RESEARCH PAPER

Contrasting physiological effects of partial root zone drying in field-grown grapevine (Vitis vinifera L. cv. Monastrell) according to total soil water availability

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Abstract

Different spatial distributions of soil moisture were imposed on field-grown grapevines by applying the same irrigation volumes to the entire (DI; deficit irrigation) or part of the (PRD; partial root zone drying) root zone. Five treatments were applied: controls irrigated at 60% ETo (crop evapotranspiration) for the whole season (308 mm year⁻¹); DI-1 and PRD-1 that received the same irrigation as controls before fruit set, 30% ETo from fruit set to harvest and 45% ETo post-harvest (192 mm year⁻¹); and DI-2 and PRD-2 that were the same, except that 15% ETo was applied from fruit set to harvest (142 mm year⁻¹). Compared with DI-1, PRD-1 maintained higher leaf area post-veraison and increased root water uptake, whole-plant hydraulic conductance, leaf transpiration, stomatal conductance, and photosynthesis, but decreased intrinsic gas exchange efficiency without causing differences in leaf xylem abscisic acid (ABA) concentration. Compared with DI-2, PRD-2 increased leaf xylem ABA concentration and decreased root water uptake, whole-plant hydraulic conductance, leaf transpiration, stomatal conductance, and photosynthesis, mainly at the beginning of PRD cycles. Distinctive PRD effects (e.g. greater stomatal closure) depended on the volumetric soil water content of the wet root zone, as predicted from a model of root-to-shoot ABA signalling.

Key words: ABA signalling, deficit irrigation, leaf water relations, partial root zone drying, root water uptake, soil water content.

Introduction

Roots in drying soil produce chemical signals such as abscisic acid (ABA) (Davies and Zhang, 1991) that can be transported to the shoots to modify their physiology. Early evidence for the existence of such signals was provided by experiments that split the root system between two pots. Plants that received irrigation to only one pot showed a similar leaf water status to those where both pots were well watered, yet stomata partially closed (Blackman and Davies, 1985) and leaf growth slowed (Gowing et al., 1990), ostensibly as a result of chemical signals transported from the roots in drying soil. Although this type of experiment has been repeated with many species, the magnitude of stomatal closure has been highly variable (reviewed in Holbrook et al., 2002), perhaps due to variation in the soil water content of the roots in ‘wet’ soil.

Recently, a model of root-to-shoot ABA signalling quantified the relationship between sap and ABA fluxes from different parts of the root system (Dodd et al., 2008a, 2008b) by grafting sunflower (Helianthus annuus L.) shoots onto the root systems of two plants grown in two separate pots.
and placing sap flow sensors on each hypocotyl (below the
graft union) of these ‘two-root one-shoot’ plants. Weighting
the ABA contributions of wet and dry root systems to leaf
xylem ABA concentration ([X-ABA]leaf) according to the
sap flow from each revealed an optimal dry pot soil water
status with a lower (Chaves et al., 2008a, b) predicted that effects of PRD would depend on root water uptake
from (and sap flow through) different parts of the root
system. Consequently, detailed spatial and temporal meas-
urements of soil water content, root water uptake from
different parts of the root zone, and [X-ABA]leaf were
necessary to interpret effects on root and leaf function.

Materials and methods

Experimental design

This research was carried out in a 1 ha vineyard at the CIFEA
experimental station in Jumilla, Murcia (SE Spain) (latitude
38°23′40″N, longitude 1°25′30″W, elevation, 350 m). The
climate is semi-arid Mediterranean, with hot and dry summers.
Rainfall at the experimental site averaged 310 mm year⁻¹ and
occurred mainly in the spring and autumn, and the average total
annual reference evapotranspiration (ETo) was 1240 mm. Vine
rows ran N-NW to S-SE and the planting density was 2.5 m
between rows and 1.25 m between vines (3200 vines ha⁻¹). The
study was performed on vines [Vitis vinifera L. Monastrell (syn.
Mourvedre) grafted on 1103 Paulsen: a vigorous and drought
tolerant rootstock (Alsina et al., 2011)] that were planted in 1997.
Irrigation water supplied from a local well had an electrical
conductivity of 1.6 dS m⁻¹. Five different irrigation treatments
were applied during three consecutive years (2006–2008) (Table 1),
from 1 April to 31 October in all years. The control treatment,
designed to obtain high productivity and to minimize vine water
stress during the whole season (April–October), received 60% ETo
crop evapotranspiration) throughout. PRD and DI treatments
were applied under drip irrigation, from just after fruit set (pea
size) (early June) until harvest (mid–late September) at 30% ETc
and 0.45 for mid-September to the end of October. Reference
evapotranspiration (ETo) values. The crop
coefficients applied were 0.35 in April, 0.45 in May, 0.5 in June, 0.75
in July and mid-August, 0.60 in the end of August to mid-September,
and 0.45 for mid-September to the end of October. Reference
evapotranspiration (ETc) was calculated weekly from the mean values
of the preceding 7–9 years using the Penman Monteith–FAO method
(Allen et al., 1998) and the daily climatic data collected in the
meteorological station located in the same experimental vineyard
belonging to the weather information service of Murcia (SIAM).

Irrigation was applied 3–5 times a week towards the end of the
day (21:00–01:00 h) and was controlled automatically by a head-
unit programmer and electro-hydraulic valves. All treatments

In this work, two different irrigation techniques (DI and
PRD) were compared at the same irrigation volumes,
aiming to distinguish effects of deficit irrigation per se (less
water) from any specific PRD effects (placement of water)
on vine physiology. Models of root-to-shoot ABA signal-
ing in split-root plants (Dodd et al., 2008a, b) revealed a further stimulus to
understand (and perhaps optimize) root-to-shoot ABA
signalling under field conditions by integrating both
physiological and agronomic research.
received the same annual fertilizer amounts (40 kg N, 20 kg P, 60 kg K, and 16 kg Mg ha⁻¹, and 1.6 g Fe chelate per vine) supplied through the irrigation system from April to July. Irrigation volumes applied to each treatment (Table 1) were measured with flow meters. Water was applied with two pressure-compensated emitters per plant (type RAM, 4 l h⁻¹), 62.5 cm apart, in one drip line per row for DI and control vines and on a double line per row for PRD vines. All drip lines were placed ~40 cm above ground. In each pipeline in PRD treatments, there were alternate zones with and without emitters, to create dry and wet root zones within each vine row (Fig. 1). In PRD treatments, water was supplied to only one part of the root system, alternating emitters every 14–16 d in 2006 and 2007 and every 6–8 d in 2008. In control and DI treatments, irrigation was supplied simultaneously to the entire root system. PRD treatments were applied throughout the whole season, comprising alternating cycles of PRD (switching irrigation on and off) during the year. The irrigation durations of PRD-1 and PRD-2 treatments were doubled compared with DI-1 and DI-2, respectively, to ensure the same irrigation volumes were applied.

### Soil water content

The soil was a 60 cm fine clay (48% clay, 30% silt, 22% sand) with 1.4% organic matter content, 18.8% active CaCO₃, EC sat (electrical conductivity) of 5.04 dS m⁻¹, and pH 7.6. Below 60–70 cm, the substrate was mainly a calcareous hard soil layer. Thirty-nine PVC tubes were installed in the vineyard in different treatments to measure soil water content periodically (Diviner) or continuously (C-probes) (see below). Although soil depth probably varied within the vineyard, <20% of the tubes could be installed deeper than 60 cm. In these cases, no root water uptake occurred at 70 cm in PRD-1 and PRD-2 vines (the only data available).

Volumetric soil water content (θ₉) was generally measured 3–4 times per week (although daily in specific periods) during the experiment with a Diviner 2000 portable soil moisture probe (Sentek Pty Ltd, Australia). PVC access tubes (5 cm diameter) were installed to a depth of 60–70 cm in one (control and DI) or both (PRD) parts of the root zone (Fig. 1). Readings were taken close to the vines, 10–15 cm from the drip head, at depths from 10 cm to 70 cm (maximum depth) for four replicates per treatments (one per block). Scaled frequency (SF) values were converted to θ₉ using a capacitance probe calibration equation (θ₉ = 47.38 SF⁻³, r² = 0.93) for clay soil (of similar texture to the vineyard soil in the present experiments) as previously proposed (Rose et al., 2001). Root water uptake rate (Δθ₀/Δt) was estimated at each depth as the changes occurring in θ₀ (with time) between two irrigation events.

In 2007 and 2008, θ₀ was also monitored using C-Probe™ FDR capacitance probes (C-Probe Corporation, Agrilink, Australia) with wireless radio telemetry (Adcon, Austria) and internet-based graphing software. PVC access tubes were installed for each probe in one (control and DI) or both (PRD) parts of the root zone, in one representative vine per treatment and placed 10–15 cm from the drip head (Fig. 1) and oriented perpendicularly to the drip lines, with sensors at depths of 10, 30, and 60 cm. Readings of θ₀ were taken every 15 min.

### Leaf water relations, gas exchange, and ABA signalling

Stem water potential (Ψₛ) was determined using a pressure chamber (Model 3000; Soil Moisture Equipment Corp., Santa Barbara, CA, USA) according to Scholander et al. (1965), weekly from the beginning of vegetative growth until leaf fall. Xylem sap osmotic pressure was not measured, but was negligible compared with the hydrostatic pressure (Lovisolo and Tramontini, 2010). Eight fully exposed and expanded mature leaves of the main shoots were taken per treatment (two leaves per block). Leaves were enclosed within foil-covered envelopes at least 2 h before measurement (McCutchan and Shackel, 1992).

On specific days in 2007 and 2008 (the morning after an evening irrigation), and after determining leaf water potential (Ψₛ), xylem sap was collected by applying an overpressure between 0.3 MPa and 0.5 MPa (using N) for 1–4 min and then lightly touching the cut petiole with a glass capillary tube. Sap was immediately transferred to an Eppendorf tube, frozen in liquid nitrogen, then stored at ~20 °C prior to ABA measurement with radioimmunoassay (Quarrie et al., 1988), using the monoclonal antibody AFRC MAC 252.

### Table 1. Irrigation systems used, deficit irrigation (DI) strategies, and annual applied water for each irrigation treatment during the experimental period (2006–2008)

| Treatment | Budburst to fruit set (early April to early June) | Fruit set to veraison (early June to end July) | Veraison to harvest (end July to mid-September) | Post-harvest (mid-September to end October) | Annual water applied (mm) |
|-----------|--------------------------------------------------|---------------------------------------------|-----------------------------------------------|--------------------------------------------|--------------------------|
| Control   | 60%                                              | 60%                                        | 60%                                          | 60%                                        | 318.5, 319.4, 285.7, 307.9 | 0.0, 38.0, 33.0, 53.0 |
| PRD-1     | 60%                                              | 30%                                        | 30%                                          | 45%                                        | 214.0, 199.9, 162.1, 192.0 | 38.0, 39.0, 38.0, 54.0 |
| DI-1      | 60%                                              | 30%                                        | 30%                                          | 45%                                        | 213.6, 197.5, 159.7, 190.3 | 38.0, 39.0, 38.0, 54.0 |
| PRD-2     | 60%                                              | 15%                                        | 15%                                          | 45%                                        | 157.6, 146.0, 122.3, 142.0 | 54.0, 55.0, 54.0, 56.0 |
| DI-2      | 60%                                              | 15%                                        | 15%                                          | 45%                                        | 174.2, 193.2, 122.9, 145.4 | 53.0, 54.0, 53.0, 55.0 |

%ETc is the percentage of crop evapotranspiration applied in each period.
During selected periods of maximum water stress in 2007, leaf water potential ($\Psi_l$) (in transpiring leaves) was measured at midday using the pressure chamber technique (as described above). After $\Psi_l$ measurements, the same leaves were covered with plastic bags, frozen and stored at $-20^\circ$C, thawed at room temperature ($20^\circ$C), and a vapour pressure osmometer (Wescor 5500, Logan, UT, USA) was used to measure osmolality (mmol kg$^{-1}$) of the cell sap expressed from a syringe. Osmolality was converted to osmotic potential ($\Psi_o$) (MPa) using the conversion factor $-0.002438$, according to the Van’t Hoff equation. Leaf turgor potential ($\Psi_t$) was calculated as the difference between $\Psi_l$ and $\Psi_o$.

Leaf relative water content (RWC) was measured at midday in transpiring leaves (similar to those used to measure $\Psi_l$ and $\Psi_t$) (two leaves per treatment and block). Sampled leaves were immediately weighed to determine fresh weight, and area was measured with a leaf area meter (Model 3000; Li-Cor, Lincoln, NE, USA). Leaves were rehydrated by submerging their petioles in deionized water for 24 h in the dark at 4°C to obtain turgid weight. Dry weight was calculated after drying the leaves to constant weight in an oven ($65^\circ$C for 48 h). RWC was calculated using the equation: RWC ($\%$) = [(fresh weight - dry weight)/(turgid weight - dry weight)] x 100.

Osmotic potential at full turgor ($\Psi_{o,full}$) at midday was measured in the same plants and in leaves similar to those used to measure RWC and $\Psi_t$. Twelve leaves per treatment (three leaves per treatment and block) were sampled, rehydrated to full turgor as described above, then immediately stored in a freezer at $-20^\circ$C for later determination of osmotic potential ($\Psi_o$) as described above.

Leaf gas exchange was measured between 09:00 h and 11:00 h weekly from April to October in all years on selected clear days. Measurements were made on healthy, fully expanded mature leaves exposed to the sun (one leaf on 8–12 vines per treatment), from main shoots in exterior mid–high canopy positions and close to those used to determine $\Psi_l$. Net CO$_2$ assimilation rate ($A$, mol m$^{-2}$ s$^{-1}$) and stomatal conductance to water vapour ($g_s$, cm$^{3}$ mol$^{-1}$ s$^{-1}$) were measured with a portable photosynthesis measurement system (LI-6400; Li-Cor) equipped with a broadleaf chamber (6 cm$^2$). During measurements, leaf chamber temperature was maintained between 25°C and 32°C, and relative humidity at 40–50%; thus leaf to air vapour pressure difference (VPD) was 2.0±0.5 kPa. Molar air flow rate inside the leaf chamber was 350 μmol mol$^{-1}$. All measurements were taken at a reference CO$_2$ concentration similar to ambient (380 μmol mol$^{-1}$) and at a saturating photosynthetic photon flux of 1500 μmol m$^{-2}$ s$^{-1}$ supplied by a red/blue light source (6400-02B LED) attached to the leaf chamber. On 7 July 2008 (pre-veraison) and 25 July 2008 (veraison) in 2008, [X-ABA] leaf, $\Psi_l$, $\Psi_t$, $A$, $E$, $g_s$, and $A/g_s$ were measured every 2–3 h in 3–4 leaves per treatment.

**Total leaf area development**

Post-veraison (early August) in all years, leaf area per vine was estimated by multiplying the average shoot-leaf area by the number of shoots on the vine for 16 vines per treatment (four per plot) using a non-destructive method. One representive shoot per vine (16 shoots per treatment) was chosen to measure main vein length of all leaves. A previous study (De la Hera et al., 2007) estimated leaf area (LI-3000, Li-Cor) of randomly selected leaves (12 shoots per treatment totalling ~200 leaves) to develop a linear regression equation that related main vein length (L) to leaf area (A) ($A = 22.10 \times L - 89.44$, $r^2 = 0.89$; $P < 0.001$, for main shoots; and $A = 18.39 \times L - 51.04$, $r^2 = 0.74$, $P < 0.001$ for lateral shoots).

**Whole-plant hydraulic conductance**

Plant hydraulic conductance ($K_{plant}$), the ratio of flow through the plant to the driving force for flow (Lo Gullo et al., 2003), was estimated at veraison in 2007 and 2008 using the ‘evaporative flux’ method (Nardini and Salles, 2000) based on Ohm’s law hydraulic analogue: $K_{plant} = E_{md}/(\Psi_{soil} - \Psi_{min})$, where $E_{md}$ is the maximum transpiration rate and $\Psi_{soil} - \Psi_{min}$ are soil and minimum diurnal leaf water potential, respectively. It was assumed that soil water potential was equal to pre-dawn leaf water potential (Lovisolo and Tramontini, 2010) while $E_{md}$ and $\Psi_{min}$ were measured between 12:00 h and 17:00 h, since plants are likely to have transpired the available soil water during this time (Lo Gullo et al., 2003). $K_{plant}$ was then scaled to total vine leaf area, following non-destructive measurements of total leaf area in the same vines used for hydraulic measurements.

**Statistical analysis**

Data were analysed using analysis of variance (ANOVA) procedures and means were separated by Duncan’s Multiple Range Test using Statgraphics 2.0 Plus software (Statistical Graphics Corp., USA). Linear regressions were fitted using SigmaPlot 2000 (Systat, Richmond, CA, USA).

**Results**

**Seasonal patterns of soil water content**

In the control treatment, volumetric soil water content (θ$_v$) at 0–60 cm depth was maintained close to field capacity, averaging 31% in 2007 and 30% in 2008 (Table 2). PRD treatments showed the expected cyclical patterns of drying and rewatering, with θ$_v$ (dry) significantly lower than θ$_v$ (wet) (Fig. 2). Longer drying cycles in 2007 (14–16 d) than in 2008 (6–8 d) dired more of the soil profile (to 40 cm depth in PRD-1 vines; data not shown) and magnified differences between θ$_v$ (dry) and θ$_v$ (wet). These differences were greater in PRD-1 vines as the irrigated root zone was wetter, while θ$_v$ at 0–30 cm depth was similar in PRD-1 and PRD-2 vines (Table 2) (Figure 2C, D).

Irrigated soil of PRD-1 vines was significantly wetter than DI-1 and other treatments in both the upper (0–30 cm where fine root density was greatest) and entire measurable (0–60 cm) parts of the soil profile (Table 2). Although average soil water content (in dry and wet parts) of the upper soil layers (0–30 cm) of PRD-1 vines was generally lower than in the DI-1 treatment, it was significantly higher when considering more of the soil profile (0–60 cm), indicating deeper water percolation through the soil under PRD-1 vines.

In both years, PRD-2 vines maintained θ$_v$ (wet) similar to DI-2 vines (Table 2). In contrast, average soil water content (dry and wet) in the entire soil profile (0–60 cm) of PRD-2 vines was generally lower than in DI-2 vines, indicative of lower total soil water availability in the entire root zone (Table 2).

**Root water uptake**

Although total root water uptake ($\Delta \theta_v/\Delta t$) of PRD-1 vines (adding wet and dry parts and averaged across all cycles) was less than that of DI-1 vines at 10 cm depth and similar at 20 cm depth, it was significantly higher at 30–40 cm (Fig. 3A). Thus total $\Delta \theta_v/\Delta t$ (at 0–30 cm) was similar to that of DI-1 vines, but significantly higher at 40–60 cm (Fig. 3A). PRD-1 vines showed a significantly higher root water extraction in the wet irrigated zone, (especially between 20 cm and 40 cm depth) compared with DI-1 vines (in 2007, Fig. 3A; and in 2008, data not shown), associated with a higher soil water content than DI-1 (Table 2). In contrast,
Table 2. Mean volumetric soil water content (θv) of the upper soil layers (0–30 cm) and entire soil profile (0–60 cm) and the average θv (mean of dry and root zones) for each treatment in two important phenological periods in 2007 and 2008. Each value is the average of different days of measurement in each period where each measurement is the mean of four vines (one soil moisture probe per vine) in each treatment.

| Treatment         | Fruit set–veraison (early June–End July 2007) | Veraison–harvest (end July–mid September 2007) | Fruit set–veraison (early June–End July 2008) | Veraison–harvest (end July–mid September 2008) |
|-------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|
|                   | θv (%) (0–30 cm)                              | θv (%) (0–60 cm)                               | θv (%) (0–30 cm)                              | θv (%) (0–60 cm)                               |
| Control (60% ETc) | 27.3 b                                        | 31.0 b                                        | 27.3 b                                        | 31.4 b                                        |
| PRD-1 (θv-dry)    | 17.7 f                                        | 26.3 d                                        | 18.2 f                                        | 26.8 d                                        |
| PRD-1 (θv-wet)    | 29.0 a                                        | 32.7 a                                        | 29.9 a                                        | 32.9 a                                        |
| PRD-1 (average θv)| 23.4 d                                        | 29.5 c                                        | 23.8 d                                        | 29.7 c                                        |
| DI-1              | 25.6 c                                        | 26.2 d                                        | 26.4 b,c                                      | 26.9 d                                        |
| PRD-2 (θv-dry)    | 17.9 f                                        | 23.1 f                                        | 18.6 f                                        | 23.2 f                                        |
| PRD-2 (θv-wet)    | 24.5 c,d                                      | 26.0 d                                        | 24.6 d                                        | 26.0 d,e                                      |
| PRD-2 (average θv)| 21.1 e                                        | 24.2 e                                        | 21.4 e                                        | 24.1 f                                        |
| DI-2              | 24.0 d                                        | 25.8 d                                        | 25.4 c,d                                      | 25.7 e                                        |
| ANOVA             | ***                                          | ***                                          | ***                                          | ***                                          |

***P < 0.001; in each column, values followed by different letters are significantly different according to Duncan’s multiple range test at the 95% confidence level.

Pre-veraison water stress period 2007 (14 days, July, 7th - July, 20th)

Fig. 2. Continuously reported volumetric soil water content (θv) at 30 cm depth using soil capacitance C-probes during a PRD cycle in 2007 (A, B). Measurements were taken every 15 min in both root zones of one representative vine per PRD treatment. Discrete measurements of volumetric soil water content θv (10–30 cm) using Diviner 2000 (C, D) during a representative PRD cycle in 2007. In C and D, each point is the mean ±SE of four measurements. Vertical dashed lines indicate the start and finish of the PRD cycle.
although $\Delta \theta_v/\Delta t$ in the irrigated root zones was similar in PRD-2 and DI-2 vines at all measured depths (Fig. 3B), total $\Delta \theta_v/\Delta t$ of PRD-2 vines was lower, mainly due to less water extraction from the upper soil layers (Fig. 3B). PRD-2 also showed a slower recovery of $\theta_v$ at 30 cm than PRD-1 after rewatering (Fig. 2A, B).

Continuous records of soil water content at 30 cm depth (in 2007) in the drying root zone showed a progressive decrease in daily root water extraction with increased soil drying (Fig. 2A, B). Detailed temporal analysis showed that during the first week of soil drying, PRD-1 vines had a lower $\theta_{v\text{-dry}}$ but similar root water uptake rate ($\Delta \theta_v/\Delta t$) to DI-1 vines (Fig. 3C). However, PRD-2 vines had a significantly lower total $\Delta \theta_v/\Delta t$ (0–60 cm) in the dry root zone compared with other treatments, in agreement with the significantly lower soil water content (Fig. 3C). Another week of soil drying further reduced $\theta_{v\text{-dry}}$ and $\Delta \theta_v/\Delta t$ to similar low levels in PRD-1 and PRD-2 treatments (Fig. 3D).

During the first half of the shorter soil drying cycles imposed in 2008, PRD-1 vines maintained similar $\theta_{v\text{-dry}}$ and

**Fig. 3.** Root water uptake rate ($\Delta \theta_v/\Delta t$) for DI-1 and PRD-1 (A) and DI-2 and PRD-2 (B) vines at each depth during 2007. Each bar represents the mean of four vines per treatment during nine irrigation cycles (from May to September), with SEs not indicated for clarity. Root water uptake rate ($\Delta \theta_v/\Delta t$) in the drying root zone, during the first and second week of drying in 2007 (C, D) and during the first and last 3–4 d in 2008 (E, F). Bold values represent mean values of volumetric soil water content ($\theta_v$) maintained in the dry root zone (0–30 cm, more active root-zone). In C–F, mean values of $\theta_v$ and $\Delta \theta_v/\Delta t$ were calculated with nine and six PRD cycles in 2007 and 2008, respectively. Treatment differences are indicated thus: ns, not significant; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. 

| Depth (cm) | Root water uptake rate ($\Delta \theta_v/\Delta t$) (mm day$^{-1}$) |
|-----------|---------------------------------------------------------------|
| 0–30 cm   | DI-1: 13.5** PRD-1: 12.4                                      |
| 40–60 cm  | DI-2: 11.7** PRD-2: 6.3                                       |

| Depth (cm) | Root water uptake rate ($\Delta \theta_v/\Delta t$) (mm day$^{-1}$) |
|-----------|---------------------------------------------------------------|
| 0–30 cm   | DI-1: 0.32** PRD-1: 2.65                                      |
| 40–60 cm  | DI-2: 1.5** PRD-2: 1.4                                        |
Seasonal variation in plant performance

DI and PRD plants receiving the same irrigation volumes maintained a similar \( \Psi_0 \) (Table 3), but \( K_{\text{plant}} \), \( \Psi_0 \), and \( g_s \) in 2007, and \( K_{\text{plant}} \), \( \Psi_0 \), and \( g_s \) in 2008 were significantly less in DI-1 than in PRD-1 vines (Table 3). The latter treatment maintained similar gas exchange to control vines. Also, \( A/g_s \) was higher in DI-1 than in PRD-1 and control vines (Table 3). This stomatal response was maintained post-veraison (~2 months) in 2008 (data not shown). Interestingly, PRD-1 vines also showed a significantly higher total leaf area than DI-1 vines when measured post-veraison (Fig. 4). However, there were no significant differences in total leaf area, vine water status, and gas exchange between PRD-2 and DI-2 vines, although in 2008 PRD-2 vines exhibited significantly lower \( K_{\text{plant}} \) (18% lower) than DI-2 vines (Table 3).

Treatments also varied significantly in leaf xylem sap ABA concentration ([X-ABA]_{\text{leaf}}) when measured during the morning at the end of the PRD cycle in 2007 and at the beginning of the PRD cycle in 2008. Control vines always showed the lowest [X-ABA]_{\text{leaf}} and there were no significant differences between PRD-1 and DI-1 vines. Interestingly, PRD-2 vines always had the highest [X-ABA]_{\text{leaf}}, which was significantly higher than DI-2 and other treatments in 2008 and the controls in 2007 (Table 3).

Table 3. Average values of \( K_{\text{plant}} \), [X-ABA]_{\text{leaf}}, \( \Psi_0 \), \( A \), \( E \), \( g_s \), and \( A/g_s \), maintained during a typical whole PRD cycle at veraison in 2007 (22 July–6 August 2007, 16 d PRD cycle) and 2008 (25 July–1 August 2008, 8 d PRD cycle)

| Year | Treatment | \( K_{\text{plant}} \) | [X-ABA]_{\text{leaf}} | \( \Psi_0 \) | \( A \) | \( E \) | \( g_s \) | \( A/g_s \) |
|------|-----------|-----------------|-----------------|-------------|------|------|------|-------|
| 2007 | Control   | 0.61 a           | 223 a           | -1.23 a     | 12.9 a | 4.83 a | 0.182 a | 72.5 a |
|      | PRD-1     | 0.66 a           | 268 a,b         | -1.37 b     | 12.0 a,b | 4.50 b | 0.163 a | 74.6 b |
|      | DI-1      | 0.44 b           | 370 a,b         | -1.37 b     | 11.0 b,c | 3.81 b,c | 0.138 b | 82.0 a,b,c |
|      | PRD-2     | 0.34 b           | 447 b           | -1.38 b     | 8.8 d   | 2.99 d   | 0.104 c | 86.5 c |
|      | DI-2      | 0.41 b           | 339 a,b         | -1.39 b     | 10.0 c,d | 3.31 c,d | 0.119 b,c | 86.0 b,c |
|      | ANOVA     | **               | *               | ***         | ***   | ***   | ***   | ***   |
| 2008 | Control   | 0.56 a           | 427 a           | -1.33 a     | 15.3 a | 4.5 a   | 0.23 a | 69.8 a |
|      | PRD-1     | 0.41 b           | 705 b           | -1.39 a,b   | 14.6 a | 4.3 a  | 0.20 a | 75.8 a |
|      | DI-1      | 0.21 d           | 618 b           | -1.36 a,b   | 12.2b   | 3.3 b   | 0.14 b | 95.2 b |
|      | PRD-2     | 0.20 d           | 893 c           | -1.47 b,c   | 10.3 c | 2.9 b   | 0.11 b | 101.0 b |
|      | DI-2      | 0.30 c           | 712 b           | -1.51 c     | 11.1   | 3.1 b   | 0.12 b | 95.9 b |
|      | ANOVA     | ***              | **              | ***         | ***   | ***   | ***   | ***   |

\(< P < 0.05; **P < 0.01; ***P < 0.001. In each column, values followed by different letters are significantly different according to Duncan’s multiple range test at the 95% confidence level.

\( K_{\text{plant}} \), whole vine hydraulic conductance (g MPa\(^{-1}\) s\(^{-1}\)); [X-ABA]_{\text{leaf}}, xylem sap ABA concentration (nM); \( \Psi_0 \), mid-day stem water potential (MPa); \( A \), net photosynthesis rate (\( \mu \text{mol} \text{ m}^{-2} \text{s}^{-1} \)); \( E \), transpiration rate (\( \text{mmol} \text{ m}^{-2} \text{s}^{-1} \)); \( g_s \), stomatal conductance (mol m\(^{-2}\) s\(^{-1}\)).
disappeared or were attenuated at the end of the PRD cycles (Table 4).

Pre-veraison, leaf water potential declined as irrigation volume declined, with no significant differences between PRD and DI treatments (Table 5). Similarly, leaf osmotic potential, turgor potential, and RWC were not clearly affected by irrigation placement either pre- or post-veraison (Table 5), although RWC was significantly higher in control vines pre-veraison, and control, PRD-1, and DI-1 vines post-veraison. Pre-veraison, osmotic potential at full turgor was significantly lower in DI and PRD treatments compared with the control, although osmotic adjustment was limited (0.28 MPa), and this effect was not detected post-veraison (Table 5).

Diurnal changes in leaf water relations, gas exchange, and ABA signalling

Throughout a typical day during a period of severe water stress (25 July 2008, <24 h after alternating wet and dry root zones), stem water potential and gas exchange of PRD-1 vines was significantly higher than those of DI-1 vines, and more similar to those of control vines (Fig. 5C,

### Table 4. Transitory effects of PRD on leaf water status and gas exchange at the beginning and end of PRD cycles in 2007 and 2008

Mean values were calculated from measurements of 4–6 PRD cycles during the growing season.

| Year | Treatment | Fruit set to harvest 2007 (14–16 d PRD cycles) | Fruit set to harvest 2008 (6–8 d PRD cycles) |
|------|-----------|--------------------------------------------|--------------------------------------------|
|      |           | 1–5 d after alternating wet and dry sides in PRD | 1–2 d after switching on/off PRD cycle | 6–8 d after switching on/off PRD cycle |
|      |           | $\Psi_s$ | $A$ | $g_s$ | $E$ | $\Psi_s$ | $A$ | $g_s$ | $E$ |
| 2007 | Control   | –1.09 a | 13.36 a | 0.189 a | 3.83 a | –1.06 a | 13.43 a | 0.173 a | 3.47 a |
|      | PRD-1     | –1.23 b | 11.43 b | 0.160 b | 3.44 a | –1.26 b | 12.10 b | 0.142 b | 2.93 b |
|      | DI-1      | –1.26 b | 11.46 b | 0.144 b | 2.96 b | –1.26 b | 11.85 b | 0.136 b | 2.82 b |
|      | PRD-2     | –1.34 c | 9.24 c  | 0.116 c | 2.51 c | –1.34 c | 9.72 c  | 0.109 c | 2.29 c |
|      | DI-2      | –1.33 c | 9.70 c  | 0.116 c | 2.54 c | –1.32 b | 9.89 c  | 0.110 c | 2.35 c |
|      | ANOVA     | ***     | ***     | ***     | ***     | ***     | ***     | ***     | ***     |

| 2008 | Control   | –1.15 a | 15.29 a | 0.227 a | 4.49 a | –1.12 a | 14.46 a | 0.205 a | 4.29 a |
|      | PRD-1     | –1.26 b | 13.98 a,b | 0.179 b | 3.90 b | –1.25 b | 13.42 a,b | 0.178 b | 3.94 a,b |
|      | DI-1      | –1.27 b,c | 13.01 b,c | 0.158 b,c | 3.58 b,c | –1.26 b | 12.70 b,c | 0.160 b,c | 3.70 b,c |
|      | PRD-2     | –1.33 c | 10.49 d | 0.110 d | 2.75 d | –1.35 c | 11.07 d | 0.124 d | 3.12 d |
|      | DI-2      | –1.33 b,c | 11.99 c | 0.140 c | 2.32 c | –1.29 b,c | 11.62 c,d | 0.139 c,d | 3.34 c,d |
|      | ANOVA     | ***     | ***     | ***     | ***     | ***     | ***     | ***     | ***     |

*** $P < 0.001$. For each column, values followed by different letters are significantly different according to Duncan’s multiple range test at the 95% confidence level.

$\Psi_s$, mid-day stem water potential, MPa; $A$, net photosynthesis rate, $\mu$mol $m^{-2}s^{-1}$; $E$, transpiration rate, $mmol m^{-2}s^{-1}$; $g_s$, stomatal conductance, $mol m^{-2}s^{-1}$.

### Table 5. Leaf water relations parameters of the different irrigation treatments in the most severe water stress periods during pre- and post-veraison in 2007

| Treatment | Pre-veraison (6–10 July 2007) | Post-veraison (10–13 August 2007) |
|-----------|-------------------------------|-----------------------------------|
|           | $\Psi_l$ (MPa) | $\Psi_m$ (MPa) | $\Psi_t$ (MPa) | RWC (%) | $\Psi_{100}^m$ (MPa) | RWC (%) | $\Psi_{100}^m$ (MPa) |
| Control   | –1.35 a | –1.89 | 0.54 | 91.6 a | –1.07 a | 94.4 a | –1.53 |
| PRD-1     | –1.44 b | –2.01 | 0.58 | 90.3 b | –1.35 b | 93.5 a,b | –1.48 |
| DI-1      | –1.49 b,c | –2.10 | 0.62 | 89.9 b | –1.34 b | 94.6 a | –1.55 |
| PRD-2     | –1.53 c | –2.11 | 0.58 | 89.8 b | –1.39 b | 92.7 b | –1.54 |
| DI-2      | –1.55 c | –2.11 | 0.56 | 89.7 b | –1.40 b | 92.8 b | –1.58 |
| ANOVA     | ***     | NS     | NS     | *       | *       | *       | NS     |

NS, not significant. * $P < 0.05$; *** $P < 0.001$. For each column, values followed by different letters are significantly different according to Duncan’s multiple range test at the 95% confidence level.

$\Psi_l$, mid-day leaf water potential; $\Psi_s$, leaf osmotic potential; $\Psi_t$, leaf turgor potential; RWC, relative water content; $\Psi_{100}^m$, leaf osmotic potential at full turgor.
Fig. 5. Diurnal course of (A, B) [X-ABA]_leaf, (C, D) stem water potential (Ψ_s), (E, F) leaf photosynthesis rate (A), (H, I) stomatal conductance (g_s), (J, K) leaf transpiration rate, and (L, M) intrinsic water use efficiency (A/g_s) at veraison on 25 July 2008, the day following irrigation and alternation of wet and dry sides in PRD plants, for each irrigation treatment. Each point is the mean ± SE of four measurements (one per plot).
E, H, J). Differences in $A$ and $g_s$ between PRD-1 and DI-1 vines were minimized at 14:00 h compared with mid-morning and afternoon, with PRD-1 vines showing faster evening recovery of gas exchange than DI-1 vines (Fig. 5E, H). However, $A/g_s$ of DI-1 vines was significantly higher than that of PRD-1 and control vines throughout the day (Fig. 5L). PRD-2 and DI-2 vines showed no significant differences in $\Psi_s$, $A$, and $g_s$, although mean leaf transpiration was significantly lower in PRD-2 than DI-2 vines during the day (Fig. 5K). In better-irrigated vines, mid-morning [X-ABA]leaf was lowest, while [X-ABA]leaf in PRD-2 and DI-2 vines was fairly constant throughout the day (Fig. 5A, B). Over the entire morning (9:00–15:00 h), mean [X-ABA]leaf was significantly higher in PRD-2 than in other treatments, with all deficit treatments higher than the control. Similar stomatal behaviour and ABA signalling to that described above was also observed after alternating wet and dry root zones of PRD vines throughout the morning of 7 July 2008 (Supplementary Fig. S1 available at JXB online). On this day, leaf water potential ($\Psi_l$), $g_s$, and $E$ significantly decreased, while $A/g_s$ significantly increased, as [X-ABA]leaf increased (Fig. 6).

**Discussion**

Partial root zone drying aims to impose soil moisture heterogeneity intentionally within the plant root zone (both spatially and temporally) to modulate root-to-shoot signalling, thereby altering shoot physiology. Yet PRD-specific physiological changes cannot always be discriminated (Marsal et al., 2008; Rodrigues et al., 2008; Intrigliolo and Castel, 2009), perhaps because heterogeneous distribution of soil moisture is not always achieved (Dodd et al., 2008b). While PRD may be more easily imposed on sandy soils that allow high infiltration rates and deep root zones (Kriedemann and Goodwin, 2003) than on poorly structured, shallower clay soils (Stewart, 2005), significant spatial and temporal variation of $\theta_s$ occurred throughout most of the growing season (Table 2). The extent of upper soil drying by PRD vines depended on drying cycle duration.

It is uncertain whether roots exposed to drying soil for long periods can survive and remain physiologically active, or lose contact with the soil and thus their ability to sense the rhizosphere environment. Root function was not irreversibly damaged despite root water uptake progressively decreasing with $\theta_s$ (minimal $\theta_s$ coincided with the lowest or no further water uptake; Fig. 2), as rewatering allowed complete recovery of water uptake. This recovery was slower in PRD-2 (2–3 d) than in PRD-1 vines (1 d) (cf. Fig. 2A, B) even though a similar minimum $\theta_s$-dry (Fig. 2C, D) was attained, probably due to different irrigation volumes applied during rewatering. Initiation of new secondary roots by rewatering (Kang and Zhang, 2004) may facilitate this recovery, and ensure sensitive responses to subsequent soil drying episodes.

Theoretically, the ‘wet’ side of PRD plants should receive sufficient water to prevent excessive soil drying and maintain a favourable plant water status (Dry et al., 2000a, b; Chaves and Oliveira, 2004). Although PRD-1 vines had

![Fig. 6. Relationships between leaf xylem sap ABA concentration and (A) leaf water potential ($\Psi_l$), (B) stomatal conductance ($g_s$), (C) transpiration rate ($E$), and (D) intrinsic water use efficiency ($A/g_s$). Each point is the mean of four replicates per treatment (one per plot). These paired measurements were made during the morning of 7 July 2008, immediately after starting a new PRD cycle. Linear regressions fitted to the data.](image-url)
Although irrigated parts of the root zone had similar heterogeneity during soil drying (Fig. 3A) as previously observed (Kriedemann et al., 2003; Gu et al., 2004; Collins et al., 2010), indicating a larger and deeper root system than DI-1 vines. Greater water uptake from roots in the wet part of the root zone in PRD-1 vines (compared with DI-1), especially between 20 cm and 40 cm deep (Fig. 3A), compensated for diminished water uptake from drier soil (Kang et al., 2002; Hu et al., 2011). Increased root hydraulic conductance of plants grown with PRD (Kang et al., 2003), putative ABA-mediated stimulation of aquaporin activity (Lovisolo et al., 2010), and induction of new roots after drying and rewetting cycles (Kang and Zhang, 2004) may be involved.

Altered spatial distribution of root water uptake, and increased whole-plant hydraulic conductance (Table 3), supported higher daily leaf water use and photosynthesis (Tables 3, 4, Fig. 5) of PRD-1 vines, but decreased transpiration efficiency (expressed as A/La). Whereas PRD often inhibits canopy leaf area and water use, and increases water use efficiency (Stoll et al., 2000; Davies et al., 2002; Santos et al., 2003; Kang and Zhang 2004; Chaves et al., 2007, 2010), greater water uptake, increased plant hydraulic conductance and leaf area, and larger canopy water use by PRD-1 vines probably reflected a greater ability of root systems to capture water (Alsina et al., 2011).

Differences in leaf turgor (Table 5) or [X-ABA]leaf (Table 3) could not account for the greater water use of PRD-1 vines. Indeed, greater water extraction from the upper layers in the wet root zone and from deeper and wetter soil layers probably diluted the ABA signal generated by roots in contact with drier soil, thereby resulting in similar [X-ABA]leaf of PRD-1 and DI-1 vines. Other non-hydraulic (cytokinins, xylem sap pH) signals and their interactions may also be involved in regulating leaf water use under PRD (Kudoyarova et al., 2007).

The responses of PRD-2 vines were more typical. Although irrigated parts of the root zone had similar \( \theta_{v\text{-wet}} \) in DI-2 and PRD-2 vines, overall the latter had less soil water available (Table 2), decreasing root water uptake from the upper soil layers and whole-plant hydraulic conductance (in 2008, Table 3). For PRD-2 vines, active roots mostly located in the upper layers (mainly at 10–30 cm) were unable to compensate by increasing water uptake from the irrigated root zone. Nevertheless, leaf water relations were similar between PRD-2 and DI-2 vines (Table 5), and the enhanced transient stomatal closure of PRD-2 vines may be due to differences in root-to-shoot ABA signalling since leaf gas exchange and [X-ABA]leaf were significantly correlated (Fig. 6). Increased [X-ABA]leaf of PRD-2 vines compared with the other treatments (Table 3) could be due to lower root water uptake (a sap concentration effect) and/or increased root ABA biosynthesis (a PRD effect) (Fig. 3C–F).

Contrasting stomatal behaviour between PRD and DI plants receiving the same irrigation volumes occurred mainly at the beginning of PRD cycles after alternation of wet and dry parts of the root zone, and was attenuated by the end of the PRD cycles (Table 4). Restricted leaf water use immediately following irrigation alternation in PRD-2 vines was closely correlated with transient (<24 h) increases in [X-ABA]leaf (Fig. 5, and Fig. S1, supporting information) and seemingly paralleled the resumption of water uptake from roots that had been in drying soil (Fig. 2). These results apparently support the hypothesis that rewatering the dry part of the root system transiently increased [X-ABA]leaf as the root ABA pool accumulated during soil drying was liberated to the transpiration stream once these roots again contributed proportionally more to total sap flow (Dodd et al., 2006, 2008a). However, root ABA export probably decreased towards the end of the drying cycles as progressive soil drying limited sap flow (and root water uptake) from those roots (Fig. 3A, B) as predicted from laboratory studies (Dodd et al., 2008a, b), causing similar stomatal behaviour of PRD and DI plants.

To conclude, distinctive physiological effects of PRD (compared with DI treatments receiving the same irrigation volumes) depended on the total soil water content available. Compared with DI-1, ample irrigation of the wet root zone in PRD-1 vines (\( \theta_{v\text{-wet}} 29–33\% \), close to field capacity) and deeper water percolation maintained deeper root water uptake, better hydraulic supply (higher \( K_{\text{plant}} \)), higher leaf area, and high transpirational fluxes. In contrast, less irrigation of the wet root zone in PRD-2 vines (\( \theta_{v\text{-wet}} \) 22–26%) prevented deep percolation and probably deeper root proliferation, decreasing total root water uptake, \( K_{\text{plant}} \), and leaf water use compared with DI-2 vines. The higher [X-ABA]leaf of PRD-2 (than PRD-1) plants despite a similar \( \theta_{v\text{-dry}} \) indicates that their stomatal behaviour was more closely related to \( \theta_{v\text{-wet}} \) (as predicted by a model of sap flow during PRD; Dodd et al. 2008a, b). Thus \( \theta_{v\text{-wet}}, [X-ABA]_{\text{leaf}}, \) and gas exchange of PRD vines were closely correlated, while \( \theta_{v\text{-dry}} \) and [X-ABA]leaf were not. Irrigation frequencies and volumes to the wet part of the root system seem critical to operating this irrigation technique successfully to increase root-to-shoot ABA signalling and crop water use efficiency. Further research will determine whether these distinctive PRD-specific physiological changes alter berry composition and wine quality.

**Supplementary data**

Supplementary data are available at JXB online.

**Figure S1.** Diurnal course of [X-ABA]leaf, mid-day stem water potential, leaf photosynthesis rate, stomatal conductance, leaf transpiration rate, and intrinsic water use efficiency on 7 July 2008 (the day following irrigation and alternation of wet and dry sides in PRD plants) for each irrigation treatment.
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