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WATER USE EFFICIENCY

Deficit irrigation in grapevine improves water-use efficiency while controlling vigour and production quality

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Abstract

Grapevine irrigation is becoming an important practice to guarantee wine quality or even plant survival in regions affected by seasonal drought. Nevertheless, irrigation has to be controlled to optimise source to sink balance and avoid excessive vigour. The results we present here in two grapevine varieties (Moscatel and Castelão) during 3 years, indicate that we can decrease the amount of water applied by 50% (as in deficit irrigation, DI, and in partial root drying, PRD) in relation to full crop's evapotranspiration (ETc) [full irrigated (FI) vines] with no negative effects on production and even get some gains of quality (in the case of PRD). We report that in non-irrigated and in several cases in PRD vines exhibit higher concentrations of berry skin anthocyanins and total phenols than those presented by DI and FI vines. We showed that these effects on quality were mediated by a reduction in vigour, leading to an increase on light interception in the cluster zone. Because plant water status during most of the dates along the season was not significantly different between PRD and DI, and when different, PRD even exhibited a higher leaf water potential than DI vines, we conclude that growth inhibition in PRD was not a result of a hydraulic control. The gain in crop water use in DI and PRD was accompanied by an increase of the $\delta^{13}C$ values in the berries in DI and PRD as compared to FI, suggesting that we can use this methodology to assess the integrated water-use efficiency over the growing season.

Introduction

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. In recent years, the number of dry days per year has increased in southern Europe (Luterbacher *et al.*, 2006), and this trend is likely to increase in the future, according to global change scenarios (Petit *et al.*, 1999; Miranda *et al.*, 2006). This will have an impact in viticulture (Schultz, 2000), with viticulturists in these regions having to rely more and more on irrigation to stabilise yield and improve wine quality. However, there is still some controversy concerning the positive and negative effects of grapevine irrigation practice in traditional viticulture because if water is applied in excess it can reduce colour and sugar content and produce acidity imbalances in the wine (Bravdo *et al.*, 1985; Matthews *et al.*, 1990; Esteban *et al.*, 2001). On the contrary, a small water supplement can increase grape yield, maintaining or even improving quality (Reynolds & Naylor, 1994; Ferreyra *et al.*, 2003; Santos *et al.*, 2003). The question of when and how much water should be applied in a given environment and variety is still standing.

A key to improve winegrape quality in irrigated vineyards is to achieve an appropriate balance between vegetative and reproductive development, as an excess of shoot vigour may have undesirable consequences for fruit composition (McCarthy, 1997). A mild water stress, maintained through partial irrigation, may reduce vine vigour and competition for carbohydrates by growing tips, as well as promoting a shift in the partition of photoassimilates towards reproductive tissues and secondary metabolites. These changes in plant metabolism by mild water stress may increase the quality of the fruit and wine produced (Matthews & Anderson, 1988, 1989).

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 (Davies *et al.*, 2002; Chaves & Oliveira, 2004; Flexas *et al.*, 2004; Cifre *et al.*, 2005; Souza *et al.*, 2005*a*). New approaches for irrigation management will have to reduce both water consumption and the detrimental environmental effects of current agricultural practices. This goal may be achieved in several ways, deficit drip irrigation being a widely used practice with the aim of saving water and simultaneously improving wine quality. Currently, the two most important irrigation tools, based on physiological knowledge of grapevine and other crops response to water stress, are regulated deficit irrigation (RDI) and partial root-zone drying (PRD).

In RDI water input is removed or reduced for specific periods during the crop cycle, improving control of vegetative vigour, to optimise fruit size, fruitfulness and fruit quality (Chalmers *et al.*, 1986; Alegre *et al.*, 1999; Dry *et al.*, 2001). RDI has been used successfully with several crops, reducing water use in crops, such as olive trees (Alegre *et al.*, 1999; Goldhamer, 1999; Wahbi *et al.*, 2005), peaches (Mitchell & Chalmers, 1982; Li *et al.*, 1989; Boland *et al.*, 1993), pears (Mitchell *et al.*, 1989; Caspari *et al.*, 1994; Marsal *et al.*, 2002) and grapevines (Goodwin & Macrae, 1990; Battilani, 2000). However, this technique needs control of water application, which is difficult to achieve in practice.

In vineyards under Mediterranean conditions it has been a common practice to manage the water deficit during the final phases of grape development (Williams & Matthews, 1990). However, in Australia, for example, the most common practice is to apply less water early in the season (McCarthy *et al.*, 2000). Both of these practices have shown to benefit wine, in one case reducing the grape size by limiting available water and in the other one by limiting the potential for grape growth. Flavour compounds, which determine wine quality, are located principally in the berry skin; therefore a smaller size in the grape berries improves fruit quality as a result of the increase in skin to flesh ratio (McCarthy, 1997). Yet, crops such as apple trees are negatively influenced by the latter (Leib *et al.*, 2006).

Partial root-zone drying is a new irrigation technique that requires approximately half of the root system to be maintained in a drying state while the remainder of the root system is irrigated. Theoretically, roots of the watered side maintain a favourable plant water status, while dehydrating roots will synthesise chemical signals, which are transported to the leaves in the transpiration stream, leading to the reduction of stomatal conductance and/or growth and bringing about an increase in water-use efficiency (WUE) (Loveys, 1984; Davies & Zhang, 1991; Dodd et al., 1996; Dry *et al.*, 1996; Davies *et al.*, 2000; Loveys *et al.*, 2000; Stoll *et al.*, 2000; Liu *et al.*, 2001; Souza *et al.*, 2003; Antolín *et al.*, 2006). There is also the indication that PRD irrigation may have impact on root growth leading to an increased root development in the deeper layers as shown by Dry *et al.* (2000) and Santos T.P., Lopes C.M., Rodrigues M.L., Souza C.R., Maroco J.P., Pereira J.S., Silva J.R., Chaves M.M. (submitted) in grapevine or in the overall root system, as shown in tomato by Mingo *et al.* (2003). It has also been reported that, as a result of drying roots in PRD, non-hydraulic signalling could occur, leading to increases in abcisic acid (ABA) production and in xylem pH (Davies & Zhang, 1991; Dry *et al.*, 1996; Dry & Loveys, 1999; Stoll *et al.*, 2000) as well as a reduction of cytokinins (Stoll *et al.*, 2000; Davies *et al.*, 2005).

The frequency of switching irrigation between rows in PRD will have to be determined according to the soil type and other factors such as rainfall, temperature and evaporative demand, but in most of the published data in grapevines, the PRD cycles were around 10–15 days (Davies *et al.*, 2000; Stoll *et al.*, 2000; Santos *et al.*, 2003). The agronomic and physiological effects of the PRD technique have been tested on several horticultural crops and fruit trees, in studies carried out either in pot or field conditions. These include apple (Gowing *et al.*, 1990), citrus (Hutton, 2000), almond (Heilmeier *et al.*, 1990), pear (Kang *et al.*, 2002, 2003), olive (Wahbi *et al.*, 2005), tomato (Davies *et al.*, 2000; Mingo *et al.*, 2003), soybean (Bahrun, 2003) and recently common bean (Wakrim *et al.*, 2005). The results are variable as a consequence of species differences and the characteristics of each experiment: soils, climate and agronomic practices. The debate in the literature over the effects and underlying causes of PRD functioning is still very intense. For example, according to Bravdo (2005), an absolute control of root drying is not possible under field conditions and also hydraulic redistribution from deeper to shallower roots may prevent that the clear results obtained in potted plants, are achieved under field conditions. Other authors, e.g. Gu *et al.* (2004), argue that the amount of water used rather than the application system explains the effects of PRD.

We studied the effects of different irrigation regimes in physiology and production of two grapevine varieties (Moscatel and Castelão), during 3 years, under the framework of the EU project IRRISPLIT. The treatments applied were full irrigation for minimum water deficit (FI, 100% of the ETc), deficit irrigated (DI, 50% of the ETc, half of water supplied to each side of the row), partial root drying (PRD, 50% of ETc periodically supplied in alternation, to only one side of the root system whereas the other one was allowed to dry) and rain fed, non-irrigated grapevines (NI). In the present paper we review the most important results obtained, illustrating them with data obtained in the two cultivars, during the 3 years of experiments.

Material and methods

Experimental conditions

Our research was conducted during three seasons (2000–2002) in a commercial vineyard at the Centro Experimental de Pegões, southern Portugal (70 km east of Lisbon). The climate is of the Mediterranean type, with hot and dry summers and mild and rainy winters. Long-term (1976–2005) mean annual rainfall is 550 mm year^{-1}, with 400 mm falling during winter months (INMG, 1991). The mean annual air temperature is 16°C. Fig. 1 shows the monthly rainfall and the mean air temperature at the experimental site during the 3 years of the experiment and the average values of 30 years (1976–2005). The soil is derived from podzols, with a sandy surface layer (0.6–1.0 m) and clay at 1 m depth. Two cultivars of *Vitis vinifera* L. were studied, cv. Moscatel (syn. Muscat of Alexandria), a white variety (used for wine and table grapes) and cv. Castelão, a red wine variety, both grafted on 1103 Paulsen rootstock in 1997 and 1996, respectively. We have chosen the two varieties because, in addition of producing different wine types (white versus red), they are the most important varieties in the wine region (98%), and they are contrasting in precocity (Castelão starting vegetation earlier than Moscatel) and in resistance to drought (Moscatel tends to resist better than Castelão). The vines were spur pruned on a bilateral Royat Cordon system (~16 buds per vine) using a vertical shoot positioning with a pair of movable wires. Shoots were trimmed at about 30 cm above the higher fixed wire, two to three times between bloom and véraison. The vineyard has a planting density of 4000 vines h^{-1}, the vines being spaced 2.5 m between and 1.0 m along rows.

Irrigation water was applied with drip emitters (4 L h^{-1} for FI and PRD and 2 L h^{-1} for DI), two per vine, positioned 30 cm from the vine trunk (out to both sides of the rows) and distributed on both sides of the root system. The water was supplied according to the crop evapotranspiration ($ET_c = ET_0 \times K_c$) calculated from the evaporation of a Class A pan (ET_0), corrected with the crop coefficient (K_c), We used the most suitable K_c for our conditions, according to Prichard (1992) and Allen *et al.* (1999). This K_c was 0.6 in June and 0.7 in July and August. The irrigation treatments were: rain fed, NI; PRD (50% of the ET_c was supplied to only one side of the root system, alternating sides each 15 days approximately); deficit irrigation (50% of the ET_c was supplied to both sides of the vine, 25% in each side); full irrigation (FI, 100% of the ETc was supplied to both the sides of the root system, 50% in each side). Water was supplied twice per week from the beginning of berry development (June) until harvest (September). Cumulative

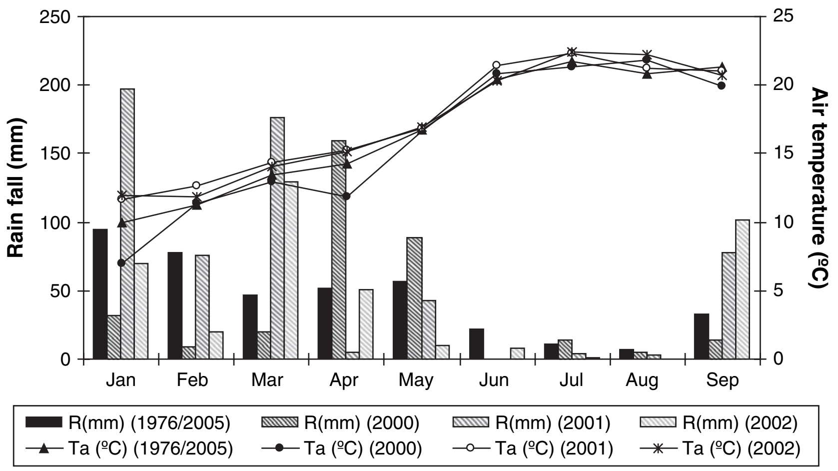

Figure 1 Total rainfall (bars) and monthly mean air temperature (lines) at the experimental site during 2000, 2001 and 2002 season and average values of 30 years (1976–2005).

rainfall during the experimental period (mid-June until the end of August) was 19.4 mm in 2000, 6.3 mm in 2001 and 0.5 mm in 2002 growing season (the driest year). The total amount of water supplied to FI, PRD and DI vines are shown in Table 5. During the growing season, mean soil moisture was on average 125% higher in FI and 65% in DI and PRD when compared to NI (see Santos *et al.*, 2005 for more details). In PRD the right side of the root zone, the first one to be irrigated, had soil moisture values around twice (95 mm) those of the left side (40 mm). The reverse occurred when the irrigation side was switched.

The experimental design was a latin square with four treatments and four replications per treatment. Each replicate (plot) had 20 vines.

Vegetative growth

Leaf area per shoot (eight shoots per treatment) was assessed periodically in shoot counts from bud break onwards in a non-destructive way, using the methodologies proposed by Lopes & Pinto (2000). In these methodologies primary leaf area was estimated using a mathematical model with four variables: shoot length, leaf number and area of the largest and the smallest leaf. Lateral leaf area estimation was performed by another model that uses the same variables with the exception of lateral shoot length. The area of single leaves was estimated using an empirical model based on the relationship between the length of the two main lateral leaf veins and leaf area on 1645 leaves of all sizes, using a leaf area meter (LI-3000; LI-COR Lincoln, NB, USA). Leaf area per plant was calculated multiplying the average leaf area per shoot by the mean shoot number.

At winter pruning, shoot number and pruning weight were recorded and shoot weight and crop load (yield/pruning weight) were calculated.

Light at the cluster zone was measured on sunny days at mid-day using a Sunflek Ceptometer (model SF-40; Delta T Devices Ltd, Cambridge, UK) inserted horizontally at cluster zone along the row. The values of incident photosynthetic photon flux density (PPFD) were expressed in percentage of a reference PPFD, measured over the canopy top.

Water relations and gas exchange

Pre-dawn (Ψ_{pd}) leaf water potential was measured weekly with a Scholander-type pressure chamber (Model 1000; PMS Instrument Co., Corvallis, OR, USA), from the beginning of berry development until harvest. The measurements were carried out in six fully expanded leaves per treatment in five dates from June to August, just before the irrigation.

Net CO_2 assimilation rate (A) and stomatal conductance (g_s) were measured on sun-exposed fully mature leaves (from primary shoots) using a portable Li-6400 IRGA (LI-COR, Lincoln, NB, USA). All measurements were replicated 4–8 times. A and g_s values were used to calculate the instantaneous intrinsic WUE (A/g_s). The relative stomatal limitation (RSL) was estimated from (A/Ci) response curve, as described in Souza *et al.* (2005*a*). The maximum ratio of Rubisco carboxylation (V_{cmax}) and maximum electron transport capacity at saturating light (J_{max}) were obtained by fitting the model of Farquhar *et al.* (1980) with modifications by Sharkey (1985) to A/Ci response curves as described by Maroco *et al.* (2002).

Carbon isotope composition

Samples to determine carbon isotope composition of mature leaves were collected in primary shoots from six plants per treatment, at harvest. Berry samples consisted of 30 berries per replicate (six replicates per treatment) taken randomly from exposed clusters. We measured whole berries in the 3 years of study, and in 2001 and 2002 the pulp berry also. The dried leaves and berry samples were ground into a fine homogeneous powder and 1 mg subsamples were analysed for $\delta^{13}C$ using an Europa Scientific ANCA-SL Stable Isotope Analysis System (Europa Scientific Ltd., Crewe, UK). Carbon isotopic composition was expressed as $\delta^{13}C = [(R_s - R_b)/R_b] \times 1000$, where R_s is the ratio $^{13}C/^{12}C$ of the sample and R_b is the $^{13}C/^{12}C$ of the PDB (Pee Dee Belemnite) standard.

Yield and fruit quality

Berry composition was studied at harvest. Sampling was carried out by collecting cluster fractions using a 200 berries sample per plot, collected in all vines (3–4 berries per cluster) and representative of all positions within the clusters (Carbonneau, 1991). Subsamples per plot were used for fresh berry analysis of weight and volume, pH, soluble solids (°Brix) by refractometry and titratable acidity by titration with NaOH as recommended by OIV (OIV, 1990). Another subsample of berries per plot was frozen at −30°C for anthocyanin and total phenolic compounds analysis. Total phenols were determined by spectrophotometry, by measuring ultraviolet absorption at 280 nm (Total Phenol Index, TPI) (OIV, 1990). Anthocyanins were measured by the sodium bisulphite discolouration method (Ribereau-Gayon & Stonestreet, 1965). At harvest, yield components were assessed, following manual harvesting and weighing the production on-site. Cluster number and yield per vine were recorded for all vines on each plot.

Statistical analyses

Factorial analyses of variance (ANOVA), with year, sampling time and/or treatments as main factors, were used to test the main effects and factor interactions on the physiological, biochemical and growth parameters evaluated. For multiple comparisons of treatments, we report also the SE and Fisher least significant differences (LSD). Statistically, significant differences were assumed for $P < 0.05$ and statistical data analysis were performed with Statistica (v5, Statsoft, Tulsa, OK, USA).

Results

Leaf water status, vegetative growth and canopy microclimate

In both varieties we observed that FI vines maintained a high Ψ_{pd} throughout the growing season (values for 2002 in Fig. 2). The minimum Ψ_{pd} was measured in middle August in 2002 (the driest year), attaining −0.22 MPa for Moscatel and −0.26 MPa Castelão (Table 1) On the contrary, NI vines showed a progressive decline in Ψ_{pd} from July onwards and the two deficit irrigation treatments (PRD and DI) had Ψ_{pd} values intermediate between FI and NI (Fig. 2). In Castelão, Ψ_{pd} of PRD vines was significantly higher than in DI. The Ψ_{pd} of Castelão NI vines at middle August reached lower values (∼−0.78 MPa) than those of NI in Moscatel (−0.64 MPa).

Water availability affected vine growth: the average weight per shoot measured during the winter pruning and the total pruning weight per vine were significantly lower in NI (and in PRD in the variety Castelão) than in FI and DI in the 3 years of studies (Table 2). Similar differences were observed in the percentage of water shoots (epicormic shoots grown from the old woody stem), with NI and PRD showing values significantly lower than FI and DI (Table 2). Total leaf area per vine at véraison presented, in both varieties, significantly higher values ($P < 0.05$) in FI than in NI and PRD vines; DI plants had intermediate values (Table 2). The differences of total leaf area observed between treatments were mainly because of differences in the lateral shoot leaf area as in some cases (Moscatel 2000, Castelão 2002) primary shoot leaf area was similar in the different watering treatments.

The reduction in vegetative growth observed in NI and in many instances in PRD resulted in a more open canopy as indicated by the significant increase in the PPFD received by the clusters in these treatments when compared to DI and FI (Fig. 3).

Photosynthetic performance and water-use efficiency

Diurnal time courses of gas exchange and intrinsic WUE in a typical day in August of 2002 are shown in Fig. 4. *A* and g_s decreased throughout the day, with differences between treatments being more marked in the late afternoon and in the variety Castelão as compared with Moscatel. NI vines showed the lowest *A* and g_s.

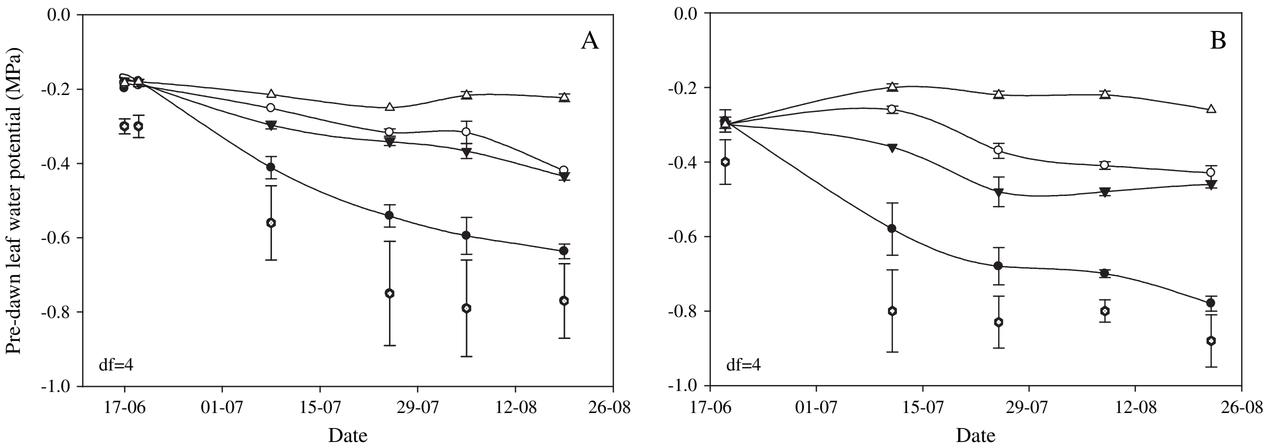

Figure 2 Seasonal evolution of pre-dawn leaf water potential for all water treatments (●, NI, ○, PRD, ▼, DI, △, FI), in Moscatel (A) and Castelão (B) during 2002 growing season. Each point represents the average of eight measurements with SE. Bars not visible indicate SE smaller than symbol. Least significant difference (LSD) bars and d.f. (degrees of freedom) are given for comparisons proposes. DI, deficit irrigation; NI, non-irrigated; FI, full irrigated; PRD, partial root drying.

Table 1 Pre-dawn leaf water potential and stomatal conductance measured at mid-day in the middle of August in Castelão and Moscatel grapevines for the four water treatments (NI, PRD, DI, NI) and the 3 years 2000, 2001 and 2002.

	2000		2001		2002	
	ψ_{pd} (MPa)	g_s (mol $m^{-2}s^{-1}$)	ψ_{pd} (MPa)	g_s (mol $m^{-2}s^{-1}$)	ψ_{pd} (MPa)	g_s (mol $m^{-2}s^{-1}$)
Moscatel						
NI	−0.58	0.10	−0.39	0.13	−0.64	0.13
PRD	−0.23	0.23	−0.29	0.15	−0.42	0.19
DI	−0.34	0.27	−0.19	0.20	−0.44	0.22
FI	−0.15	0.29	−0.11	0.25	−0.22	0.23
LSD (d.f.)	0.04 (4)	0.11 (3)	0.12 (4)	0.05 (3)	0.12 (4)	0.10 (3)
Castelão						
NI	−0.68	0.15	−0.51	0.05	−0.78	0.05
PRD	−0.37	0.20	−0.30	0.15	−0.43	0.08
DI	−0.40	0.20	−0.28	0.23	−0.46	0.08
FI	−0.28	0.30	−0.15	0.30	−0.26	0.11
LSD (d.f.)	0.06 (4)	0.04 (3)	0.13 (4)	0.04 (3)	0.08 (4)	0.05 (3)

d.f., degrees of freedom; LSD, least significant difference; DI, deficit irrigation; NI, non-irrigated; FI, full irrigated; PRD, partial root drying.

Although most differences between PRD and DI were not statistically significant, the values of g_s in PRD were closer to NI than to DI vines. Midday g_s values recorded in mid-August for the two varieties and the 3 years are shown in Table 1. Because they represent the lowest attained stomatal conductances, we conclude that only in NI treatments g_s reached values close to or lower than 0.1 mol m^{-2} s^{-1}.

A/g_s (2002 values) did not show significant differences among treatments in Moscatel, except in the afternoon (16.00 h), where FI exhibit lower A/g_s than the other treatments (Fig. 4). In Castelão, the highest values in A/g_s throughout the day were observed in NI.

Stomatal limitation of gas exchange (RSL) of Moscatel NI vines was significantly higher than of FI and DI vines in two out of the three years studied (2000 and 2002, Table 3). PRD was not significantly different either from NI or from FI and DI. In Castelão (only measured in 2002) RSL of NI vines was significantly higher than of FI, DI and PRD vines (Table 3).

The estimated maximal velocity of carboxylation (V_{cmax}) was not significantly different between treatments in the variety Moscatel, in any of the years of study (Table 3). The same result was obtained for Castelão, in measurements made in 2002.

However, in the variety Moscatel, the rate of electron transport (J_{max}) was lower in NI than in FI in the 3 years, with PRD being closer to NI and DI closer to FI in 2000. In Castelão no differences between treatments were observed (Table 3).

Carbon isotopic composition ($\delta^{13}C$)

The effects of the treatments on the $\delta^{13}C$ values of bulk leaf tissue (primary and lateral leaves), whole berry and pulp berry are shown in Table 4 for the two varieties, and, in the case of Moscatel, for the 3 years. The tissues of NI plants were less depleted in ^{13}C (higher $\delta^{13}C$, lowest discrimination against ^{13}C) than the other treatments, and FI vines showed the lowest $\delta^{13}C$ (higher discrimination against ^{13}C). Deficit irrigation treatments (PRD and DI) showed intermediate values. In general, significant differences between NI and FI were observed in berries and pulp where a substantial enrichment of ^{13}C is apparent as compared with the other tissues. The highest values of $\delta^{13}C$ were shown in berry pulp as compared to leaves. A good relationship was established between pulp $\delta^{13}C$ and intrinsic WUE (Fig. 5). This is not the case between A/gs and $\delta^{13}C$ in leaves.

Yield and fruit composition

As for the yield components, the number of clusters per vine was independent of soil water availability. However, cluster weight was significantly lower in NI than in FI (except in Moscatel in 2001) resulting in a significant yield decrease in the former. The three irrigated treatments showed no significant differences among them in 2001 and 2002 (Table 5).

Berry composition at harvest changed with treatments. In Castelão, skin anthocyanins accumulation was higher in NI and PRD (only significantly different in 2002) grapevines as compared to DI and FI. NI and PRD presented the highest total phenols when compared with the other treatments, and FI and DI the lowest (except in 2001 in Moscatel when no differences between treatments were observed) (Table 5). Irrigation had no significant effect on berry total soluble solids (°Brix) and pH. However, must titratable acidity increased significantly in FI as related to NI, in both varieties and in 2 years (2000 and

Table 2 Vigour parameters measured at pruning time or at véraison (the case of leaf parameters) in Castelão and Moscatel grapevines for the four water treatments (NI, PRD, DI, FI) in 2000, 2001 and 2002.

	2000					2001					2002				
	NI	PRD	DI	FI	LSD	NI	PRD	DI	FI	LSD	NI	PRD	DI	FI	LSD
Moscatel															
Shoot															
Shoot number per vine	11	11	9	9	1.06 (6)	13	12	13	12	0.78 (6)	16	17	18	17	0.03 (6)
Pruning weight (kg/vine^{-1})	0.52	0.56	0.57	0.64	0.08 (6)	0.46	0.51	0.52	0.58	0.05 (6)	0.45	0.48	0.52	0.54	0.67 (6)
Shoot weight (g)	49.0	53.4	64.3	69.0	8.23 (6)	36.4	41.2	42.6	50.8	4.37 (6)	29.2	28.8	31.1	33.4	2.16 (6)
Water shoots (%)	na	na	na	na		8.0	9.4	12.7	12.9	2.01 (6)	9.5	12.0	16.9	17.7	1.65 (6)
Leaf															
Leaf layer number (véraison)	2.6	3.2	3.8	3.8	0.30 (6)	2.4	2.7	3.6	3.8	0.29 (6)	2.1	2.2	3.2	3.6	0.25 (6)
Main leaf area (m^2 vine^{-1})	2.0	1.9	2.1	1.9	0.55 (6)	Na	na	na	na		2.5	3.1	3.4	4.0	0.80 (6)
Lateral leaf area (m^2 vine^{-1})	1.6	2.4	2.8	4.4	1.29 (6)	Na	na	na	na		1.9	1.7	1.8	3.7	1.22 (6)
Total leaf area (m^2 vine^{-1})	3.6	4.3	4.9	6.3	1.24 (6)	Na	na	na	na		4.3	4.9	5.2	7.6	1.60 (6)
Castelão															
Shoot															
Shoot number per vine	14	16	16	17	1.32 (6)	16	18	20	19	1.78 (6)	19	19	21	20	2.20 (6)
Pruning weight (kg vine^{-1})	1.1	1.4	1.6	1.8	0.19 (6)	1.1	1.2	1.5	1.5	0.22 (6)	0.9	1.1	1.5	1.5	0.22 (6)
Shoot weight (g)	70.1	89.8	102.5	105.8	11.72 (6)	64.9	67.8	76.8	77.8	10.54 (6)	47.9	56.1	76.2	74.9	11.42 (6)
Water shoots (%)	na	na	na	na		11.2	14.0	21.5	20.8	2.82 (6)	13.6	15.2	25.9	23.2	4.12 (6)
Leaf															
Leaf layer number (véraison)	2.3	2.6	3.4	3.4	0.28 (6)	2.4	2.6	3.4	3.6	0.25 (6)	1.6	2.3	3.3	3.7	0.24 (6)
Main leaf area (m^2 vine^{-1})	2.6	3.2	3.4	3.6	0.73 (6)	Na	na	na	na		4.4	4.6	5.5	6.2	0.73 (6)
Lateral leaf area (m^2 vine^{-1})	0.8	1.3	1.3	2.5	1.14 (6)	Na	na	na	na		0.8	1.0	1.5	1.5	1.14 (6)
Total leaf area (m^2 vine^{-1})	3.4	4.5	4.7	6.0	1.55 (6)	Na	na	na	na		5.2	5.6	7.0	7.7	1.55 (6)

d.f., degrees of freedom; LSD, least significant difference; DI, deficit irrigation; NI, non-irrigated; FI, full irrigated; PRD, partial root drying.

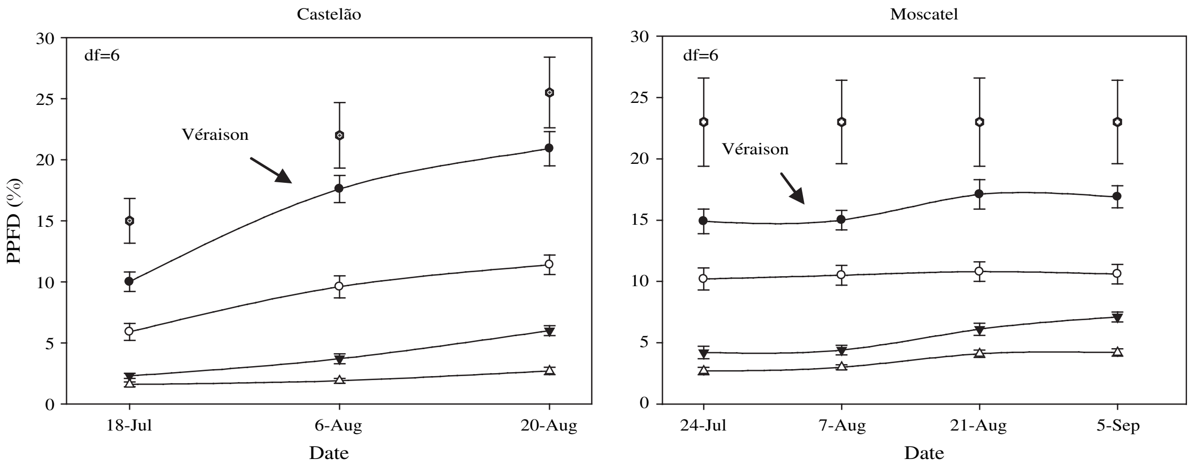

Figure 3 Incident photosynthetic photon flux density (PPFD) at the cluster zone expressed as a percentage of a reference (PPFD at the top of the canopy) in Castelão and Moscatel grapevines under four water treatments (●, NI, ○, PRD, ▼, DI, △, FI) during the 2002 growing season. Values shown represent the mean of 80 measurements with SE. Least significant difference (LSD) bars and d.f. are given for comparisons proposes. DI, deficit irrigation; NI, non-irrigated; FI, full irrigated; PRD, partial root drying.

2002). PRD and DI also presented higher must titratable acidity than NI in the variety Castelão in 2000 and 2001 (Table 5).

Discussion

Our results show the potential to utilise deficit irrigation, particularly PRD, to control the redistribution of photoassimilates, through a reduction in vigour, with a positive effect on light interception in the cluster zone and in the berry composition. We showed also that the pattern of physiological responses to water deficits was identical in both varieties, but most of the effects of deficit irrigation are more pronounced in the variety Castelão than in Moscatel. This can be explained by the low sensitivity to water stress in Moscatel plants (Regina & Carbonneau, 1996). By irrigating PRD and DI grapevines with 50% of ET_c, we imposed a mild water deficit that led to leaf predawn water potentials at the end of the season, which were intermediate (−0.2 to −0.4 MPa in both treatments and the two varieties) between FI (−0.1 to −0.3 MPa) and NI vines (−0.6 to −0.8 MPa) (Table 1). In July 2002, we observed that PRD vines exhibited slightly higher ψ_{pd} than in DI (Fig. 2), which might be explained by the tendency for some stomatal closure (lower g_s) during the afternoon in PRD, as shown in Fig. 4. Another evidence for the mild water deficits induced in PRD and DI vines was that the estimated RSL of photosynthesis in PRD and DI was not significantly higher than in FI (Table 3).

Crop ***WUE (amount of fruit produced per unit of water applied) in PRD and DI was twice that in FI, as a result of these plants (PRD and DI) having utilised half of the irrigation water for a similar yield in FI (Table 5). However, the intrinsic WUE estimated throughout the day or as an integral along the season (Souza *et al.*, 2005*b*) was not significantly different in the three irrigated treatments (PRD, DI and FI). These results might be explained by the fact that flowering buds are preset and half water supply was enough to maintain a 'normal' sink supply and because the effects of water deficits on stomata and photosynthesis were proportional, as it seems to be the case in both varieties (Fig. 4).

Interestingly, $\delta^{13}C$ values in the berries of DI and PRD vines were intermediate between FI and NI (Table 4 and Fig. 5), suggesting a higher integrated WUE over the season in DI and PRD than in FI. This might be the result of stomata of DI and PRD remaining closed for more hours in the day than in FI along the growing season. The correlation between $\delta^{13}C$ and WUE has been well documented in several crops (Farquhar & Richards, 1984), including grapevines (Gaudillère *et al.*, 2002; Souza *et al.*, 2005*b*). The results that we obtained point out to the interest of using integrated measures of physiological performance in order to evaluate long-term responses of plants to the environment and to agricultural practices.

The higher $\delta^{13}C$ values found in berries as compared to leaves may have two explanations, (1) the fact that berry filling results from current photosynthates, which were produced during the summer, reflecting the effects of mild water stress on stomatal closure as compared to the spring when leaves were formed; (2) the $\delta^{13}C$ of leaves may be more depleted than that of berries

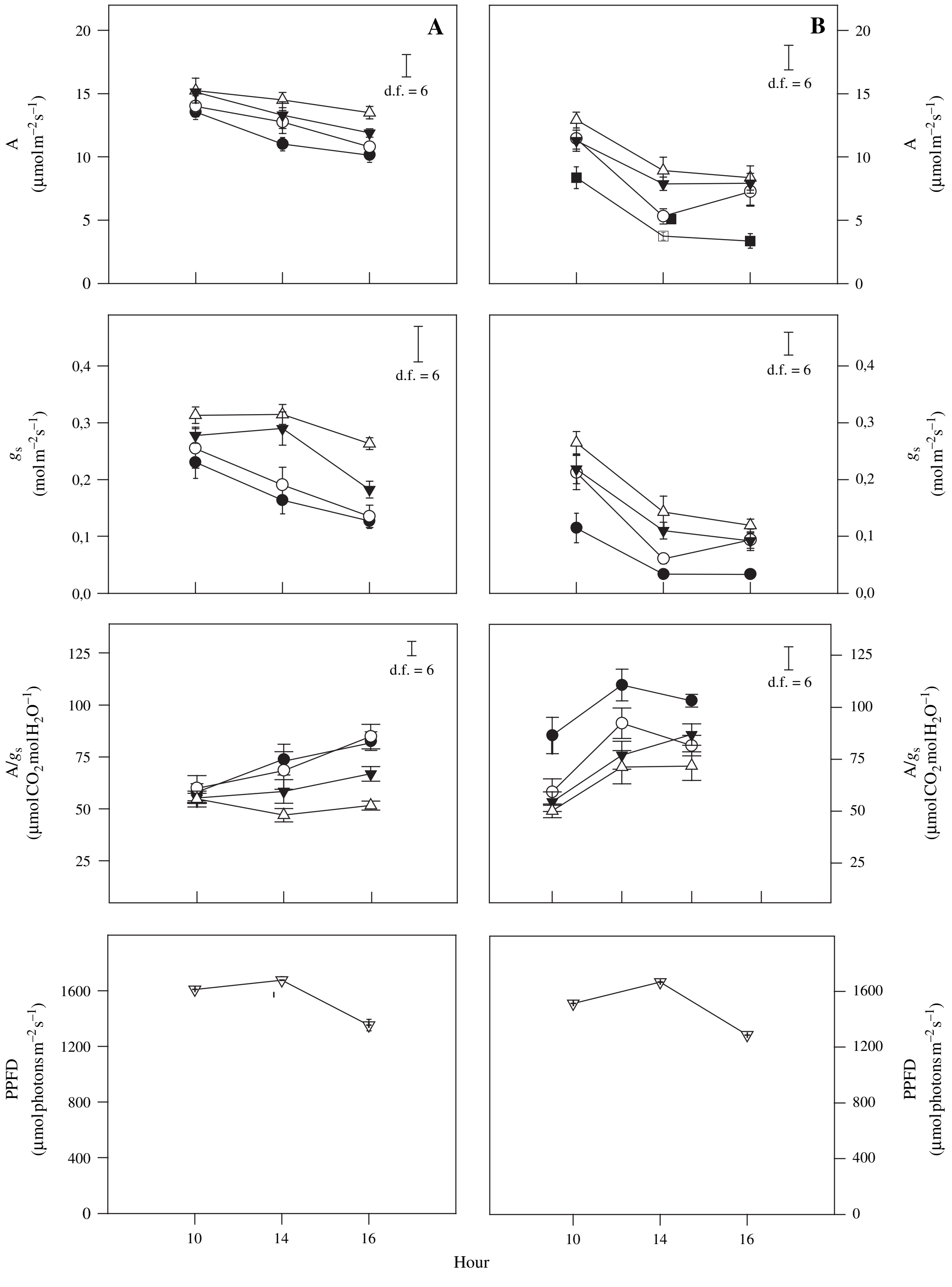

Figure 4 Diurnal course of photosynthesis (*A*), stomatal conductance (g_s), intrinsic water use efficiency (A/g_s) and photosynthetic photon flux density (PPFD) in cultivars Moscatel (A) and Castelão (B) measured, respectively on 5 and 8 of August 2002 for all water treatments (●, NI, ○, PRD, ▼, DI, △, FI). Values are the means ± SE. Least significant difference (LSD) bars and d.f. (degrees of freedom) are given for comparisons proposes. DI, deficit irrigation; NI, non-irrigated; FI, full irrigated; PRD, partial root drying.

Table 3 Estimated model parameters (V_{cmax} and J_{max}) and relative stomatal limitations (RSL) for the irrigation treatments in Moscatel during years 2000, 2001 and 2002, and in Castelão during 2002.

Treatment	V_{Cmax} (μmol m^{-2} s^{-1})	J_{max} (μmol m^{-2} s^{-1})	RSL (%)
Moscatel			
2000			
NI	45.68	130.08	35.75
PRD	46.10	149.99	32.49
DI	47.56	153.63	23.77
FI	55.84	170.64	23.24
LSD (d.f.)	16.54 (3)	21.41 (3)	7.68 (3)
2001			
NI	44.89	154.41	37.33
PRD	54.14	186.14	31.33
DI	49.23	177.22	24.65
FI	53.42	206.43	25.75
LSD (d.f.)	12.14 (3)	23.34 (3)	9.92 (3)
2002			
NI	44.96	127.50	37.14
PRD	42.88	219.16	27.68
DI	44.35	203.13	18.88
FI	53.99	235.11	19.77
LSD (d.f.)	10.30 (3)	28.44 (3)	13.54 (3)
Castelão			
2002			
NI	53.81	217.97	38.96
PRD	50.24	196.49	25.75
DI	48.82	193.90	25.47
FI	61.65	220.33	26.69
LSD (d.f.)	13.07 (3)	34.44 (3)	8.36 (3)

d.f., degrees of freedom; LSD, least significant difference; DI, deficit irrigation; NI, non-irrigated; FI, full irrigated; PRD, partial root drying.

Table 4 Carbon isotope composition ($\delta^{13}C$) in leaves, whole berries and pulp of grape subjected to different water treatments.

	$\delta^{13}C$		
Treatment	Leaves	Berries	Pulp
Moscatel			
2000			
NI	−25.75	−24.33	na
PRD	−26.63	−25.43	na
DI	−26.67	−25.88	na
FI	−27.26	−26.34	na
LSD (d.f.)	0.55 (3)	0.47 (3)	
2001			
NI	−26.83	−25.02	−24.61
PRD	−27.08	−25.37	−25.14
DI	−26.82	−25.41	−25.30
FI	−26.91	−25.71	−25.54
LSD (d.f.)	0.49 (3)	0.20 (3)	0.18 (3)
2002			
NI	−26.23	−24.68	−24.43
PRD	−26.77	−25.18	−25.22
DI	−26.72	−25.45	−25.31
FI	−27.03	−25.86	−25.79
LSD (d.f.)	0.32 (3)	0.45 (3)	0.38 (3)
Castelão			
2002			
NI	−26.83	−24.04	−23.23
PRD	−27.53	−25.72	−24.89
DI	−28.08	−25.43	−25.22
FI	−28.34	−26.61	−26.04
LSD (d.f.)	0.43 (3)	0.74 (3)	0.62 (3)

d.f., degrees of freedom; LSD, least significant difference; DI, deficit irrigation; na, not analyzed; NI, non-irrigated; FI, full irrigated; PRD, partial root drying.

because there are more post-photosynthetic fractionation processes (namely respiration) in berries, which might result in differences in the carbon isotope composition of the two organs (Badeck *et al.*, 2005).

When comparing the two deficit irrigation treatments, one of the striking observations made in the three years of the study was the reduction in vigour observed in PRD as compared to FI, which did not occur in DI vines (Table 2). As stated above, this effect was more marked in variety Castelão than in Moscatel. Because plant water status during most of the dates along the season was not significantly different between the two treatments, and when different, PRD even exhibited a higher leaf water potential than DI vines, we conclude that these effects are not a result of an hydraulic control, but rather support the hypothesis of a long distance signalling originated in dehydrating roots. Indeed, in recent years strong evidence has accumulated suggesting that stomatal closure and growth slow-down observed in the early stages of soil water deficits (Hsiao, 1973; Kramer, 1983) may be mediated by chemical signals produced in drying roots, namely ABA or cytokinins and transported to the shoot in the transpiration stream (Wilkinson & Davies, 2002). Even though some studies reported an increase in xylem ABA concentration in PRD plants (Stoll *et al.*, 2000), which we did not find in the present study (Rodrigues M.L., Santos T., Rodrigues A., Souza C.R., Lopes C., Maroco J., Pereira J.S., Chaves M.M., unpublished data), we think that other chemical signals, such as cytokinins, ethylene, alterations in ion contents of the xylem sap or changes in apoplastic pH in the leaves might be involved in that regulation (Wilkinson & Davies, 2002; Sobeih *et al.*, 2004).

We cannot discard the interpretation that applying the water only in one side of the plant may affect plant water status as a result of alterations in the dimension and architecture of the root system. In fact, we observed some changes in the pattern of root distribution, PRD vines showing a tendency for producing more roots in the deeper layers than the other treatments (Santos T.P., Lopes C.M., Rodrigues M.L., Souza C.R., Maroco J.P., Pereira J.S., Silva J.R., Chaves M.M., submitted). Effects

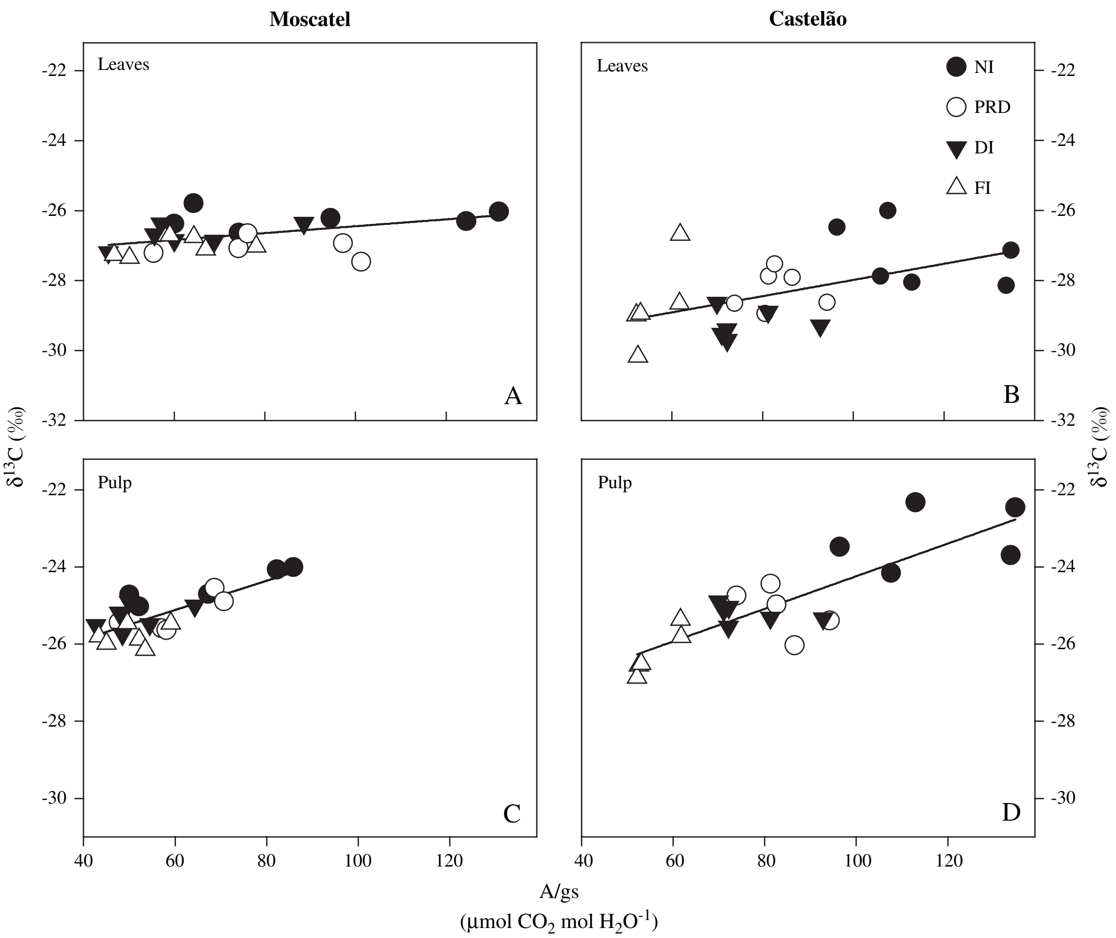

Figure 5 Relationship of δ^{13}C with intrinsic water use efficiency (A/g_s) in leaves and berry pulp of Moscatel, respectively, ($y = 26.37 + 0.002x$, $R^2 = 0.01$ (A); $y = 27.42 - 0.04x$, $R^2 = 0.60$** (C)) and in leaves an pulp of Castelão ($y = 27.81 - 0.02x$, $R^2 = 0.26$ (B); $y = 28.47 - 0.04x$, $R^2 = 0.70$** (D)). Each point represents one replicate of the water treatments. The measurements of A/g_s were made in August 2002.** indicates significant difference at level of 0.01. DI, deficit irrigation; NI, non-irrigated; FI, full irrigated; PRD, partial root drying.

of PRD in the root system were also reported by Dry *et al.* (2000) in grapevines and by Mingo *et al.* (2003) showing an overall increase in root biomass in potted tomato plants growing under PRD.

Taken together our results showed that the effects of PRD are dependent on the variety studied and the climatic conditions during the growing season (see also Santos *et al.*, 2003, 2005; Souza *et al.*, 2003, 2005*a,b*). This is consistent with the knowledge that environmental factors (such as PPFD, temperature or VPD) that influence shoot physiological processes will interact with factors that affect the rhizosphere, determining the final nature and intensity of chemical signalling (Wilkinson, 2004). As a consequence, plant WUE will reflect the multiple environmental stimuli perceived and the ability of the particular genotype to sense the onset of changes in moisture availability and therefore fine-tune its water status in response to the environment. This complexity of responses to the environment together with the difficulty in maintaining an effective partial root drying under field conditions as a result of root hydraulic redistribution (Smart *et al.*, 2005), as it was pointed out by Bravdo (2005), makes the impact of PRD not so clear as under controlled conditions. Soil type may also play a role in the intensity of the response to PRD. Sandy-type soils, as the one in our experiment, may produce effects closer to controlled conditions because lateral diffusion of irrigation water is lower than under clay-type soils (data not shown from an ongoing experiment).

Finally, our results also indicate that, for the region where our study took place (moderately subjected to water deficits), the differences in yield between irrigated (FI, PRD and DI) and rainfed vines (NI) only occurred in the driest year (2002). As for fruit quality, NI and PRD

Table 5 Yield components, berry composition and irrigation amount at harvest in Moscatel and Castelão grapevines for four water treatments (NI, PRD, DI, FI) in 2000, 2001 and 2002.

	2000					2001					2002				
	NI	PRD	DI	FI	LSD	NI	PRD	DI	FI	LSD	NI	PRD	DI	FI	LSD
Moscatel															
Parameter															
Yield components															
Mean cluster number per vine	15.6	15.0	15.8	15.3	1.19 (6)	18.2	18.5	20.0	19.6	1.32 (6)	27.4	28.7	28.8	28.7	2.22 (6)
Mean cluster weight (g)	475.9	515.9	502.0	592.8	55.65 (6)	472.2	506.0	473.4	502.5	26.67 (6)	377.5	407.0	398.0	395.3	3.86 (6)
Yield (ton ha^{-1})	28.9	30.9	31.6	36.0	3.87 (6)s	33.2	36.4	36.8	38.8	2.40 (6)	36.7	45.8	46.1	45.8	24.42 (6)
Berry composition															
Total soluble solids (°Brix)	21.0	21.8	20.6	20.6	1.03 (7)	17.7	18.6	17.9	18.4	1.69 (7)	15.8	17.0	15.9	15.6	1.70 (7)
Anthocyanins (mg L^{-1} must)	na	na	na	na		na	na	na	na		na	na	na	na	
TPI	15.6	15.8	13.0	12.8	1.73 (7)	17.6	16.8	17.2	16.9	1.02 (7)	8.7	8.7	8.0	7.7	0.68 (7)
Titratable acidity (g L^{-1})	3.5	3.6	3.8	3.9	0.26 (7)	4.0	4.0	4.0	4.2	0.33 (7)	3.4	3.4	3.5	3.8	0.29 (7)
pH	4.07	4.07	3.99	3.97	0.04 (7)	3.95	3.95	3.91	3.90	0.14 (7)	3.81	3.84	3.84	3.78	0.14 (7)
Irrigation amount (L $vine^{-1}$)	0	183.0	183.0	366.1		0	210.7	210.7	421.4		0	246.5	246.5	493.0	
Castelão															
Parameter															
Yield components															
Mean cluster number per vine	15.5	15.6	17.2	16.2	2.19 (6)	19.9	18.8	19.9	21.5	3.72 (6)	21.7	23.9	23.1	24.9	3.47 (6)
Mean cluster weight (g)	114.9	141.1	122.3	151.5	18.32 (6)	203.9	245.8	236.2	236.2	32.85 (6)	188.0	260.8	275.9	254.2	4.25 (6)
Yield (ton ha^{-1})	7.2	8.8	8.4	10.0	1.76 (6)	16.2	18.5	18.8	20.3	4.27 (6)	16.1	24.6	25.3	254.2	26.93 (6)
Berry composition															
Total soluble solids (°Brix)	23.4	24.1	23.5	23.1	0.98 (7)	22.4	22.3	23.0	22.2	0.97 (7)	19.0	19.7	18.7	18.9	2.37 (7)
Anthocyanins (mg L^{-1}must)	646.4	490.2	453.7	351.2	72.25 (7)	703.6	445.2	438.4	364.0	148.71 (7)	799.1	820.6	682.2	646.4	158.61 (7)
TPI	21.8	17.0	15.9	12.2	2.67 (7)	14.2	13.6	10.4	11.4	2.44 (7)	20.6	23.2	19.2	18.9	2.52 (7)
Titratable acidity (g L^{-1})	3.48	3.90	4.08	4.48	0.28 (7)	3.3	4.3	4.1	3.9	0.27 (7)	3.9	3.9	4.3	4.8	0.76 (7)
pH	4.22	4.22	4.16	4.07	0.10 (7)	4.21	4.13	4.22	4.16	0.05 (7)	3.92	3.88	3.81	3.82	0.20 (7)
Irrigation amount (L $vine^{-1}$)	0	183.0	183.0	366.1		0	210.7	210.7	421.4		0	246.5	246.5	493.0	

d.f., degrees of freedom; LSD, least significant difference; DI, deficit irrigation; NI, non-irrigated; FI, full irrigated; PRD, partial root drying; TPI, total phenols index.

tended to exhibit higher concentrations of berry skin anthocyanins and total phenols than those presented by DI and FI vines. This suggests that the main impact of the type of irrigation was produced via the effect of vigour on the light interception and the overall microclimate in the cluster zone (Williams & Matthews, 1990).

Irrigation did not significantly affect berry sugar accumulation and pH. These results are in contrast with those obtained by other authors who observed either an increase (Schultz, 1996; Lopes *et al.*, 2001) or a decrease (Jordão *et al.*, 1998; Pire & Ojeda, 1999) in berry sugars induced by high soil water availability. So in our experiment berries acted as a preferential sink for carbohydrates under the moderate water deficits (as occurred in DI and PRD) and even under full irrigation conditions as observed in FI vines.

Conclusions

It was demonstrated that large fluxes of water are not essential to optimal plant performance for agricultural purposes and that moderate water deficits, induced under deficit irrigation practices, might be used successfully in grapevine production to control sink–source relationships, maintaining or ameliorating fruit quality, while improving WUE in relation to full irrigated crops. Our data point out to subtle physiological differences between PRD receiving 50% of ETc (given in alternation to each side of the root system) and DI (the deficit irrigation receiving equal amount of water as PRD, but distributed by the two sides of the root system). These differences include slight reductions of stomatal aperture in PRD as compared to DI, recorded at some dates, but a clear depression of vegetative growth in PRD. Growth inhibition occurs in spite of similar or even better plant water status in PRD plants, suggesting a non-hydraulic regulation mechanism. On the other hand, no significant differences in photosynthetic rates, chlorophyll fluorescence parameters and WUE were observed between DI and PRD. Growth inhibition in PRD as compared to DI led to an increase in cluster exposure to solar radiation, with some potential to improve fruit quality. In fact, we report that NI and in several instances in PRD, vines exhibit higher concentrations of berry skin anthocyanins and total phenols than those presented by DI and FI vines. We have also observed that plant responses to deficit irrigation are dependent on the variety and the environmental conditions during the growing season.

Acknowledgements

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