

1 **Physiological response of post-veraison deficit irrigation strategies and**
2 **growth patterns of table grapes (cv. Crimson Seedless)**

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28 **Running title:** Comparing PRD and RDI strategies in table grapes

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33 **Abstract**

34 To determine whether partial root-zone drying (PRD) offers physiological advantages
35 compared with regulated deficit irrigation (RDI), a 3 year long-experiment was
36 conducted on a commercial vineyard of ‘Crimson Seedless’ table grapes (*Vitis vinifera*
37 *L.*). Four different drip irrigation treatments were imposed: (i) a Control treatment
38 irrigated at 110% of seasonal crop evapotranspiration (ET_c), (ii), a regulated deficit
39 irrigation (RDI) treatment irrigated similar to Control before veraison and at 50% of the
40 Control treatment post-veraison, (iii) a partial root-zone drying (PRD) irrigated similar
41 to RDI but alternating (every 10-14 days) the dry and wet side of the root-zone, and (iv)
42 a null irrigation treatment (NI) which only received the natural precipitation and
43 occasional supplementary irrigation when midday stem water potential (Ψ_s) dropped
44 below -1.2 MPa. Post-veraison, PRD vines accumulated greater localized soil and plant
45 water deficit at midday than RDI vines, but maintained similar pre-dawn water potential
46 (Ψ_{pd}) values. Stomatal conductance (g_s) of PRD vines remained high, likely because
47 there was sufficient root water uptake from irrigated soil. Xylem ABA concentration
48 ($[ABA]_{xylem}$) did not change yet intrinsic WUE (WUE_i) decreased compared to RDI
49 vines, probably because PRD induce greater root density and root development
50 Vegetative growth was only decreased by severe deficit irrigation (NI) although total
51 leaf area index (LAI) was also affected in PRD in the 1st and 3rd year. PRD can be
52 considered a useful strategy in semiarid areas with limited water resources because
53 sustained water use maintained assimilation rates despite greater stress than
54 conventional RDI strategy, which may be related to root and morphological adjustment.

55 **Keywords:** Partial root-zone drying; leaf gas exchange; water relations; leaf area index;
56 $[ABA]_{xylem}$; *Vitis vinifera*

57 **Abbreviations:** DI, deficit irrigation; RDI, regulated deficit irrigation; PRD, partial
58 root-zone drying, A, net CO₂ assimilation rate; g_s, stomatal conductance; E, transpiration
59 rate; A/g_s, intrinsic water use efficiency; [ABA]_{xylem}, xylem abscisic acid concentration;
60 S-ABA, exogenous abscisic acid; θ_v, soil volumetric water content; Ψ_{stem}, stem water
61 potential at midday, Ψ_{pd}, predawn leaf water potential; Ψ_o, predawn leaf osmotic
62 potential; Ψ_{os}, predawn leaf osmotic potential at full turgor; Ψ_t, predawn leaf turgor
63 potential; LAI, leaf area index; TCSA, trunk cross-section area; ΔTCSA, annual
64 increment trunk-section area; PE, productivity efficiency.

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79 **1. INTRODUCTION**

80 Irrigated agriculture is known as the primary user of diverted water globally,
81 reaching a proportion that exceeds 70–80% of the total in arid and semiarid zones. Since
82 water withdrawals are forecast to sharply increase in the future, it is obvious that
83 irrigated agriculture will become a primary consumer of water especially in emergency
84 drought situations (Williams et al., 2010a,b). Moreover, other factors such as the
85 booming global population and the progress of climate change will require increased
86 food production under water deficit situations. Therefore, the challenge for the coming
87 years will be to increase or at least maintain fruit production and quality with less
88 irrigation water, which could be achieved by implementing different irrigation strategies
89 that enhance irrigation water efficiency.

90 Table grapes need more water than grapevines because they require a greater
91 leaf area to supply photoassimilates to developing berries, allowing large berries for
92 fresh consumption (Williams and Ayars, 2005; Silva-Contreras et al., 2012). Thus, the
93 determination of crop water requirements is essential to apply deficit irrigation (DI). In
94 fact, the demand for seedless varieties (e.g. ‘Crimson Seedless’) has increased
95 considerably in recent years as a result of increased international demand and new
96 plantings.

97 Applying deficit irrigation (DI) practices can limit irrigation requirements while
98 maintaining the yield and quality standards required by the fruit market (Ruiz-Sánchez
99 et al., 2010, Pérez-Pastor et al., 2016). Two main techniques are regulated deficit
100 irrigation (RDI) and partial root-zone drying (PRD). Both supply less irrigation during
101 periods of the growing season when the crop is less sensitive to fruit growth (Chalmers
102 et al., 1981; Dry et al., 1996). In this sense, table grapes are generally considered
103 sensitive to water stress from fruit setting to veraison, since this determines the final

104 yield and fruit quality. Thus, RDI and PRD should be applied post-veraison to minimise
105 adverse effects on productivity (Conesa et al., 2016a).

106 Soil water deficit imposed by DI techniques alters vine physiology and plant
107 hydraulic and chemical signalling systems, thereby affording commercial benefits such
108 as increased water use efficiency (WUE) and decreased vegetative vigour (Romero et
109 al., 2014). Stomatal conductance (gs) can be decreased by the synthesis of chemical
110 signals (predominantly abscisic acid - ABA) in the roots in response to drying soil, and
111 their subsequent transport to the leaves via the transpiration stream to effect stomatal
112 closure (Dodd et al., 2015; Puértolas et al., 2015). During PRD, typically one part of the
113 root-zone is irrigated at a time, with the wet and dry parts of the root zone periodically
114 alternated to transiently enhance ABA signalling (Dodd et al., 2006) and/or prevent
115 excessive soil drying diminishing the transport of chemical signals to the shoot (Romero
116 et al., 2012). ABA-induced stomatal closure limits transpiration and xylem cavitation
117 (Beis and Patakas, 2010), even though prolonged stomatal closure also limits
118 photosynthetic activity by decreasing Rubisco carboxylation activity (Chaves et al.,
119 2010; Salazar-Parra et al., 2015). Conversely, prolonged soil drying cycles during PRD
120 may limit ABA transport from roots in drying soil (Pérez-Pérez and Dodd, 2015),
121 thereby minimising stomatal limitation of photosynthesis (Downton et al., 1988), which
122 may enhance yield of PRD plants compared to conventional RDI plants (Antolín et al.,
123 2006; Dodd, 2009). Thus, it is not clear whether ABA-induced stomatal closure (and
124 effects on photosynthetic carbon gain) is enhanced or attenuated by PRD relative to
125 RDI.

126 Typically, water stress limits leaf area expansion prior to any decrease in
127 photosynthetic assimilation (Beis and Patakas, 2015) and canopy development and
128 vegetative growth are more sensitive to water deficit than fruit growth. Insufficient

129 canopy development may also limit berry development in low vigour varieties (Ruiz-
130 Sánchez et al., 2010). Moreover, decreased vegetative growth under RDI or PRD might
131 be also due to limited cell expansion mediated by lower cellular turgor (Chaves et al.,
132 2010). When PRD and RDI vines received the same irrigation volumes, only subtle
133 differences in leaf water relations, WUE, crop yield and fruit quality were detected (dos
134 Santos et al., 2005; de Souza et al., 2005; Romero et al., 2012). However, in some cases,
135 PRD vines appeared to maintain higher water status with a lower (Chaves et al., 2010;
136 Rodrigues et al., 2008), higher (Antolín et al., 2006), or similar (Antolín et al., 2008)
137 leaf area than RDI vines. Therefore, it is not clear whether leaf water relations are
138 regulating canopy development (Lovisolo et al., 2010) or *vice versa*.

139 Earlier studies that compared PRD and RDI under the same irrigation volumes
140 revealed differential physiological and biochemical responses in wine grapes (Romero
141 et al., 2012, 2014; Beis and Patakas, 2015), but there is little information on table
142 grapes. While there is no reason to suppose table grapes and wine grapes should differ
143 in their physiological responses to PRD and RDI, irrigation is typically withheld from
144 table grapes post-veraison (Conesa et al., 2016a; Pinillos et al., 2016) and from wine
145 grapes throughout berry development (Chaves et al., 2010; Costello and Patterson,
146 2012). Interestingly, stomatal closure of winegrapes was less sensitive to ABA post-
147 veraison (dos Santos et al., 2005), suggesting that the timing of deficit irrigation may
148 modify stomatal responses (Torres-Ruiz et al., 2016). Furthermore, grower
149 implementation of PRD in favour of conventional RDI requires positive agronomic
150 effects, especially due to higher costs of infrastructure installation and complex
151 irrigation management (Marsal et al., 2008; García García et al., 2012; Romero et al.,
152 2016; Permanhani et al., 2016). Nevertheless, PRD enhanced berry coloration and
153 health-promoting bioactive compounds (e.g. anthocyanins, resveratrol and antioxidant

154 capacity) compared to RDI in the table grape Crimson Seedless (Conesa et al., 2016a).
155 To determine whether these biochemical differences were coincident with altered vine
156 physiology, the physiological responses and vegetative growth of RDI and PRD vines

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158 **2. MATERIAL AND METHODS**

159 **2.1. Experimental conditions, plant material and irrigation treatments**

160 The experimental design, soil characteristics, climate parameters, fertilization
161 and standard cultural practices have been described in detail (Conesa et al. 2015; 2016
162 a, b). Briefly, this research was carried out in a 1-ha vineyard at Cieza, Murcia (SE
163 Spain, 38°15'N; 1°33'W) during three consecutive years (2011-2013). The table grapes
164 were 11-year-old Crimson Seedless (*Vitis vinifera L.*), grafted onto 1103 Paulsen
165 rootstock. The training system was a bilateral cordon trellised to a three-wire vertical
166 system. The vine rows ran N–NW to S–SE and the planting density was 4 m both
167 between rows and between vines (625 vines ha⁻¹). The experiment involved four
168 different irrigation treatments which were irrigated daily in the early evening from April
169 to October. A Control treatment irrigated to satisfy maximum crop water requirements
170 (ET_c-110%) through the whole growing season; (ii) a RDI treatment was irrigated as the
171 Control except post-veraison, when the vines were irrigated at 50% of Control levels
172 (iii) a PRD treatment that received the same irrigation amount as RDI, but applied to
173 only part of the rootzone, with the dry and wet sides of the root-zone alternated every
174 10-14 days, when the dry side of the rootzone reached 75% of field capacity (~34 % θ_v);
175 and (iv) a null irrigation (NI) treatment, which only received rainfall and supplementary
176 irrigation when the daily stem water potential (Ψ_s) exceeded the established threshold
177 value of -1.2 MPa (Conesa et al., 2012). In Control, RDI and NI treatments, the

178 irrigation system comprised one drip-line in each vine row, with four self-compensating
179 drippers (4L h^{-1}) 0.50 m apart, whereas the PRD treatment utilised two drip-lines with
180 two drippers (4L h^{-1}) per vine to each side of the root system. Crop evapotranspiration
181 ($\text{ET}_c = \text{ET}_0 \times \text{kc}$) was estimated using crop coefficients (kc) based on Williams et al.
182 (2003) varying from 0.2 to 0.8 according to the phenological stage, whereas reference
183 crop evapotranspiration (ET_0) was calculated with the Penman Montheith-FAO method
184 (Allen et al., 1998), with daily climatic data recorded by an automatic weather station of
185 the Servicio de Información Agraria de Murcia, located 8.5 km from the experimental
186 plot (CIA-42, www.siam.es).

187 **2.2. Soil water status**

188 Soil volumetric water content (θ_v) was measured to a maximum depth of 1 m
189 every 0.1 m with a frequency domain reflectometry (FDR) probe (Diviner 2000[®],
190 Sentek Pty. Ltd., South Australia). Measurements were expressed in the profile 0-50
191 cm, coinciding with the effective root depth (data not shown). Three access tubes (1 per
192 each replicate, $n = 3$) located 25 cm from the drippers, were installed within the wetting
193 area on randomly selected vines. In PRD treatment, FDR probes were installed on both
194 sides of the vine row (2 per each replicate, $n=6$). Measurements were taken every 7-10
195 days between 10:00 h-12:00 h during the experimental period.

196 **2.3. Water relations and $\text{ABA}_{\text{xylem}}$**

197 Pre-dawn leaf water potential (Ψ_{pd}) and midday stem water potential (Ψ_s) were
198 monitored every 7-10 days with a pressure chamber (Model 3000, Soil Moisture
199 Equipment, Santa Barbara, CA) from the beginning of berry development until harvest
200 on at least two leaves per replicate and three replicates per irrigation treatment ($n=6$),
201 located on the middle third of the branches, with a pressure chamber (Soil Moisture

202 Equipment Co., Model 3000) following the recommendations of Hsiao (1990). For Ψ_s ,
 203 leaves were enclosed in plastic bag two hours before measurement, and placed in the
 204 chamber within 20 s of collection. After measuring Ψ_{pd} , xylem sap was collected by
 205 applying an over-pressure of between 0.3 and 0.5 MPa for 1-3 min. Sap was
 206 immediately transferred to an Eppendorf tube, frozen in liquid nitrogen and stored at -
 207 20°C prior to ABA measurement [ABA_{xylem}] with radioimmunoassay (Quarrie et al.,
 208 1988) using the monoclonal antibody AFRC MAC52. After measuring Ψ_{pd} , the leaves
 209 were frozen in liquid nitrogen and predawn osmotic potential (Ψ_o) was measured on
 210 expressed sap of frozen and thawed leaves using a WESCOR 5520 vapour pressure
 211 osmometer (Wescor Inc., Logan, UT, USA), according to Gucci et al. (1991). Predawn
 212 leaf turgor potential (Ψ_t) was estimated as the difference between predawn leaf osmotic
 213 (Ψ_o) and predawn water potential (Ψ_{pd}).

214 Predawn leaf osmotic potential at full turgor (Ψ_{os}) was measured on leaves
 215 adjacent to those used to measure Ψ_{pd} . The leaves were excised with their petioles and
 216 placed in distilled water overnight to reach full saturation before being frozen in liquid
 217 nitrogen and stored at -30 °C, following the same methodology as for Ψ_o . Osmotic
 218 adjustment was estimated as the difference between the Ψ_{os} of stressed and Control
 219 vines. To estimate the intensity of stress endured by deficit irrigation treatments, the
 220 water stress integral was calculated from the values of Ψ_s , according to the equation
 221 defined by Myers (1988).

$$222 \quad S_{\Psi} = \left| \sum_{i=0}^{i=t} (\bar{\Psi}_{i,i+1} - \Psi_c) n \right| \quad \text{[Equation 1]}$$

223 where t is the number of measurements of Ψ_s ; $\Psi_{i,i+1}$ is the mean Ψ_s for any measurement
 224 i and i+1; Ψ_c is the maximum Ψ_s measured during each phenological period (pre and

225 post-veraison); n is the number of days in the interval. All values were referred to
226 Control treatment. S_{Ψ} obtained in the whole season is the sum of those observed in pre-
227 and post-veraison.

228 **2.4. Leaf gas exchange**

229 Gas exchange measurements were taken every 7-10 days between 09:00 and
230 11:30 h in daylight hours on at least two sun-exposed leaves per replicate and three
231 replicates per irrigation treatment ($n = 6$), at a consistent time with reference to the PRD
232 cycle. Maximum net CO_2 assimilation rate (A_{CO_2} , $\mu\text{mol m}^{-2} \text{s}^{-1}$), maximum stomatal
233 conductance (g_s , $\text{mmol m}^{-2} \text{s}^{-1}$), and transpiration rate (E_m , $\text{mmol m}^{-2} \text{s}^{-1}$) were measured
234 at a photosynthetic photon flux density (PPFD) $\approx 1500 \mu\text{mol m}^{-2} \text{s}^{-1}$, near constant
235 ambient CO_2 concentration ($C_a \approx 380 \mu\text{mol mol}^{-1}$) and leaf temperature ($T_{\text{leaf}} \approx 30 \text{ }^\circ\text{C}$)
236 with a portable gas exchange system CIRAS-2 (PP Systems, Hitchin, Hertfordshire,
237 UK). Intrinsic water use efficiency (WUEi) was calculated as the ratio between A and g_s
238 ($\mu\text{mol mol}^{-1}$), respectively.

239 **2.5. Vine growth patterns**

240 Micrometric trunk diameter fluctuations (TDF), first described by Kozłowski
241 and Winget (1964), were monitored throughout the experimental period in six selected
242 trees, using a set of linear variable displacement transducers (LVDT; Solartron
243 Metrology, Bognor Regis, UK, model DF ± 2.5 mm, precision $\pm 10 \mu\text{m}$) installed on the
244 trunk northern side at 120 cm above-ground and mounted on holders built of aluminum
245 and invar – an alloy comprising 64 % Fe and 35 % Ni that has minimal thermal
246 expansion. Several indices were derived from trunk diameter fluctuations according to
247 Goldhamer and Fereres, (2001): maximum daily trunk diameter (MXTD), minimum
248 daily trunk diameter (MNTD), maximum daily shrinkage (MDS = MXTD – MNTD)

249 and trunk daily growth rate (TGR, calculated as the difference between MXTD of two
250 consecutive days). The vines used for Ψ_s monitoring were also used for TDF
251 determinations. Data from LVDT sensors were collected using wireless technology. The
252 sensor nodes were provided by the company WIDHOC (WIDHOC Smart Solutions
253 S.L.), and sent data approximately every 20 minutes to a coordinator node which was
254 connected to a computer. Each node was provided by one SD card to store the data and
255 powered by lithium polymer batteries (5000 mAh) and small solar panels (5V/80 mA)
256 which allowed autonomous operation. Three nodes per irrigation treatment (one per
257 replicate) were used.

258 Leaf area index (LAI as %) was measured in one vine per replicate before
259 veraison using a canopy analyzer instrument (Model LAI 2000®, Li-Cor, Lincoln,
260 Nebraska, USA), and assuming no leaf growth (only canopy senescence) after veraison.
261 Previously, a grid of 16 points (of 4 x 4 measurements, each spaced 0.5 m and 0.25 m
262 from the main trunk) was established on the ground around the vine selected. The final
263 measurement averaged these 16 points.

264 Trunk perimeter was measured by tape-measure before harvesting on 6 vines per
265 replicate at a marked location around 1.2 m from the soil surface to determine trunk
266 cross-section area (TCSA, cm²). The annual increment in TCSA (Δ TCSA) was
267 calculated as the difference between two consecutive TCSA measurements. The
268 productivity efficiency (PE) was also calculated as the ratio between yield and TCSA⁻¹
269 Pruning weight was determined annually during winter dormancy in all the vines of the
270 experiment.

271 **2.7. Statistical analysis**

272 The experimental layout was a randomized complete block design with three
273 block-replicates per irrigation treatment. Each replicate consisted of three adjacent rows
274 of vines with six vines per row. The four central vines of the central row were used for
275 monitoring vine water relations, while the others served as guard vines. The data were
276 analyzed by one-way ANOVA using Statgraphics Plus for Windows version 5.1
277 (Manugistics, Inc., Rockville MD, USA). *Post hoc* pairwise comparison between all
278 means was performed by Duncan's multiple range test at $p < 0.05$.

279

280 **3. RESULTS**

281 **3.1. Irrigation, climate conditions and soil water content**

282 Averaged over the 3 years of the study, the Control treatment received 685 mm
283 of irrigation. Both RDI and PRD treatments applied 35% less water than well-watered
284 vines, while the NI treatment applied 72% less water, corresponding to a severe water
285 deficit (Table 1). Meteorological conditions (ET_0 and rainfall) differed between years,
286 with 2012 the wettest (375 mm annual rainfall), receiving twice as much as 2011, the
287 driest year (188 mm annual rainfall). Atmospheric evaporative (ET_0) was highest pre-
288 veraison (from early-June to early-August).

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Table 1. Reference evapotranspiration (ET₀), precipitation (P), irrigation water applied (from April to the end of October) to Control (full irrigation treatment) vines, and irrigation savings relative to the Control in RDI (regulated deficit irrigation, moderate deficit); PRD (partial rootzone drying, moderate deficit), and NI (null irrigation treatment, severe deficit) treatments during pre and post-veraison periods of the study period (2011-2013).

Year	Phenological period	ET ₀ (mm)	P (mm)	Irrigation (mm) Control	Irrigation savings compared to Control (%)		
					RDI	PRD	NI
2011	Pre-veraison	390	63	285	12	20	-----
	Post-veraison	886	125	363	62	57	48
	Total	1195	188	648	40	41	71
2012	Pre-veraison	388	209	288	-6	-2	79
	Post-veraison	886	166	398	52	47	81
	Total	1274	375	686	28	27	81
2013	Pre-veraison	393	130	315	5	16	50
	Post-veraison	860	65	407	61	64	76
	Total	1253	195	722	37	43	65
Average (2011-2013)		1241	253	685	35	37	72

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297 **Table 2.** Mean values of soil volumetric water content (θ_v , %) in the upper soil profile (0-50 cm) for Control (full irrigation); RDI (regulated
 298 deficit irrigation); PRD_{right} (partial rootzone drying in the right side, moderate deficit), PRD_{left} (partial rootzone drying in the left side, moderate
 299 deficit) and NI (null irrigation treatment, severe deficit) during the three years assessed (2011-2013). RDI vs. PRD_{total} was also compared
 300 individually.

Year	Phenological period	θ_v (%)						
		Control	RDI	PRD _{right}	PRD _{left}	NI	RDI	PRD _{total}
2011	Pre-veraison	32.55 a	33.38 a	33.92 a	30.44 a	32.82 a	33.38 a	32.18 a
	Post-veraison	35.23 c	31.92 b	32.15 b	28.49 a	28.09 a	31.92 a	30.32 a
	Whole-season	34.06c	32.56 b	32.93 b	29.35 ab	29.78 a	32.56 a	31.14 a
2012	Pre-veraison	31.94 b	37.52 c	35.85 c	31.84 b	28.09 a	37.52 b	33.84 a
	Post-veraison	40.86 b	32.04 a	32.99 a	30.90 a	30.45 a	32.04 a	31.94 a
	Whole-season	36.19 b	34.91 b	34.49 b	31.39 ab	28.52 a	34.91 b	32.94 a
2013	Pre-veraison	35.99 b	34.83 b	35.51 b	34.89 b	30.45 a	34.83 a	35,20 a
	Post-veraison	37.47 d	35.86 c	27.86 ab	31.95 b	28.93 a	35.86 b	29.90 a
	Whole-season	36.64 d	35.24 c	32.16 b	33.60 b	29.84 a	35.24 b	32.88 a
2011-2013	Average	35.63	34.24	33.2	31.45	29.38	34.24	32.32

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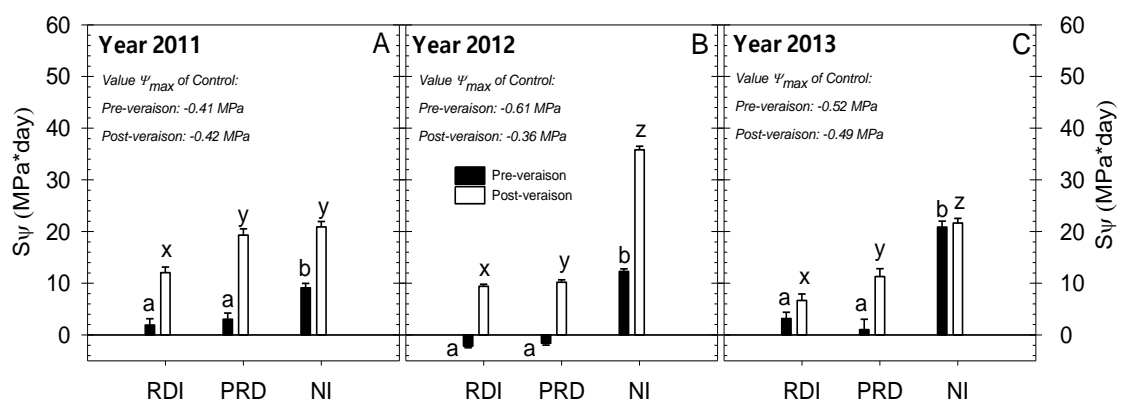
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Means within rows followed by a different letter were significantly different according to Duncan multiple range test (P<0.05).

303 In the Control treatment, irrigation maintained θ_v above field capacity at 0-50
 304 cm depth, averaging 35.6% during the study period (Table 2). As expected, θ_v values in
 305 RDI and PRD treatments were significantly lower than in the Control post-veraison
 306 (from early-August to the end of October). Although soil drying during PRD caused
 307 greater local soil water deficits than RDI, integrated θ_v values (averaged over both sides
 308 of the rootzone) were similar between PRD and RDI treatments post-veraison in 2011,
 309 with RDI showing greater θ_v post-veraison in 2012 and 2013. Furthermore, θ_v in the NI
 310 treatment was always lower than the Control treatment as expected, with a 17%
 311 reduction in θ_v during the study (Table 2).

312 3.2. Leaf water relations

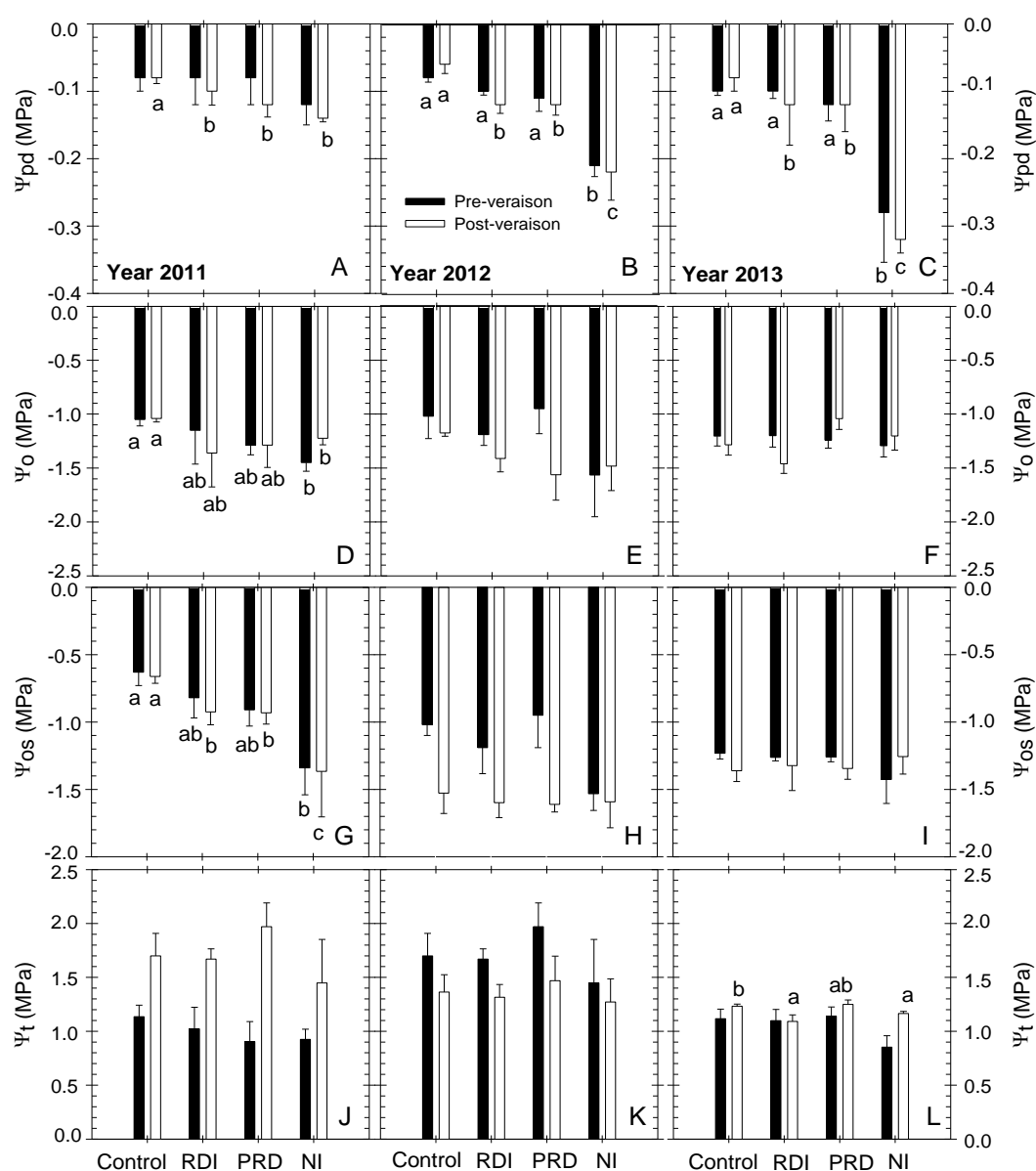
313 Pre-veraison, the water stress integral (S_Ψ) in RDI and PRD vines remained
 314 close to 0 as they received the same irrigation amount as Control vines. Post-veraison,
 315 the PRD treatment showed significantly higher S_Ψ values than the RDI treatment in all 3
 316 years (Fig. 1). As expected, regardless of the phenological period considered, the NI
 317 treatment had the highest S_Ψ in all years, with the values corresponding with annual
 318 rainfall.



319
 320 **Figure 1.** Relative water stress integral (S_Ψ) in deficit irrigation treatments compared to
 321 the control treatment (=0) for RDI (regulated deficit irrigation, moderate deficit); PRD
 322 (partial rootzone drying, moderate deficit); and NI (null irrigation treatment, severe

323 deficit) treatments during the years 2011 (A); 2012 (B) and 2013 (C), respectively. Stem
324 water potential (Ψ_s) was measured at midday. Black and white bars correspond to pre-
325 and post-veraison respectively. Within a year, different letters indicate statistically
326 significant differences among treatments of each phenological period: pre-veraison (a,
327 b,c) or post-veraison (x, y, z) by Duncan's multiple range test ($P < 0.05$).
328

329 Predawn leaf water potential (Ψ_{pd}) values for the Control treatment were around
330 -0.08 MPa (Figs. 2 A-C). Pre-veraison, the NI treatment had a significantly lower Ψ_{pd}
331 during 2012 and 2013. Post-veraison, all deficit irrigation treatments exhibited moderate
332 (in RDI, PRD) and severe (NI) water deficit, with, average Ψ_{pd} values of -0.14 and -0.28
333 MPa, respectively. Leaf osmotic and osmotic saturated potentials (Ψ_o and Ψ_{os}), only
334 differed between control and the other treatments (RDI, PRD and NI) during 2011 (Fig.
335 2D). Solute accumulation of RDI and PRD vines was not enabling to compensate the
336 deficit reached after veraison, whereas NI treatment maintained this trend during both
337 phenological periods (Fig. 2G). In 2013, RDI and NI vines had lower Ψ_t than Control
338 vines, but otherwise there were no significant treatment differences in leaf turgor. Thus,
339 there were minimal differences in leaf water relations between PRD, RDI and NI vines.



340

341 **Figure 2.** Seasonal evolution of (A-C) predawn leaf water potential (Ψ_{pd}), (D-F)
 342 predawn leaf osmotic potential (Ψ_o), (G-I) predawn leaf osmotic potential at full turgor
 343 (Ψ_{os}), and (J-L) predawn leaf turgor potential (Ψ_t) during the three years assayed (2011-
 344 2013) for all the irrigation treatments: Control (full irrigated treatment); RDI (regulated
 345 deficit irrigation, moderate deficit); PRD (partial rootzone drying, moderate deficit); and
 346 NI (null irrigation treatment, severe deficit). Values are means \pm SE during each
 347 phenological period of pre-veraison (black bars) and post-veraison (white bars).
 348 Different letters indicate statistically significant differences between treatments during
 349 pre-veraison (black bars) and post-veraison (white bars) by Duncan's multiple range test
 350 ($P < 0.05$).
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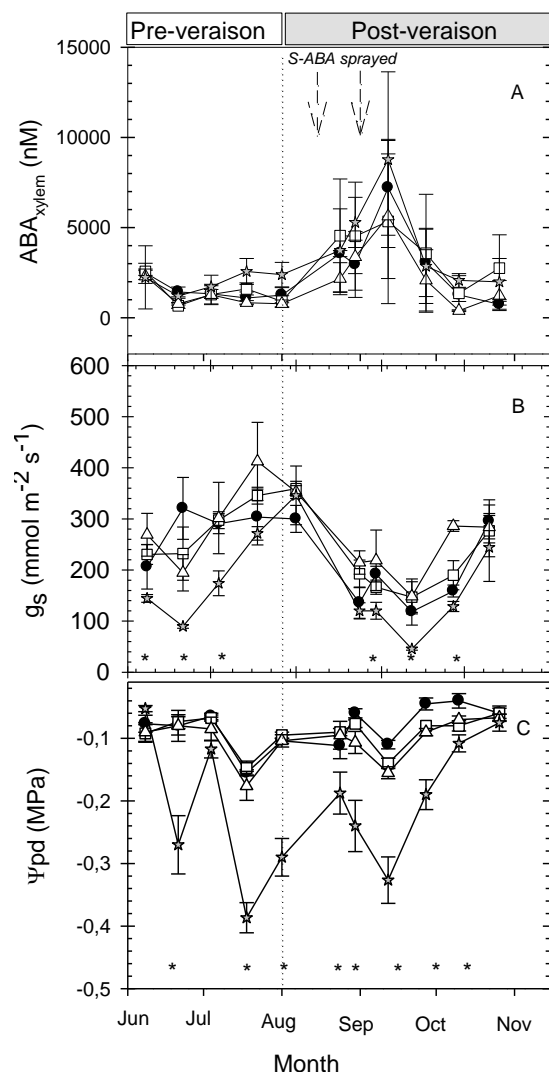
354 **3.3. Gas exchange parameters and ABA_{xylem}**

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356 Net CO₂ assimilation (A) was not affected by irrigation treatment, except pre-
357 veraison in 2012 when the NI treatment had the lowest values (Table 3). In contrast,
358 deficit irrigation decreased stomatal conductance (g_s) throughout the study, with
359 significant effects in 2011 and 2012. Stomatal closure was greatest in NI vines and least
360 in PRD vines, with RDI vines generally showing intermediate values despite receiving
361 the same irrigation volumes as PRD vines. Intrinsic water use efficiency (WUE_i) did
362 not statistically differ between treatments. Gas exchange parameters were more affected
363 by the period considered (pre-and post-veraison), regardless of the water availability
364 (Table 3).

365 Seasonal evolution of xylem ABA concentration ($[ABA_{xylem}]$) was dominated
366 by two exogenous applications of S-ABA in August and September to increase berry
367 coloration. By the end of September, $[ABA_{xylem}]$ had decreased to the levels observed
368 pre-veraison (Fig. 3A). $[ABA_{xylem}]$ tended to increase towards the end of the pre-
369 veraison period in NI vines. Although treatment did not significantly affect ($[ABA_{xylem}]$)
370 on any measurement date, averaging values both pre- and post-veraison indicated that
371 PRD vines maintained lower $[ABA_{xylem}]$ than NI vines (Fig. 3A). Across all irrigation
372 treatments, g_s declined as $[ABA]_{xylem}$ increased ($r^2 = 0.50$; $P < 0.001$), as seen in Romero
373 (2012). In contrast, g_s was not correlated with Ψ_{pd} ($r^2 = 0.04$; $P = 0.215$), while Ψ_{pd} was
374 not correlated with $[ABA]_{xylem}$ ($r^2 = 0.12$; $P < 0.01$) (Fig. 4).

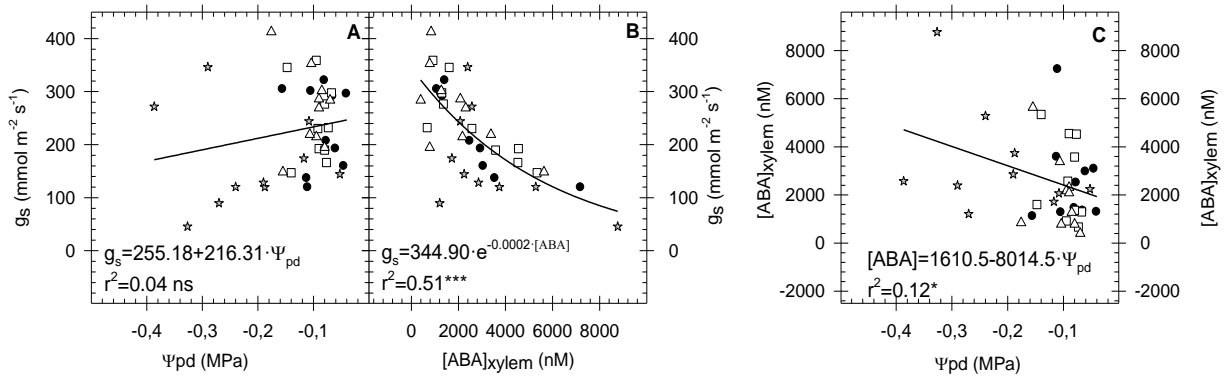
375 Diurnal time courses of gas exchange and vine water status in two typical post-
376 veraison days (24th August 2012 and 3rd September 2013) demonstrated relatively few
377 treatment differences in leaf gas exchange (Fig. 3).



378

379 **Figure 3.** Seasonal evolution of (A) xylem abscisic acid concentration (ABA_{xylem}), (B)
 380 stomatal conductance and (C) predawn leaf water potential for all the irrigation
 381 treatments (Control, \bullet , RDI, \square , PRD \triangle and, NI \star) during the year 2012.
 382 Arrows indicate the time of the application of exogenous ABA (S-ABA) by the
 383 commercial farm. Each point is mean \pm SE from 6 leaves or sap samples per irrigation
 384 treatment. Asterisks indicate statistically significant differences between treatments by
 385 Duncan's multiple range test ($P < 0.05$).

386



388

389 **Figure 4.** Relationship between (A) g_s vs. Ψ_{pd} , (B), g_s vs. $[\text{ABA}]_{\text{xylem}}$, and (C) $[\text{ABA}]_{\text{xylem}}$ vs. Ψ_{pd} for all the irrigation treatments (Control, \bullet , RDI, \square , PRD
390 \triangle and, NI \star). Each point is mean \pm SE from 6 leaves or sap samples per irrigation
391 treatment.
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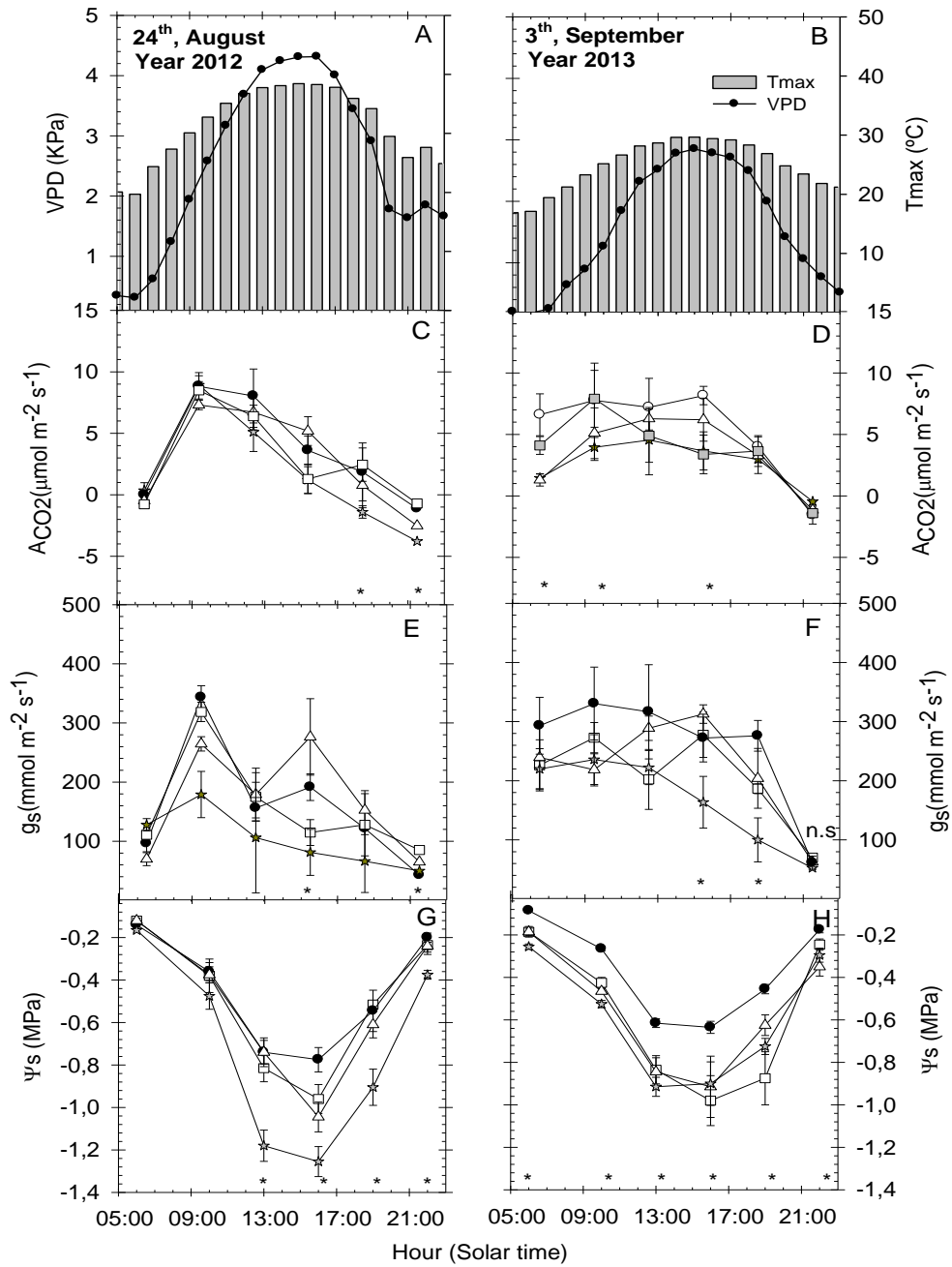
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In contrast, pronounced treatment differences in Ψ_s occurred mid-afternoon in
both years (Fig 4G-H). Indeed, RDI, PRD and NI treatments dropped sharply during the
morning (\sim 09:00–13:00 hours) and did not start to recover until late afternoon in both
years (Fig. 4G-H). The A_{CO_2} was slightly higher in Control than in the deficit treatments
even though these differences were less than those corresponding with g_s . Although, no
clear differences were found in daily g_s between RDI and PRD, the latter vines
recovered their gas exchange more rapidly than in RDI treatment, especially in 2012. As
expected, NI vines had the lowest values of A_{CO_2} and g_s averaged over the whole day
(Table 3 and Fig. 5).



405

406 **Figure 5.** Daily variation in (A-B) vapour deficit pressure (VPD) and maximum
 407 temperature (T_{max}), (C-D) net CO_2 assimilation rate (A_{CO_2}), (E-F) stomatal conductance
 408 (g_s), and (G-H) stem water potential (Ψ_{stem}) during two post-veraison days in 2012 and
 409 2013. Values are means \pm SE of 6 leaves per irrigation treatment (Control, \bullet , RDI,
 410 \square , PRD \triangle and, NI \star). Asterisks indicate statistically significant differences
 411 between treatments by Duncan's multiple range test ($P < 0.05$).

412

413

414

415 **Table 3.** Means values for the gas exchange parameters (Net CO₂ assimilation rate (A,
 416 $\mu\text{mol m}^{-2} \text{s}^{-1}$); Stomatal conductance (gs, $\text{mmol m}^{-2} \text{s}^{-1}$), Intrinsic water use efficiency
 417 (WUE, $\mu\text{mol mol}^{-1}$), of all irrigation treatments: Control (full irrigation treatment); RDI
 418 (regulated deficit irrigation, moderate deficit); PRD (partial rootzone drying, moderate
 419 deficit), and NI (null irrigation treatment, severe deficit) evaluated at pre-veraison, post-
 420 veraison during the study period (2011-2013).

421

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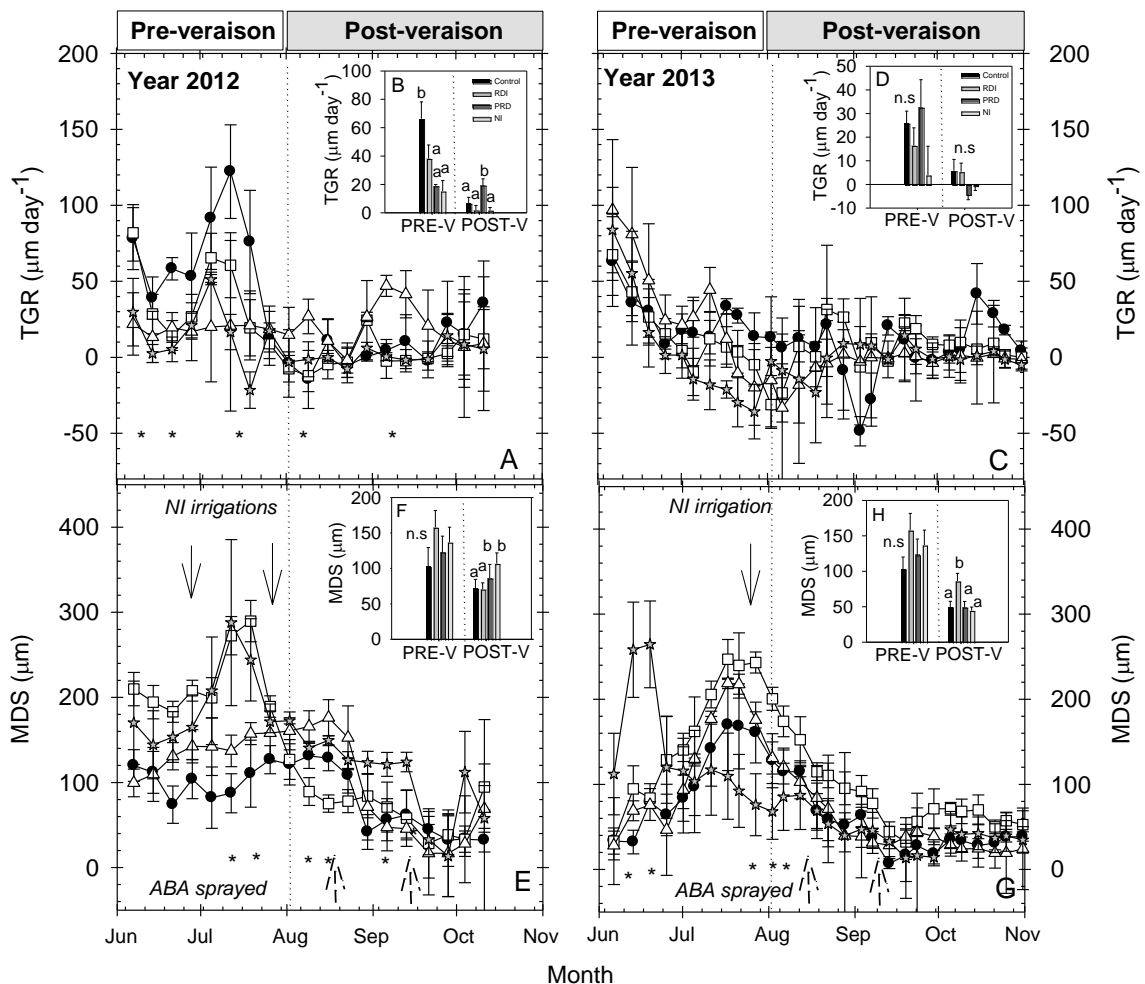
Year and Treatment	Pre-veraison			Post-veraison		
	A	gs	WUE	A	gs	WUE
2011						
Control	6.3	103.1 bc	60.9	7.7	104.5	74.5
RDI	5.9	78.3 b	75.6	4.7	72.3	84.1
PRD	6.9	164.6 c	50.0	5.3	155.8	36.5
NI	4.6	41.9 a	116.1	5.5	127.3	70.8
2012						
Control	9.9 a	309.4	31.9	8.0	365.1 c	23.5
RDI	9.7 a	345.8	29.1	8.5	292.2 b	28.3
PRD	9.1 a	328.1	28.9	8.1	288.0 b	28.4
NI	5.7 b	233.5	28.3	6.3	182.0 a	38.4
2013						
Control	7.1	192.5	43.9	6.6	243.9	27.1
RDI	7.3	240.3	30.0	6.5	150.8	43.1
PRD	6.9	187.1	40.0	6.1	258.6	23.9
NI	6.4	142.3	45.3	4.6	157.7	29.7
Analysis of variance:						
Treatment (T)	*	*	n.s	n.s	*	n.s
Year (y)	**	***	***	**	***	**
T x y	n.s	n.s	n.s	n.s	n.s	n.s
Average (2011-2013)						
Control	7.8	201.7	45.6	7.4	237.8	41.7
RDI	7.6	221.5	44.9	6.6	171.8	51.8
PRD	7.6	226.6	39.6	6.5	234.1	29.6
NI	5.6	139.2	63.2	5.5	155.7	46.3

423

424 Within a year, means within columns followed by a different letter were significantly
 425 different according to Duncan multiple range test ($P < 0.05$). *, **, *** significant effect
 426 at $P = 0.05$; $P = 0.01$ or 0.001 , respectively. n.s= not significant. Analysis of variance
 427 indicates a comparison across the years using a treatment (T) and a year (y) as factors.

428 **3.4. Vegetative growth patterns**

429 Treatment differences in trunk growth rate (TGR) were more pronounced pre-
 430 veraison in 2012, with Control vines showing the highest values ($\approx 120 \mu\text{m day}^{-1}$) (Figs.
 431 6A-C). Irrespective of the treatment considered, trunk growth apparently ceases 7-10
 432 days before veraison, with negative values (trunk shrinkage) occurring around veraison
 433 in both years (Fig. 6A-C). After veraison, there were few treatment differences in TGR
 434 and low growth rates. Noteworthy, PRD vines had the highest trunk growth rate post-
 435 veraison in 2012 (Fig. 6B).



436

437 **Figure 6.** Seasonal evolution of (A and C) trunk growth rate (TGR) and (E and G)
 438 maximum daily shrinkage (MDS) during 2012 and 2013, respectively for all the
 439 irrigation treatments (Control, \bullet , RDI, \square , PRD \triangle and, NI \ast). For TGR and
 440 MDS, inset graphs are means of each irrigation treatment for pre-and post veraison

441 during the year (B and D) 2012 and (F and H) 2013, respectively. Each point of MDS
442 and TGR represents weekly means \pm SE from 6 LVDT sensors per treatment. Arrows
443 indicate the time when the supplementary irrigations in NI treatment were applied.
444 Discontinuous arrows indicate the time of the application of exogenous xylem ABA (S-
445 ABA) by the commercial farm. Asterisks and different letter (in inset graphs) indicate
446 statistically significant differences between treatments by Duncan's multiple range test
447 ($P < 0.05$).

448

449 MDS values increased towards veraison, then decreased post-veraison, generally
450 remaining between 50 and 100 μ m in all treatments (Figs. 5C-D). Control and PRD
451 treatments showed the lowest MDS values pre-veraison in 2012, but in 2013 NI plants
452 also showed low MDS despite two supplementary irrigations. NI plants had
453 significantly lower MDS than the other irrigation treatments pre-veraison, especially in
454 2013. When irrigation was applied post-veraison, MDS was significantly higher in PRD
455 than RDI vines (Fig. 6F-H).

456 Pruning dry weight varied more between years than irrigation treatment, even
457 though the absolute values in NI plants were 24% lower than in Control vines (Table 4).
458 In contrast, leaf area index (LAI) was affected more by irrigation treatment than year.
459 Averaged across years, LAI of PRD and NI treatments were 9 and 27% lower
460 respectively than in Control vines. While trunk cross-sectional area (TCSA) did not
461 significantly differ between Control, RDI and PRD vines in any year, TCSA increments
462 of RDI, PRD and NI vines were 28, 26 and 77% lower than Control vines respectively.
463 In 2011, the productivity efficiency (PE) decreased in the order Control > RDI = PRD >
464 NI, but in the other two years only NI vines had significantly lower PE (Table 4).

465

466

467

468 **Table 4.** Seasonal evolution of pruning weight, leaf area index (LAI), annual increment
 469 trunk cross-section area (Δ TCSA) and productivity efficiency (PE) calculated as the
 470 ratio between yield and Δ TCSA in Control (full irrigation treatment); RDI (regulated
 471 deficit irrigation, moderate deficit); PRD (partial rootzone drying, moderate deficit), and
 472 NI (null irrigation treatment, severe deficit).

473

Year and Treatment	Pruning (kg vine⁻¹)	LAI (%)	ΔTCSA (cm² y⁻¹)	PE (kg cm⁻² y⁻¹)
2011				
Control	7.18	83.57 b	4.92 b	14.83 a
RDI	6.82	84.55 b	2.70 ab	31.11 b
PRD	6.57	75.26 ab	2.90 ab	26.89 b
NI	5.64	61.98 a	0.90 a	74.44 c
2012				
Control	6.9	71.64 b	4.31 b	18.32 a
RDI	7.12	66.26 b	3.10 ab	23.22 a
PRD	6.27	67.73 b	2.98 ab	20.80 a
NI	5.22	41.15 a	1.18 a	38.13 b
2013				
Control	4.43	82.15 b	3.41 b	19.94 a
RDI	4.55	72.99 b	3.30 b	20.01 a
PRD	4.46	79.79 ab	3.40 b	19.11 a
NI	3.32	69.71 a	0.88 a	51.13 b
Analysis of variance:				
Treatment (T)	n.s	***	***	***
Year (y)	***	*	n.s	*
Txy	*	***	n.s	**
Average (2011-2013)				
Control	6.19	79.12 b	4.21 c	17.69 a
RDI	6.16	74.60 b	3.03 b	24.78 a
PRD	5.77	74.26 b	3.09 b	22.26 a
NI	4.72	57.61 a	0.98 a	54.56 b

474

475 Within a year, means within columns followed by a different letter were significantly different
 476 according to Duncan multiple range test ($P < 0.05$). *, **, *** significant effect at $P = 0.05$, 0.01
 477 or 0.001, respectively; n.s = not significant. Analysis of variance indicates a comparison across
 478 the years using a treatment (T) and a year (y) as factors.

479

480

481

482 4. DISCUSSION

483 Although PRD and RDI received the same irrigation volume post-veraison (50%
484 of Control) and throughout the experiment (\approx 35% less water than Control, Table 1),
485 both treatments had different water uptake patterns (see Conesa et al., 2016a) and hence,
486 accumulated water stress measured as midday stem water potential (Fig. 1). However,
487 predawn water potential measurements did not differ between RDI and PRD (Conesa et
488 al., 2015) even though PRD vines experienced greater localized soil drying (Table 2).
489 However, pre-dawn water potential of PRD vines should be greater at a given soil water
490 content as water uptake is principally from the wet side (Kang and Zhang, 2004). Since
491 PRD vines received twice the irrigation volume applied to part of the rootzone
492 compared to that applied to either side of the RDI treatment, irrigation events during
493 PRD might penetrate deeper into the soil profile (50-100 cm - data not shown) (Dry et
494 al., 2000). Nevertheless, average θ_v was generally equivalent between PRD_{total} and RDI
495 vines (Table 2), suggesting that localized soil drying during the day increases hydraulic
496 resistance (Rodrigues et al., 2008; Romero et al., 2012) in the soil-plant-atmosphere
497 pathway.

498 Soil drying can stimulate root ABA biosynthesis (Speirs et al. 2013) and ABA
499 transport from roots to shoots (Dodd et al., 2008) to cause stomatal closure and reduce
500 transpiration rates (Stoll et al., 2000; Speirs et al. 2013), thereby increasing water use
501 efficiency (Flexas et al., 2010). Nonetheless, soil water availability (Table 2) was not
502 directly correlated with plant physiological behavior (Table 3), probably due to the
503 relatively narrow range of soil moisture, in contrast to previous studies (Chaves et al.,
504 2010; Romero et al., 2012). Although PRD plants had greater post-veraison plant water
505 deficits than RDI plants (Fig. 1), leaf gas exchange and $[ABA_{xylem}]$ showed minimal

506 treatment differences (Fig. 3A and Table 3). Contrary to expectations (Medrano et al.,
507 2015), PRD vines showed decreased leaf-level water use efficiency compared to RDI
508 and Control vines. Similarity of gas exchange between PRD and RDI vines may be
509 because soil moisture distribution in PRD under field settings depends on multiple
510 factors such as the soil type (Sepaskhah and Ahmadi, 2010, Permanhani et al., 2016),
511 the grapevine variety and the environmental conditions (Romero et al., 2012), and/or
512 genotypic differences in stomatal behavior to water deficit (Chaves et al., 2010;
513 Permanhani et al., 2016). Nevertheless, halving the water application to PRD vines
514 partially closed the stomata and prevented severe leaf water deficit because half of the
515 roots still receive water (Dry et al., 1996, 2000). Although PRD decreased plant water
516 status compared to control vines, roots in wet soil absorbed sufficient water to maintain
517 a higher shoot water status than non-irrigated vines (Fig. 1). Thus, physiological
518 impacts of PRD on leaf gas exchange depended on the basis of comparison, with
519 irrigation volume (PRD *versus* Control) having greater impacts than irrigation
520 placement (PRD *versus* RDI).

521 Irrigation treatment affected trunk diameter variations pre-veraison whereas
522 stem diameter changes diminished post-veraison (Fig. 6). Similarly, trunk growth
523 stopped \approx 20 days before veraison in both non-irrigated and well-irrigated grapevines,
524 thus grapevine water status could not be related to TDF-indices (Intrigliolo and Castel,
525 2007), likely due to high competition for photoassimilates between fruit and vegetative
526 growth and decreased trunk elasticity which reduced MDS and TGR values (Conesa et
527 al., 2016b). In contrast, irreversible stem shrinkage in grapevines caused by periderm
528 formation was not linked to grape berry development (Van de Wal et al. 2017). Finally,
529 irrigation treatments had limited effects on TGR and MDS post-veraison (Fig. 6),
530 suggesting they may be unsuitable in table grapes as water stress indicators.

531 Although PRD has less effect on leaf gas exchange than RDI, vegetative growth
532 (determined by LAI) was more affected in the 1st and 3rd year (Table 4), likely due to
533 the greater water stress experienced by PRD vines (Fig 1). These differences suggest
534 that hydraulic signalling regulated vegetative development (Santos et al., 20005), even
535 though both treatments received the same irrigation volumes. In addition, PRD
536 maintained crop yield and even improved quality when compared with RDI and Control
537 treatments (Conesa et al., 2016 a), indicating that the small decrease in LAI in PRD
538 plants had no detrimental effect on crop production. In this sense, Kang and Zhang
539 (2004) reported that PRD may influence carbohydrates partitioning among different
540 plant organs and contribute positively to fruit quality (as in Conesa et al., 2016a).

541 In conclusion, although PRD and RDI vines received the same irrigation
542 volumes and PRD showed greater plant and localized soil water deficit, physiological
543 (stomatal closure and ABA_{xylem}) and agronomic (fruit yields – Conesa et al. 2016a)
544 indicators were similar to RDI vines. These data dispute the utility of midday stem
545 water potential (Ψ_s) as a predictor of physiological performance, likely since enhanced
546 root growth (Dry et al., 2000; Mingo et al., 2004) allowed greater efficiency of water
547 uptake under PRD. Total leaf area was the vegetative parameter more affected by PRD
548 as there were no differences in TCSA or trunk growth rate. Moreover, the trunk
549 diameter fluctuations indices (MDS and TGR) can only be considered as a good water
550 stress indicators before veraison to ascertain plant water status. Therefore PRD seems a
551 suitable irrigation technique for table grapes to sustain water, modifying growth (Table
552 4) and improve berry physical quality (Conesa et al., 2015) and bioactive compounds
553 (Conesa et al., 2016) compared with conventional RDI,

554

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563

564 **Conflicts of Interest:** We have not any conflict of interest.

565

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