists and agronomists is to detect stomatal closure and estimate g_s , which avoids the use of gas-exchange measurements and allows the assessment of stomatal conductance over large areas of a crop.

The existing methods used to estimate g_s from leaf temperature were developed on the basis of the leaf energy balance (Jones et al., 2002). In the field, thermal imaging measurements are influenced by the surrounding environment (sun radiation, wind speed, air temperature, VPD). Because of this, thermal imaging measurements have been optimized by the use of thermal indices (e.g., crop water stress index - CWSI or the index of stomatal conductance (I_g), which is proportional to stomatal conductance (for a constant boundary layer conductance) and is calculated from canopy temperatures in relation to the temperature of dry (T_{dry}) and wet references (T_{wet}) (Jones et al., 2002; Grant et al., 2006). Nevertheless, remote sensing approaches such as thermal imaging also have limitations concerning their application in the field (e.g., under conditions of overcast skies or excessive wind). Image analysis and processing and the price of the instruments are other types of limitations. Thermal imaging can also be relevant as means to carry out the phenotyping of existing and also of new cultivars in breeding programs (Costa et al., 2010).

Hydraulic and Long Distance Chemical Signalling

Vitis vinifera shows a decrease in shoot's hydraulic conductivity under water deficits (Schultz and Matthews, 1988; Lovisolo et al., 2002). Under mild water stress it was shown to be linearly correlated with stomatal conductance (Lovisolo and Schubert, 1998). Lower leaf water potential may enhance stomatal sensitivity to ABA and would explain the midday decrease in stomatal conductance observed in field grown vines, including the well-watered ones, in spite of the constant diurnal concentration of ABA in the xylem stream (Rodrigues et al., 2008). Root-to-shoot hydraulic signals are followed by a larger synthesis of ABA, which regulates stomatal aperture (Dodd et al., 1996; Wilkinson and Davies, 2002; Christmann et al., 2007) and leaf growth (Neumann et al., 1997). Stomata may also be regulated by the activity of ABA precursors (Sauter et al., 2002; Jiang and Hartung, 2008), the concentration of cytokinins (Shashidhar et al., 1994; Stoll et al., 2000) or by xylem's pH or mineral composition (Wilkinson and Davies, 1997; Jia and Davies, 2007).

The relative importance under mild water deficit of hydraulic and chemical signals on stomatal control and leaf growth is still not clear (Davies et al., 1994; Dodd et al., 1996). Depending on the species and/or experimental conditions the hydraulic limitation may dominate over root chemical signalling or vice-versa (Comstock, 2002; Neumann, 2008). Some studies show a pronounced decrease of g_s in PRD grapevines in comparison to conventionally irrigated vines, for a similar shoot water status (Dry and Loveys, 1999; Du et al., 2006). This behaviour suggests that a non-hydraulic signal affects stomatal aperture. Meanwhile, other findings show that stomatal closure was similar in PRD and in DI vines (Souza et al., 2003; De la Hera et al., 2007; Rodrigues et al., 2008). Consequently, we may assume that the improved water status of PRD plants derives from reduced vegetative growth (Santos et al., 2003; Chaves et al., 2007) that decreases plant water use and increases availability of soil water to the roots.

BERRY METABOLISM UNDER MILD WATER DEFICIT

Water deficits influence berry growth/development, metabolism and final composition. Furthermore, the timing and intensity of the deficit influences the extent of alterations occurring in wine composition, such as colour and flavour. Mild water deficit improved wine quality derived from red cultivars (Bravdo et al., 1985). However, the effects of deficit irrigation on berry and wine quality depend on climatic conditions during the growing season, the soil type, the cultivar and the timing of irrigation (Santos et al., 2003; Keller, 2005). Flavonoids (anthocyanins, flavonols and proanthocyanidins) are the most important phenolic compounds present in grape berries. Water deficit enhanced anthocyanins accumulation via stimulation of anthocyanin hydroxylation and probably by up-regulating the gene encoding the enzyme F3'5'H (Mattivi et al., 2006; Castellarin et al., 2007a). Coordination between the beginning of sugar accumulation and the increase in anthocyanin-related transcripts was reported (Castellarin et al., 2007b). According to these authors the biosynthesis of anthocyanins in grape berries seems to be triggered in a sugar-dependent manner, probably due to the presence of 'sucrose boxes' in the promoters of anthocyanin-related genes (Gollop et al., 2002).

Transcriptional analysis of grape berries from vines subjected to moderate water deficits at the end-ripening stage showed changes on mRNA expression patterns particularly related to the cell wall and sugar and hormone metabolism (Deluc et al., 2007). The most profound alterations related to hormone metabolism occur in ethylene, auxin and ABA but the expression of several genes of the phenylpropanoid pathway was shown also to increase (Deluc et al., 2007). The impact of water deficit on grape berry proteome (defined as all proteins produced by the genome of an organism or tissue) has also been studied. Grimplet and colleagues (2009) analysed the skin, pulp and seed proteomes of fully ripen berries from non irrigated and well-irrigated vines (irrigation from pre-veraison to the end of berry maturity). They observed that 7% of pericarp (skin and pulp tissues) proteins respond to water-stress. Using an identical approach Francisco (2011) studied the dynamics of berry proteome for the cultivar 'Aragonez' (syn. 'Tempranillo') along development of berries from non-irrigated (NI), well-irrigated (FI) and RDI plants. Comparison of berries from well irrigated vines with RDI and NI vines, allowed for the identification of several proteins considered water-deficit responsive. One of those proteins was a vacuolar invertase (GIN1), which was down-regulated under non-irrigated and RDI conditions when compared to FI conditions. These results were observed at pre-veraison (green stage) and at veraison and are in accordance with the early hexoses accumulation observed under water deficit conditions, in the same study. Also relevant was the fact that changes occurring at very early stages of berry development (green berry stage) may affect final berry maturity (Francisco, 2011).

CONCLUSIONS

A major challenge for the wine industry is to maintain and/or improve berry quality and yield under more unfavourable climate conditions and a more restricted use of water. This is particularly the case of south European viticulture. Moreover, consumer and governmental awareness with regards to more sustainable agricultural production is increasing and puts pressure on the horticultural industry to optimize the use of inputs like water, fertilizers or energy (Stefanelli et al., 2010). In the case of the wine industry, the assessment of wine's water foot print for different "terroirs" and management conditions is needed to clarify the environmental impact of irrigated viticulture and the image of the sector towards consumers, especially to those of more developed countries.

In dry climates, and where vines are usually grown without irrigation (e.g., south Mediterranean Europe), deficit irrigation can improve profitability and optimise water use. This is especially relevant due to the problem of water scarcity and to the tendency for more restricted water use and predicted higher water prices as consequence of the implementation of the EU Water Directive. Differences among genotypes in terms of their response to mild/moderate water deficits imposed by deficit irrigation strategies still need to be clarified in order to respond to the requirements of different environments and

management practices (e.g., canopy and soil management, rootstock). Future research should focus on studying and identifying reasons behind this variation in response. Improved knowledge on berry development (e.g., timing for accumulation of various berry components, and their dependence on water availability) is critical for the adoption of optimal irrigation strategies and needs further research.

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Literature Cited

- Aldaya, M.M., Martinez-Santos, P. and Llamas, M.R. 2010. Incorporating the water footprint and virtual water into policy: reflections from the Mancha Occidental Region, Spain. *Water Resources Manage.* 24:941-958.
- Bota, J., Flexas, J. and Medrano, H. 2001. Genetic variability of photosynthesis and water use in Balearic grapevine cultivars. *Ann. Appl. Biol.* 138:353-361.
- Bravdo, B., Hepner, Y., Loinger, C. and Tabacman H. 1985. Effect of irrigation and crop level on growth, yield and wine quality of Cabernet Sauvignon. *Am. J. Enol. Vit.* 36:132-139.
- Bravdo, B., Naor, A., Zahavi, T. and Gal, Y. 2004. The effects of water stress applied alternatively to part of the wetting zone along the season (PRD-partial rootzone drying) on wine quality, yield, and water relations of red wine grapes. *Acta Hort.* 664:101-109.
- Bravdo, B. 2005. Physiological mechanisms involved in the production of non-hydraulic root signals by partial rootzone drying - a review. *Acta Hort.* 689:267-275.
- Carvalho, S.M.P. 2000. Water availability in Almeria. p.39-47. In: J.M. Costa and E. Heuvelink (eds.), *Greenhouse Horticulture in Almeria - Report on a study tour. Horticultural Production Chains*, Wageningen University, The Netherlands.
- Castellarin, S.D., Pfeiffer, A., Sivilotti, P., Degan, M., Peterlunger, E. and Di Gaspero, G. 2007a. Transcriptional regulation of anthocyanin biosynthesis in ripening fruit of grapevine under seasonal water deficit. *Plant Cell Environ.* 30:1381-1399.
- Castellarin, S.D., Matthews, M.A., Di Gaspero, G. and Gambetta, G.A. 2007b. Water deficits accelerate ripening and induce changes in gene expression regulating flavonoid biosynthesis in grape berries. *Planta* 227:101-112.
- Chaves, M.M., Santos, T.P., Souza, C.R., Ortuño, M.F., Rodrigues, M.L., Lopes, C.M., Maroco, J.P. and Pereira, J.S. 2007. Deficit irrigation in grapevine improves water-use efficiency while controlling vigour and production quality. *Ann. Applied Biol.* 150:237-252.
- 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. *Ann. Bot.* 105:661-676.
- Chapagain, A. and Orr, S. 2008. UK water footprint: the impact of the UK's food and fibre consumption on global water resources. Volume one. World Wildlife Fund, Godalming, UK, 44p.
- Chouzouri, A. and Schultz, H.R. 2005. Hydraulic anatomy, cavitation susceptibility and gas-exchange of several grapevine varieties. *Acta Hort.* 689:71-78.
- Christmann, A., Weiler, E.W., Steudle, E. and Grill, E. 2007. A hydraulic signal in root-to-shoot signalling of water shortage. *The Plant J.* 52:167-174.
- Cifre, J., Bota, J., Escalona, J.M., Medrano, H. and Flexas, J. 2005. Physiological tools for irrigation scheduling in grapevine (*Vitis vinifera* L.). An open gate to improve water-use efficiency? *Agr. Ecosyst. Environ.* 106:159-170.

- Clothier, B., Green, S. and Deurer, M. 2010. Reducing water foot print of fruit production. Actas X Symposium Hispano-Portugues de Relaciones Hídricas en las Plantas, <http://www.cebas.csic.es/webCongresoHispa/archivos/Libro%20X-SHPRHP.pdf>. (Accessed on 15 December 2010), p.15-17.
- Collins, R., Kristensen, P. and Thyssen, N. 2009. Water resources across Europe - confronting water scarcity and drought. European Environmental Agency (EEA) Report series. N. 2/2009. ISSN 1725-9177, 55p.
- Cominelli, E., Galbiati, M., Tonelli, C. and Bowler, C. 2009. Water: the invisible problem. *EMBO Rep.* 10:671-676.
- Comstock, J.P. 2002. Hydraulic and chemical signalling in the control of stomatal conductance and transpiration. *J. Exp. Bot.* 53:195-200.
- Costa, J.M., Ortuño, M.F. and Chaves, M.M. 2007. Deficit irrigation as strategy to save water: physiology and potential application to horticulture. *J. Int. Plant Biol.* 49:1421-1434.
- Costa, J.M., Grant, O.M. and Chaves, M.M. 2010. Use of thermal imaging in viticulture: current application and future prospects. p.135-150. In: S. Delrot, H. Medrano, E. Or, L. Bavaresco and S. Grando (eds.), *Methodologies and Results in Grapevine Research*. Springer.
- Davies, W.J., Tardieu, F. and Trejo, C.L. 1994. How do chemical signals work in plants that grow in drying soil. *Plant Physiol.* 104:309-314.
- Davies, W.J., Wilkinson, S. and Loveys, B. 2002. Stomatal control by chemical signalling and the exploitation of this mechanism to increase water use efficiency in agriculture. *The New Phyt.* 153:449-460.
- De la Hera, M.L., Romero, P., Gómez-Plaza, E. and Martinez, A. 2007. Is partial root-zone drying an effective irrigation technique to improve water use efficiency and fruit quality in field-grown wine grapes under semiarid conditions? *Agric. Water Manage.* 87:261-274.
- Deluc, L.G., Grimplet, J., Wheatley, M.D., Tillett, R.L., Quilici, D.R., Osborne, C., Schooley, D.A., Schlauch, K.A., Cushman, J.C. and Cramer, G.R. 2007. Transcriptomic and metabolite analyses of Cabernet Sauvignon grape berry development. *BMC Genomics* 8:429.
- Dodd, I.C., Stikic, R. and Davies, W.J. 1996. Chemical regulation of gas exchange and growth of plants in drying soil in the field. *J. Exp. Bot.* 47:1475-1490.
- Dokoozlian, N.K. and Kliever, W.M. 1996. Influence of light on grape berry growth and composition varies during fruit development. *J. Am. Soc. Hortic. Sci.* 121:869-874.
- Dry, P.R. and Loveys, B.R. 1999. Grapevine shoot growth and stomatal conductance are reduced when part of the root system is dried. *Vitis* 38:151-156.
- Dry, P.R., Loveys, B.R., McCarthy, M.G. and Stoll, M. 2001. Strategic irrigation management in Australian vineyards. *J. Int. Sci. Vigne Vin* 35:129-139.
- Du, T., Kang, S., Zhang, J., Li, F. and Hu, X. 2006. Yield and physiological responses of cotton to partial root-zone irrigation in the oasis field of northwest China. *Agric. Water Manage.* 84:41-52.
- Escalona, J.M., Flexas, J. and Medrano, H. 1999. Stomatal and non-stomatal limitations of photosynthesis under water stress in field-grown grapevines. *Austr. J. Plant Physiol.* 26:421-433.
- Fereres, E. and Soriano, M.A. 2007. Deficit irrigation for reducing agricultural water use, *J. Exp. Bot.* 58:147-159.
- Flexas, J., Bota, J., Escalona, J.M., Sampol, B. and Medrano, H. 2002. Effects of drought on photosynthesis in grapevines under field conditions: an evaluation of stomatal and mesophyll limitations. *Func. Plant Biol.* 29:461-471.
- Flexas, J., Galmés, J., Gallé, A., Gulías, J., Pou, A., Ribas-Carbo, M., Tomàs, M. and Medrano, H. 2009. Improving water-use-efficiency in grapevines: potential physiological targets for biotechnological improvement. *Aust. J. Grape Wine Res.* 16:106-121.
- Francisco, R. 2011. Biochemistry of grape berries: post-genomics approaches to uncover

- the effects of water deficits on ripening. Ph. D. Thesis, Instituto de Tecnologia Química e Biológica, ITQB-UNL, Oeiras, Portugal, 191p.
- Gaudillère, J.P., Van Leeuwen, C. and Ollat, N. 2002. Carbon isotope composition of sugars in grapevine, an integrated indicator of vineyard water status. *J. Exp. Bot.* 53:757-763.
- Goldhamer, D.A., Viveros, M. and Salinas, M. 2006. Regulated deficit irrigation in almonds: effects of variations in applied water and stress timing on yield and yield components. *Irrig. Sci.* 24:101-114.
- Gollop, R., Even, S., Colova-Tsolova, V. and Perl, A. 2002. Expression of the grape dihydroflavonol reductase gene and analysis of its promoter region. *J. Exp. Bot.* 53:1397-1409.
- Grant, O.M., Chaves, M.M. and Jones, H.G. 2006. Optimizing thermal imaging as a technique for detecting stomatal closure induced by drought stress under greenhouse conditions. *Physiol. Plantarum* 127:507-518.
- Grimes, D.W. and Williams, L.E. 1990. Irrigation effects on plant water relations and productivity of 'Thompson Seedless' grapevines. *Crop Sci.* 30:255-260.
- Grimplet, J., Wheatley, M.D., Jouira, H.B., Deluc, L.G., Cramer, G.R. and Cushman, J.C. 2009. Proteomic and selected metabolite analysis of grape berry tissues under well-watered and water-deficit stress conditions. *Proteomics* 9:2503-2528.
- Gu, S.L., Du, G.Q., Zoldoske, D., Hakim, A., Cochran, R., Fugelsang, K. and Jorgensen, G. 2004. Effects of irrigation amount on water relations, vegetative growth, yield and fruit composition of Sauvignon Blanc grapevines under partial rootzone drying and conventional irrigation in the San Joaquin Valley of California, USA. *J. Hort. Sci. Biotech.* 79:26-33.
- Hoekstra, A.Y., Chapagain, A.K., Aldaya, M.A. and Mekonnen, M.M. 2009. Water Footprint Manual. State of the Art 2009. <http://doc.utwente.nl/77211/1/Hoekstra09WaterFootprintManual.pdf> (Accessed on 30 June 2011).
- Hoekstra, A. 2010. The water foot print: water in the supply chain. *The Environmentalist* 93:12-13.
- Hunter, J.J., Archer, E. and Volschenk, C.G. 2010. Vineyard management for environmental valorisation. Proceedings 7th International Zoning Congress, Soave, Italy 7:3-15.
- IPPC. 2008. Climate change and water. <http://www.ipcc.ch/pdf/technical-papers/climate-change-water-en.pdf>.
- Jia, W. and Davies, W.J. 2007. Modification of leaf apoplastic pH in relation to stomatal sensitivity to root-sourced abscisic acid signals. *Plant Physiol.* 143:68-77.
- Jiang, F. and Hartung, W. 2008. Long-distance signalling of abscisic acid (ABA): the factors regulating the intensity of the ABA signal. *J. Exp. Bot.* 59:37-43.
- Jones, H.G., Stoll, M., Santos, T., Sousa, C., Chaves, M.M. and Grant, O.M. 2002. Use of infra-red thermography for monitoring stomatal closure in the field: application to grapevine. *J. Exp. Bot.* 53:2249-2260.
- Jones, H.G. 2004. Irrigation Scheduling: advantages and pitfalls of plant-based methods. *J. Exp. Bot.* 55:2427-2436.
- Keller, M. 2005. Deficit irrigation and vine mineral nutrition. *Am. J. Enol. Vitic.* 56:265-283.
- Lopes, C.M., Santos, T.P., Monteiro, A., Rodrigues, M.L., Costa, J.M. and Chaves, M.M. 2011. Combining cover cropping with deficit irrigation in a Mediterranean low vigor vineyard. *Sci. Hort.* doi:10.1016/j.scienta.2011.04.033.
- Lovisolo, C. and Schubert, A. 1998. Effects of water stress on vessel size and xylem hydraulic conductivity in *Vitis vinifera* L. *J. Exp. Bot.* 49:693-700.
- Lovisolo, C., Hartung, W. and Schubert, A. 2002. Whole-plant hydraulic conductance and root-to-shoot flow of abscisic acid are independently affected by water stress in grapevines. *Func. Plant Biol.* 29:1349-1356.
- 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. *Func. Plant Biol.* 37:98-116.
- Maroco, J.P., Rodrigues, M.L., Lopes, C. and Chaves M.M. 2002. Limitations to leaf photosynthesis in field-grown grapevine under drought - metabolic and modelling approaches. *Func. Plant Biol.* 29:451-459.
- Mattivi, F., Guzzon, R., Vrhovsek, U., Stefanini, M. and Velasco, R. 2006. Metabolite profiling of grape: flavonols and anthocyanins. *J. Agric. Food Chem.* 54:7692-7702.
- McCarthy, M.G., Loveys, B.R., Dry, P.R. and Stoll, M. 2002. Regulated deficit irrigation and partial rootzone drying as irrigation management techniques for grapevines. *FAO Water Reports* 22:79-87.
- Medrano, H., Escalona, J.M., Cifre, J., Bota, J. and Flexas, J. 2003. Regulated deficit irrigation effects in cv. 'Tempranillo' vineyards grown under semiarid conditions in mid-Ebro river valley (Spain). *Func. Plant Biol.* 30:607-619.
- Möller, M., Alchanatis, V., Cohen, Y., Meron, M., Tsipris, J., Naor, A., Ostrovsky, V., Sprintsin, M. and Cohen, S. 2007. Use of thermal and visible imagery for estimating crop water status of irrigated grapevine. *J. Exp. Bot.* 58:827-838.
- Neumann, P., Chazen, O., Bogoslavsky, L. and Hartung, W. 1997. Role of root-derived ABA in regulating early leaf growth responses to water deficits. p.147-154. In: A. Altman and Y. Waisel (eds.), *Biology of root formation and development*. New York: Plenum Press.
- Neumann, P.M. 2008. Coping mechanisms for crop plants in drought-prone environments. *Ann. Bot.* 101:901-907.
- Patakas, A. and Noitsakis, B. 1999. Mechanisms involved in diurnal changes of osmotic potential in grapevines under drought conditions. *J. Plant Physiol.* 154:767-774.
- Rodrigues, M.L., Santos, T., Rodrigues, A.P., de Souza, C.R., Lopes, C.M., Maroco, J.P., Pereira, J.S. and Chaves, M.M. 2008. Hydraulic and chemical signalling in the regulation of stomatal conductance and plant water use of field grapevines growing under deficit irrigation. *Func. Plant Biol.* 35:565-579.
- Santos, T., Lopes, C., Rodrigues, M.L., Souza, C.R., Maroco, J.P., Pereira, J.S., Silva, J.M.R. and Chaves, M.M. 2003. Partial rootzone drying effects on growth and fruit quality of field-grown grapevines (*Vitis vinifera*). *Func. Plant Biol.* 30:663-671.
- Sauter, A., Dietz, K.J. and Hartung, W. 2002. A possible stress physiological role of abscisic acid conjugates in root to shoot signalling. *Plant Cell Environ.* 25:233-228.
- Schultz, H.R. and Matthews, M.A. 1988. Resistance to water transport in shoots of *Vitis vinifera* L. *Plant Physiol.* 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 Environ.* 26:1393-1405.
- Schultz, H.R. and Stoll, M. 2010. Some critical issues in environmental physiology of grapevines: future challenges and current limitations. *Aust. J. Grape Wine Res.* 16:4-24.
- Shashidhar, V.R., Prasad, T.G. and Sudharshan, L. 1994. Hormonal signals from roots to shoots of sunflower (*Helianthus annuus* L.) moderate soil drying increases delivery of abscisic acid and depresses delivery of cytokinins in the xylem sap. *Ann. Bot.* 78:151-155.
- Soar, C.J., Speirs, J., Maffei, S.M., Penrose, A.B., McCarthy, M.G. and Loveys, B.R. 2006. Grape vine varieties Shiraz and Grenache differ in their stomatal response to VPD: apparent links with ABA physiology and gene expression in leaf tissue. *Aust. J. Grape Wine Res.* 12:2-12.
- Souza, C.R., Maroco, J.P., Santos, T., Rodrigues, M.L., Lopes, C., Pereira, J.S. and Chaves M.M. 2003. Partial rootzone-drying: regulation of stomatal aperture and carbon assimilation in field grown grapevines (*Vitis vinifera* cv. 'Moscatel'). *Funct. Plant Biol.* 30:653-662.
- Sperry, J.S., Hacke, U.G., Comstock, J.P. and Oren, R. 2002. Water deficits and hydraulic limits to leaf water supply. *Plant Cell Environ.* 25:251-264.

- Stefanelli, D., Goodwin, I. and Jones, R. 2010. Minimal nitrogen and water use in horticulture: effects on quality and content of selected nutrients. *Food Res. Int.* 43:1833-1843.
- Stoll, M., Loveys, B. and Dry, P. 2000. Hormonal changes induced by partial rootzone drying of irrigated grapevine. *J. Exp. Bot.* 51:1627-1634.
- Tin, T. 2008. Climate Change: faster, stronger, sooner, World Wildlife Foundation. http://assets.wwf.org.uk/downloads/cc_science_paper_october_2008_1.pdf (Accessed on 2 December 2010).
- Water Foot Print Network 2010. <http://www.waterfootprint.org/?page=files/home> (Accessed on 2 December 2010).
- Wilkinson, S. and Davies, W.J. 2002. ABA-based chemical signalling: the co-ordination of responses to stress in plants. *Plant Cell Environ.* 25:195-210.
- Wine Institute. 2010. World Statistics. <http://www.wineinstitute.org/resources/statistics> (Accessed on 2 December 2010).

Tables

Table 1. Major cultivation area of grapevine (in hectares) and wine production (hectoliters) worldwide, relative to the years 2004 and 2008 (adapted from the Wine Institute, 2010).

Continent/Country	Area (10 ³ ha)	Wine (10 ³ hl)	Area (10 ³ ha)	Wine (10 ³ hl)
	2004		2008	
Europe/Mediterranean				
Spain	1167	41,843	1,113	36,781
France	852	57,386	817	45,692
Italy	787	44,086	805	51,500
Turkey	597	250	587	260
Portugal	223	7,340	220	6,049
Asia and Middle East				
China	459	11,700	551	14,500
Iran	339	-	352	-
America				
USA	378	24,110	380	24,274
Chile	175	6,550	194	8,690
Africa				
South Africa	117	9,279	120	10,300
Oceania				
Australia	157	15,048	173	14,750
World total	7,904	291,987	7,864	283,898

Figures

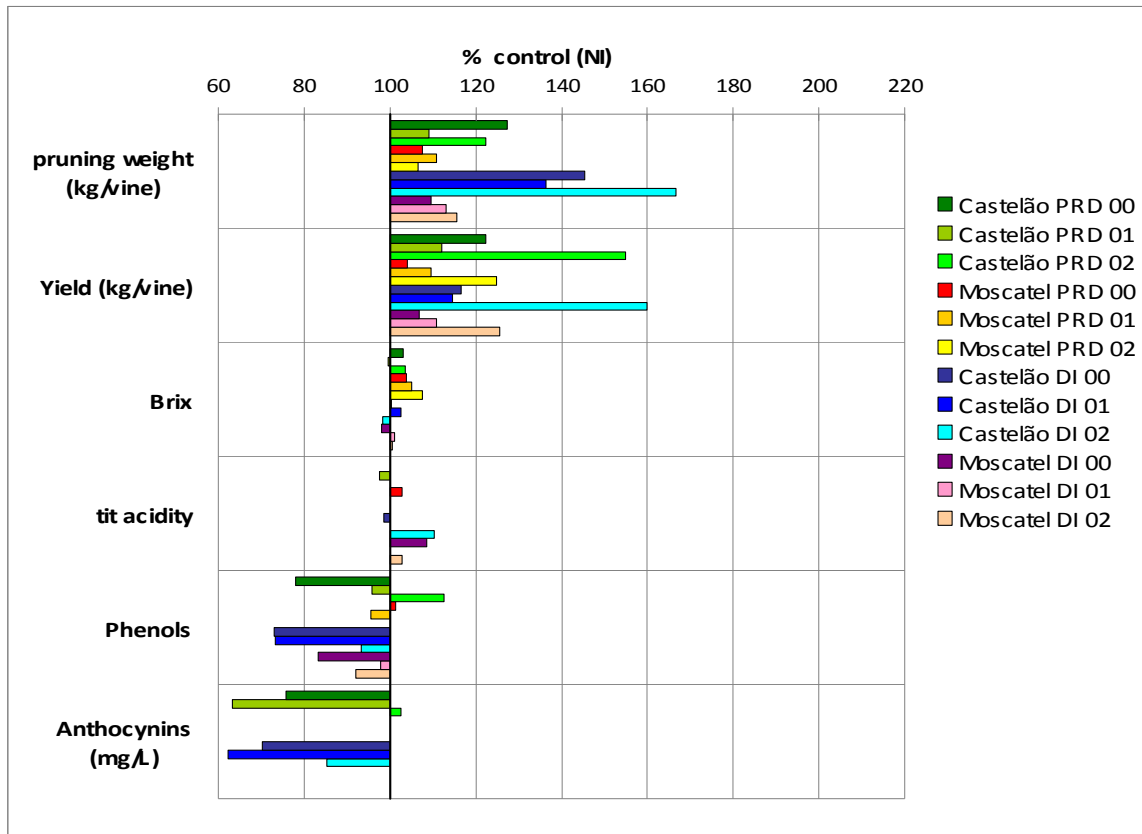


Fig. 1. Pruning weight, yield and berry quality parameters in PRD and DI grapevines calculated as a function of the same parameters measured for non irrigated (NI) vines, in two *V. vinifera* cultivars, 'Moscatel' and 'Castelão', during three years. The experiment took place in a sandy soil in Pegões, Central Portugal (redrawn from Chaves et al., 2007).

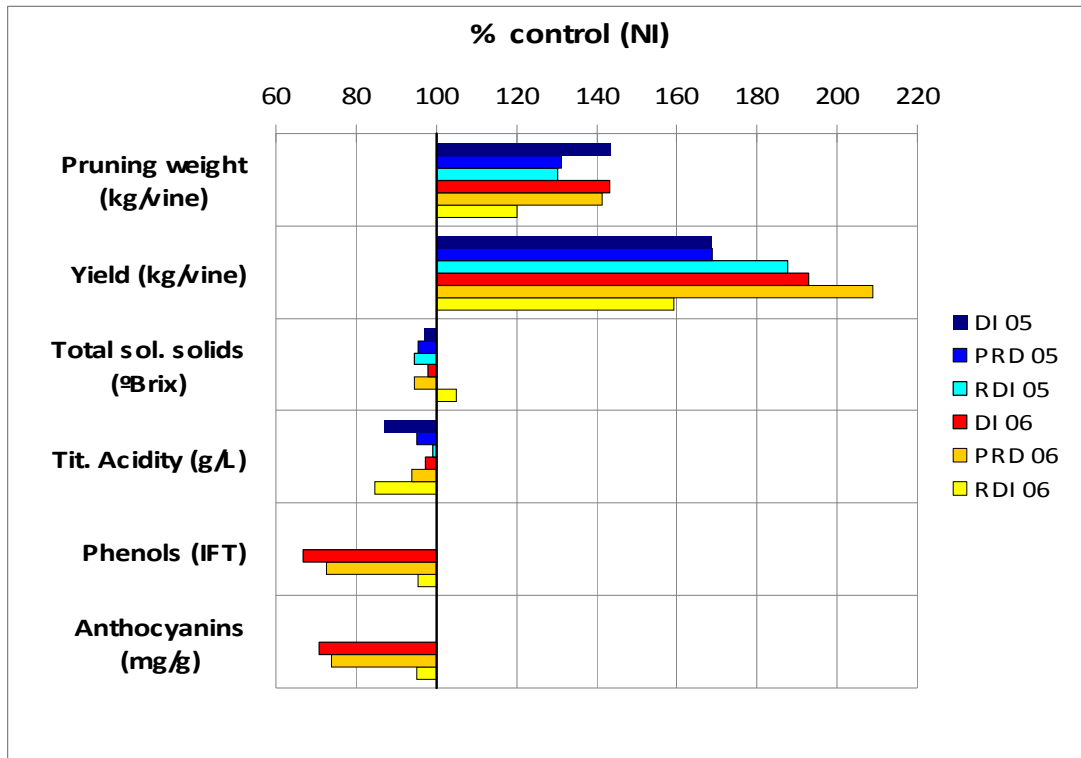


Fig. 2. Pruning weight, yield and quality parameters in PRD, RDI and DI vines as percentage (%) of the same parameters measured for non irrigated (NI) plants studied in the *V. vinifera* cultivar ‘Aragonez’ (syn. ‘Tempranilho’) during two particularly dry years (2005 and 2006), in a loamy soil in a commercial vineyard (Herdade Seis Reis), Alentejo, South Portugal (Lopes et al., unpublished). Data relative to phenols and anthocyanins are not available for 2006.