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RESEARCH ARTICLE

Water relations and gas exchange in olive trees under regulated deficit irrigation and partial rootzone drying

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Abstract It is widely believed that partial root drying (PRD) reduces water losses by transpiration without affecting yield. However, experimental work carried out to date does not always support this hypothesis. In many cases a PRD treatment has been compared to a full irrigated treatment, so doubt remains on whether the observed benefits correspond to the switching of irrigation or just to PRD being a deficit irrigation treatment. In addition, not always a PRD treatment has been found advantageous as compared to a companion regulated deficit irrigation (RDI) treatment. In this work we have compared the response of mature 'Manzanilla' olive trees to a PRD and an RDI treatment in which about 50% of the crop evapotranspiration (ET_c) was supplied daily by localised irrigation. We alternated irrigation in the PRD treatment every 2 weeks in 2003 and every 3 weeks in 2004. Measurements of stem water potential (Ψ_{stem}), stomatal conductance (g_s) and net CO_2 assimilation rate (A) were made in trees of both treatments, as well as in trees irrigated to 100% of ET_c (Control trees) and in Rain-fed trees. Sap flow was also measured in different conductive organs of trees under both PRD and RDI treatments, to evaluate the influence of alternating irrigation on root water uptake and tree water consumption. We found small and random differences in Ψ_{stem}, g_s and A, which gave no evidence of PRD causing a positive effect on the olive tree performance, as compared to RDI. Stomatal conductance decreased in PRD trees as compared to Control trees, but a similar decrease in g_s was also recorded in the RDI trees. Sap flow measurements, which reflected water use throughout the irrigation period, also showed no evidence of g_s being more reduced in PRD than in RDI trees. Daily water consumption was also similar in the trees of the deficit irrigation treatments, for most days, throughout the irrigation period. Alternating irrigation in PRD trees did not cause a change in either water taken up by main roots at each side of the trees, or in the sap flow of both trunk locations and main branches of each side. Results from this work, and from previous work conducted in this orchard, suggest that transpiration is restricted in trees under deficit irrigation, in which roots are left in drying soil when water is applied by localised irrigation, and that there is no need to alternate irrigation for achieving this effect.

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Introduction

The response of the olive tree to reduced irrigation is well known. Different deficit irrigation strategies applied to olive orchards have been evaluated, from the supplementary (Abdel-Rahman and El-Sharkawi 1974) and complementary irrigation (Lavee et al. 1990; Pastor and Orgaz 1994) to what Chalmers et al. (1986) named as regulated deficit irrigation, RDI (Goldhamer 1999; Girona 2001). Most deficit irrigation strategies in olive orchards use RDI to apply irrigation water when the tree is least tolerant of water stress. However, RDI techniques have been increasingly perfected and used in parallel with the increased knowledge on crop water response at different physiological and phenological stages. Nowadays the RDI approach is widely accepted for supplying water to many fruit tree species (Fereres et al. 2003). In olive, Motilva et al. (2000) studied the effect of RDI strategies on oil yield and oil composition of 'Arbequina' olive trees. There are also a variety of papers showing the response of different varieties to other deficit irrigation strategies, such as those by Fernández et al. (1997), Moriana et al. (2003), d'Andria et al. (2004) and Tognetti et al. (2004, 2005).

Another deficit irrigation technique that has also become common in recent years is partial root drying, PRD (Dry et al. 1996). With this technique half of the rootzone is kept under dry soil, by alternating irrigation from one half to the other every 2–3 weeks. In many species, when exposing a part of the rootzone to soil drying a root-to-shoot signalling mechanism is triggered, which induces partial stomata closure. This reduces water loss by transpiration, which increases the water use efficiency (Dry et al. 1996, 2001; Stikic et al. 2003). The nature of the signals is complex. Most published work refers to chemical signals (Gowing et al. 1990; Davies et al. 2001; Sobeih et al. 2004), some to hydraulic signals (Yao et al. 2001), and some to the interaction of both of them (Tardieu and Davies 1992, 1993; Augé and Moore 2002). The PRD technique has been tested in many species, including both herbaceous (Davies et al. 2000; Yao et al. 2001; Stikic et al. 2003; Kirda et al. 2004; Wakrim et al. 2005) and woody crops.

Most PRD in woody crops has been on grapevine, which seems to be a species that responds well to this deficit irrigation strategy. Dry et al. (1996) report PRD reduced shoot growth but not fruit yield, while the fruit quality was improved. Dry and Loveys (1999) used PRD in two different grape cultivars growing in split-root containers. They observed a reduction in shoot growth and stomatal conductance. Additional studies in containers-grown and field-grown grapevines have also been published (Dry et al. 2000a, b, 2001; Loveys et al. 2000; Stoll et al. 2000). Recently dos Santos et al. (2003) and de Souza et al. (2003, 2005) have provided more information on the effect of PRD on field-grown grapevines. Their results support the hypothesis that PRD decreases stomatal conductance without reducing carbon assimilation, which increases water use efficiency. They concluded, however, that the differences between their PRD and other deficit irrigation treatments were subtle, and that further research with different varieties and weather conditions is required before recommending the use of PRD in commercial vineyards. In a recent review on the effect of soil water status on grapevines, Cifre et al. (2005) also point out the need for more research before confirming the usefulness of PRD at the agronomic level.

Concerning fruit tree species, the PRD approach has been tested, to our knowledge, in pear, peach and olive. Kang et al. (2002, 2003a, b) observed positive effects after applying PRD to pear trees, as compared to a fully irrigated treatment, but they did not have an RDI treatment comparison. Goldhamer et al. (2002) compared PRD with RDI in young peach trees. They found no differences between treatments, except for a slightly less negative early morning stem water potential measured in PRD trees at the end of stage 2. They concluded that ''more information is needed to elucidate root signal mechanism and if any, identify opportunities for exploring them to improve fruit tree culture''. More recently, Wahbi et al. (2005) and Centritto et al. (2005) published the only pieces of work we have found on PRD applied to the olive tree. They used the same orchard, with 'Picholine marocaine' olive trees. Centritto et al. (2005) found, in a PRD treatment in which 50% of the crop water evapotranspiration (ET_c) was applied, a significant decrease in time-course leaf water potential, although leaf relative water content and photosynthetic capacity were similar to that of the control plants irrigated in both sides to 100% of ET_c. Wahbi et al. (2005) found, for the same conditions, a PRD-induced yield reduction of 15–20% only, and no reduction on yield quality. Unfortunately, as pointed out by these authors in their conclusions, they did not have a companion RDI treatment, so once again we do not know whether similar benefits could have been obtained with RDI. To clarify whether PRD has any advantage on RDI is important for orchardists, since PRD implies the use of double tubing, making the irrigation system more expensive and difficult to manage than that required for RDI.

The aim of this work was to compare the response of mature 'Manzanilla' olive trees to two deficit irrigation treatments in which about half of the crop water needs were supplied daily by localised irrigation. In one treatment we used the PRD approach, and in the other the RDI one. Measurements of stem water potential, stomatal conductance and net CO_2 assimilation rate were made in trees of both treatments, as well as in trees both under dry farming conditions and irrigation to replace 100% of the crop water needs. Sap flow measurements were also made in different conductive organs of the two deficit irrigation treatments, to evaluate the influence of alternating irrigation on root water uptake and tree water consumption.

Materials and methods

Orchard characteristics

The experiments were conducted during 2003 and 2004, in an 0.5 ha olive orchard at *La Hampa*, an experimental farm of the Spanish Research Council (CSIC) 15 km South of Seville, in southwest Spain (37°17′ N, 6°3′ W, elevation 30 m). The trees (*Olea europaea* 'Manzanilla de Sevilla', from now on 'Manzanilla'), planted at 7 m × 5 m, were 35 years old in 2003. They have a single trunk and two main branches from 0.7 to 1.5 m above ground. The canopies, of spherical shape and a diameter of about 4.5 m, are usually open at the top, due to the type of pruning applied in the area. The trees were pruned every year, reaching a maximum leaf area index of about 1.7 at the end of the growing season. The ground cover was about 34% throughout the experiments. The rest of management practices also align with those recommended for the area. Trees of the irrigated part of the orchard were well adapted to localised irrigation from the beginning of the experiment (Palomo et al. 2002). During the dry season the soil was left free of weeds using herbicide.

The slope of the orchard ranges from 3% to 6%. The soil is a sandy loam (Xerochrept) with depth ranging from 0.9 to 2 m. Below this a hard limy sandstone pan impedes root and water penetration. The texture is quite homogeneous with depth, with average values from the surface to the pan of 14.8% clay, 7.0% silt, 4.7% fine sand and 73.5% coarse sand. Laboratory measurements showed that the volumetric soil water content (θ, $m^3\ m^{-3}$) is 0.33 $m^3\ m^{-3}$ for a soil matric potential of 0 MPa, and 0.10 $m^3\ m^{-3}$ for −1.5 MPa. Field values of θ close to the drippers a few hours after irrigation were rarely greater than 0.20 $m^3\ m^{-3}$. The climate of the area is typically Mediterranean, with a mild, wet season from October to April, and being hot and dry from May to September. The average rainfall and evapotranspiration values for the period 1971–2004 are 501 mm and 1445 mm, respectively.

Irrigation treatments

The orchard was divided into four plots of similar size, each receiving a different water treatment. In treatment 1 (Control) trees were irrigated daily for the whole season, from May to October. Enough water to replace ET_c was supplied with a single pipe per row with five 3 $l\ h^{-1}$ drippers per tree, 1 m apart. The following equation was used to calculate ET_c:

$$ET_C = K_C\ K_r\ ET_O, \quad (1)$$

where the coefficient related to the percentage of ground covered by the crop (K_r) was determined after Fereres and Castel (1981), resulting a value of 0.7 for the ground cover in the orchard; ET_o is the reference evapotranspiration calculated with the FAO56

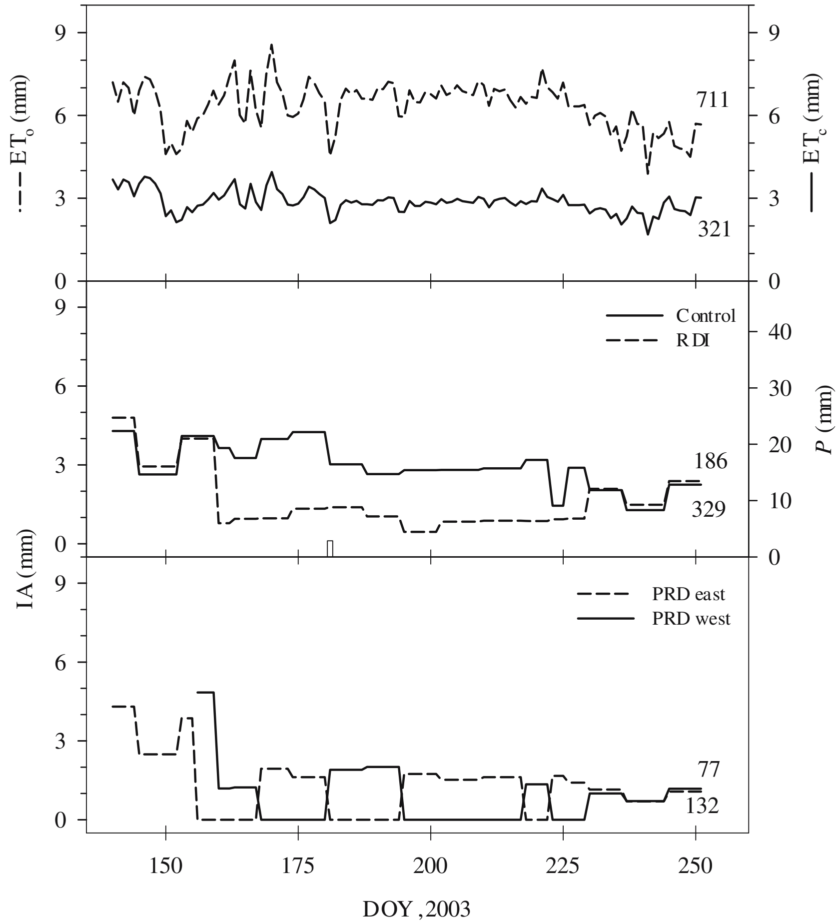

Fig. 1 Irrigation amounts (IA) supplied to the olive trees of the three irrigated treatments (see text for details) during the irrigation season of 2003. The numbers at the right end of the lines indicate the total amount of water supplied to each treatment (mm), and the total reference (ET$_o$, mm) and crop evapotranspiration (ET$_c$, mm) for the measurement period. The precipitation (*P*) amounts are shown in the central graph. The top graph shows the daily evolutions of ET$_o$ and ET$_c$. The values of ET$_o$ were calculated from the records of the meteorological station in the farm and the FAO56 Penman–Monteith equation. The values of ET$_c$ were calculated with Eq. (1) described in the text. DOY=day of year (DOY 150 = May 30)

Penman–Monteith equation (Allen et al. 1998). Meteorological data was collected from a site next to the orchard (see below). We calculated ET$_o$ every week, based on the meteorological data of the previous week, and adjusted the daily irrigation doses of each irrigation treatment accordingly. The values of the crop coefficient (K_c) were determined in previous years for the orchard conditions, resulting 0.76 in May, 0.70 in June, 0.63 in July and August, 0.72 in September and 0.77 in October. In a previous paper (Fernández and Moreno 1999) we give lower K_c values for the same orchard; this is because those values were calculated for the case of ET$_o$ being determined by the FAO–Penman equation (Doorenbos and Pruitt 1977), which Mantovani et al. (1991) evaluated as the most suitable for our area. Gavilán and Berengena (2000) presented results showing that the most accurate values of ET$_o$ are determined in the area by using the FAO56 Penman–Monteith equation. We have therefore corrected our K_c values. Treatment 2 (RDI) was based on values given by Girona (2001); enough water was supplied to replace ET$_c$ for 3 weeks at the beginning of pit hardening and again on the 3 weeks before harvest (flowering occurred within the rainy season). At both periods the trees are less tolerant to water stress; for the rest of the time we adjusted the irrigation amounts (IA, mm) to replace 30% of ET$_c$. In treatment 3

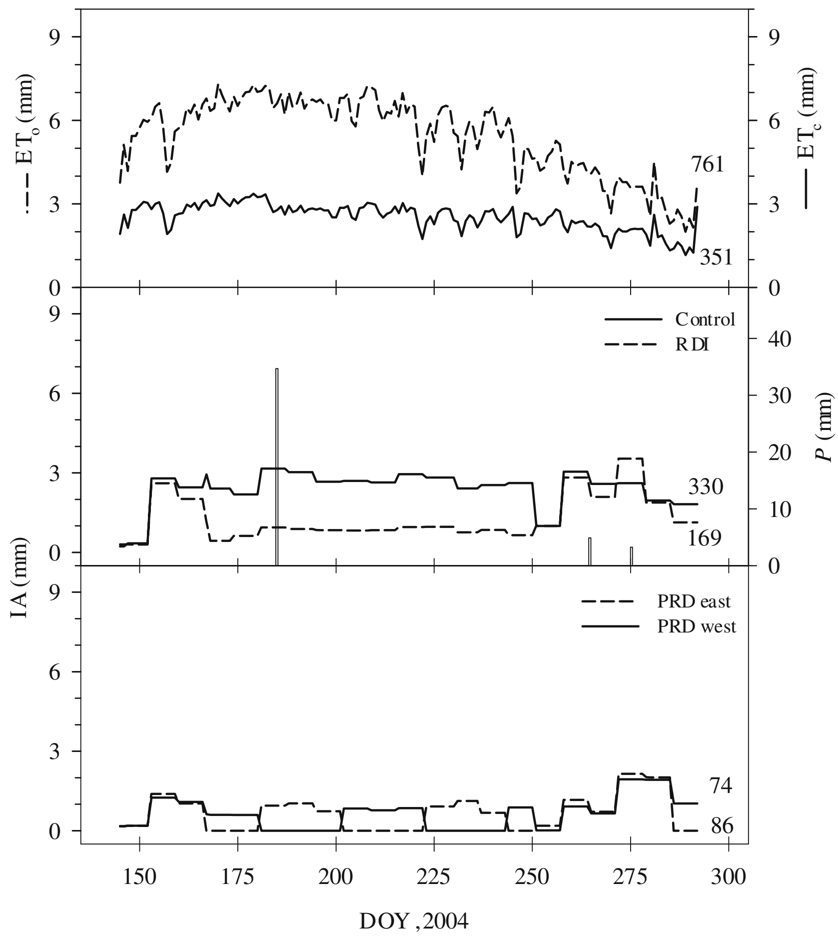

Fig. 2 As in Fig. 1, but for 2004

(PRD) two laterals per tree row were used, each equipped with three 3 l h^{-1} drippers 0.6 m apart, being the one closer to the trunk at 0.8 m from it. Each lateral had the drippers at a different side of the tree, east and west, which allowed irrigation to each side independently. As in the RDI treatment, we irrigated to 100% of ET$_c$ on the 3 weeks at the beginning of pit hardening and on the 3 weeks before harvest. For the rest of the irrigation season, we adjusted irrigation to supply 30% of ET$_c$ to one side of the tree, switching to the other every 2 weeks in 2003 and every 3 weeks in 2004. Details on the applied IA are given in Fig. 1 for 2003 and in Fig. 2 for 2004. Also shown in the figures are the calculated ET$_o$ and ET$_c$ values for each experimental season. In Treatment 4 (Rain-fed) trees were under dry-farming conditions. The only water supply for those trees was that of precipitation (*P*, mm), shown in Figs. 1 and 2.

All treatments were generously fertilized, to avoid the influence of any possible nutritional deficiency on the observed variables. Each tree received about 0.60 kg of N, and 0.25 kg of both K and P per year. The fertilizers also contained enough amounts of Fe, B and other elements to cover the crop needs, as described by Fernández-Escobar (2001). In the irrigated trees the fertilizers were injected in the irrigation system, six days a week, throughout all the irrigation period. In the Rain-fed trees two fertilizer applications were made, in mid February and early June; in both cases the fertilizers were distributed on the whole ground area covered by the canopies.

Measurements

Three trees per treatment were instrumented with access tubes for the neutron probe (Troxler 3300, Research Triangle Park, NC, USA); in one of the trees, four access tubes were installed at distances of 0.5, 1.5, 2.5 and 3.5 m from the trunk along the tree row; in the other two trees, two access tubes were installed at 1.5 and 2.5 m from the trunk, along the tree row. The θ measurements were made every 0.1 m, from 0.2 m down to the maximum depth of the rootzone (2 m). In the top 0.2 m, θ was calculated from gravimetric measurements and the average values of soil bulk density measured in the field: 1.43 Mg m^{-3} for the 0.0–0.1 m soil layer and 1.59 Mg m^{-3} for the 0.1–0.2 m soil layer. Soil water profiles were recorded every week for the RDI and PRD treatments, and every two weeks for the Rain-fed and Control treatments, throughout the two irrigation seasons. These values were used to calculate a depth equivalent of water, expressed as the level of relative extractable water (REW, mm) defined by the equation (Granier 1987):

$$\mathrm{REW} = \frac{R - R_{\min}}{R_{\max} - R_{\min}}, \quad (2)$$

where R (mm) is the actual soil water content, $R_{\min}$ (mm) the minimum soil water content measured during the experiments, and $R_{\max}$ (mm) is the soil water content at field capacity. The values of $R_{\min}$ and $R_{\max}$ were 218 and 388 mm, respectively. Based on our soil water measurements, and on a previous work we did in the same orchard (Palomo et al. 2002), we assumed a negligible runoff during the experimental periods, and less than 10% water lost by drainage in the Control treatment. From the wetted ground areas and the soil evaporation model derived by Díaz-Espejo et al. (2004) for the orchard conditions, we estimated an average difference between treatments in soil evaporation values of about 1.5 l per tree and day, which is a small amount as compared to the applied IA (Figs. 1, 2).

The response of the trees to the imposed water treatments was characterised by measurements of the plant water status, leaf gas exchange and sap flow in different conductive organs. We recorded diurnal time courses of stem water potential (Ψ_{stem}, MPa), which was assumed to be equal to the xylem pressure potential at the petiole of leaves wrapped in aluminium foil some 2 h before the measurements with a pressure chamber (Soilmoisture Equipment Corp., Santa Bárbara, California, USA) in 6 leaves per treatment (2 leaves per tree, 3 trees per treatment). The sampled leaves were the fourth or fifth from the apex of sunlit, healthy twig at about 1.5–1.9 m above ground. In 2003, these measurements were made in the Rain-fed and Control treatments in one day of each month all throughout the irrigation season, and in the RDI and PRD treatments one or two days after. In 2004, all the treatments were measured on the day. At the same times Ψ_{stem} was measured, we used a portable photosynthesis system (LI-6400, Li-Cor, Inc., Lincoln, NE, USA) to record stomatal conductance (g_s, mol m^{-2} s^{-1}) and net CO_2 assimilation (A, μmol m^{-2} s^{-1}) in the same number and type of leaves. In 2003, sap flow was recorded in the trunk of a representative PRD tree. We used the compensation heat-pulse method, with probes, associated electronics and software made by the Environmental and Risk Management Group of the HortResearch in Palmerston North, New Zealand. Details of gear and method are given in Green et al. (2003). The method was calibrated for olive by Fernández et al. (2006). One probe set was installed in the main branch, in the trunk and in a main root (about 0.04 m diameter) in each of the two sides affected by irrigation of a PRD tree (three probes in the east side and another three in the west side of each tree). Sap flow readings were taken every half hour, from August 11 to September 1. In 2004, we used the same method and probe distribution to record sap flow in 3 RDI trees and 3 PRD trees, throughout the experimental season, from May 12 to September 15. In the RDI trees, we installed three probe sets at about equal spacing around the circumference of each trunk. In the PRD trees, we used the same probe distribution as in 2003. From the sap flow data and leaf area measurements (LA, m^2) we estimated the total daily transpiration per unit leaf area (E_p, l day^{-1} m^{-2}) of each instrumented tree. To do so we estimated LA of the three RDI and PRD trees in which sap flow was recorded in 2004. In March 25 we counted the leaves of a sector of the canopy of each of the six trees, accounting for some one fifth of the total volume; then we estimated the LA of each sector from the measurement with a leaf area meter of the LA of some 300 leaves randomly taken from the experimental trees; the total LA of the trees was eventually estimated by extrapolation from the measured sector to the rest of the canopy of each tree. The evolution of the total LA of each tree throughout the period in which sap flow recorded was

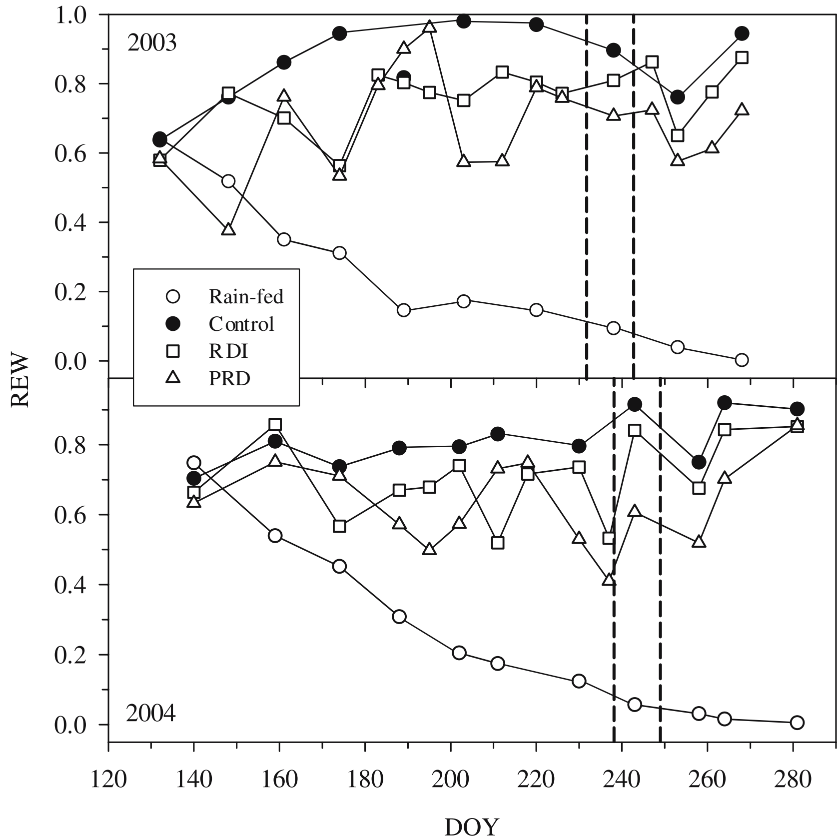

Fig. 3 Seasonal evolution of the relative extractable water (REW, calculated with Eq. (2) as described in the text) recorded for each treatment (see text for details) during the irrigation seasons of 2003 and 2004. Broken lines show the periods of both irrigation seasons for which the sap flow measurements are shown in Figs. 8 and 9. In the PRD treatment, measurements of soil water content were made in the west half of the rootzone. DOY=day of year

estimated from the LA of 20 twigs per instrumented tree, measured in June 2, July 1, August 4 and September 15.

Meteorological measurements were continuously carried out with an automatic station (Campbell Scientific Ltd., Shepshed, UK) located next to the orchard, and ET_o was calculated with the REF-ET Reference Evapotranspiration Software (Allen 2002).

Data analysis

Rather than replicating the treatment plots we relied on the detailed measurements made within each of them. We were bound to do so due to the high cost of the instrumentation required for recording sap flow, one of the main variables, and for the high labour and time required for the LA measurements. The distribution of the Ψ_{stem}, g_s and A sets of data was tested for normality by Kolmogorov–Smirnov test, kurtosis and skewness. A Student's *t*-test was used to assess differences between mean values. Statistical analyses were made with the program SPSS 11.5 for Windows.

Results

The IA added to the Control treatment throughout the irrigation periods amounted to 102% of the calculated ET_c in 2003 (Fig. 1) and to 94% of the calculated ET_c in 2004 (Fig. 2). For the RDI treatment, the IA supplied at the period in which the crop was more tolerant to water stress, assumed as the whole irrigation season except 3 weeks at the beginning of pit hardening and another 3 weeks before harvest, amounted to 33% of ET_c in 2003 and 30% of ET_c in 2004. In the PRD treatment, the

Table 1 Mean values (n = 6) of stem water potential (Ψ_{stem}) measured in trees of the four studied treatments throughout the irrigation seasons of 2003 and 2004

Month	Treatment	Mean Ψ_{stem} (MPa)			
		2003		2004	
		Predawn	Daily minimum	Predawn	Daily minimum
May	Rain-fed	−0.31a	−0.85a		
	Control	−0.28a	−0.75a		
	RDI	−0.29a	−1.27b		
	PRD	−0.22a	−1.15b		
June	Rain-fed	−0.55a	−1.56b	−0.36a	−1.73a
	Control	−0.52a	−1.15a	−0.38a	−1.71a
	RDI	−0.51a	−1.74b	−0.49a	−1.58a
	PRD	−0.50a	−1.89b	−0.42a	−1.44a
July	Rain-fed	−0.30a	−1.52a	−0.68a	−1.88b
	Control	−0.28a	−1.34a	−0.55a	−1.40a
	RDI	−0.39a	−1.38a	−0.77a	−1.49b
	PRD	−0.36a	−1.59a	−0.65a	−1.52b
August	Rain-fed	−0.70b	−1.75b		
	Control	−0.48a	−1.17a		
	RDI	−0.48a	−1.87b		
	PRD	−0.61ab	−1.77b		
September	Rain-fed	−0.61b	−2.04b	−1.48b	−2.70b
	Control	−0.37a	−1.38a	−0.70a	−1.35a
	RDI	−0.42a	−1.44a	−0.77a	−1.27a
	PRD	−0.46ab	−1.77b	−0.81a	−1.50a

In 2003, measurements were made in the Rain-fed and Control treatments in one day of each month, and in the RDI and PRD treatments one or two days after. In 2004, all the treatments were measured on the same day. See text both for details on the measurements and definition of treatments. Means followed by a common letter are not significantly different at the 5% level

amounts of water supplied by irrigation on the same periods were 33% of ET_c in 2003 and 29% of ET_c in 2004. These data shows that we managed irrigation reasonably well. The amount of water supplied to the RDI trees during the whole irrigation season was 58% of ET_c in 2003 and 48% of ET_c in 2004; in the PRD treatment, we supplied a total of 65% of ET_c in 2003 and 46% of ET_c in 2004.

Figure 3 shows the seasonal evolution of the REW values calculated with Eq. (2) for each one of the treatments, both for 2003 and 2004. In the Rain-fed treatment the soil dried up all throughout the dry seasons, the average value of θ in the rootzone at the end of the dry season being 0.11 $m^3 m^{-3}$, both in 2003 and 2004. In the Control treatment, REW values were usually over 0.8. The average value of θ in the wet bulbs for the whole irrigation season was 0.19 $m^3 m^{-3}$, both in 2003 and 2004. The REW values of the RDI and PRD treatments fluctuated between 0.5 and 0.8. The average value of θ all throughout the irrigation season of 2003, in the wet bulbs of both deficit irrigation treatments, was 0.17 $m^3 m^{-3}$. In the irrigation season of 2004, we recorded an average of 0.17 $m^3 m^{-3}$ for the RDI treatment and 0.16 $m^3 m^{-3}$ for the PRD treatment.

Data on the seasonal evolution of Ψ_{stem} at predawn and midday are shown in Table 1. In 2003, differences between irrigated and unirrigated trees became significant from the first week of August. As expected, the values closer to zero were recorded in the Control trees, both at predawn and midday. Differences in predawn Ψ_{stem} between irrigated treatments were never significant. At midday in August, the values recorded in the trees of the two deficit irrigation treatments were significantly lower ($P < 0.05$) than that of the Control trees. These differences were lower in September, probably because IA matched 100% of ET_c in both treatments since August 18, DOY 230 (Fig. 1). In addition, the atmospheric demand in September 4, the day in which we measured Ψ_{stem} in the deficit irrigation treatments, was lower than in September 2, the day in which we measured in the Rain-fed and Control trees (Fig. 4). No differences in Ψ_{stem} between the RDI and PRD treatments were

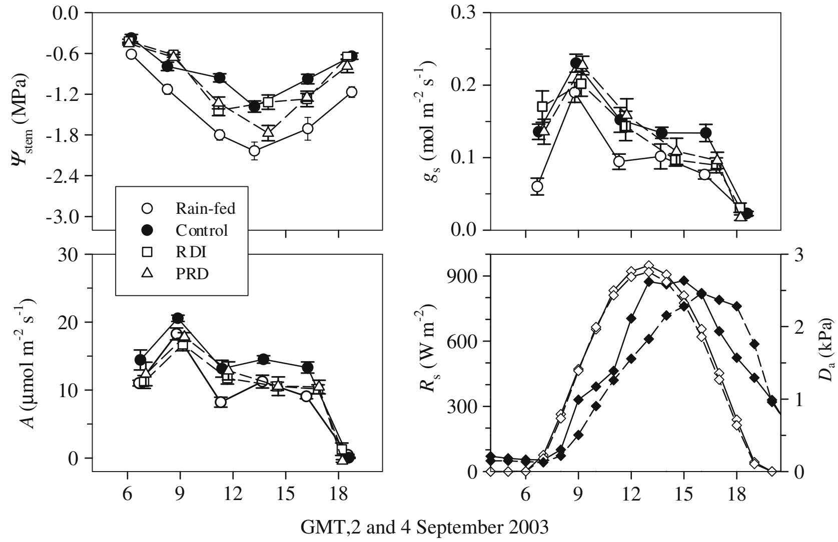

Fig. 4 Diurnal time courses of stem water potential (Ψ_{stem}), stomatal conductance (g_s) and assimilation rate (A) recorded in trees of the four studied treatments, on 2 (treatments Rain-fed and Control) and 4 (treatments RDI and PRD) September 2003. Each point represents the average of six values per treatment. Vertical bars indicate twice the standard error. Values of solar global radiation (R_s, open symbols) and vapour pressure deficit of the air (D_a, closed symbols) recorded on the measurement days are also plotted (dashed lines correspond to 4 September). GMT=Greenwich mean time

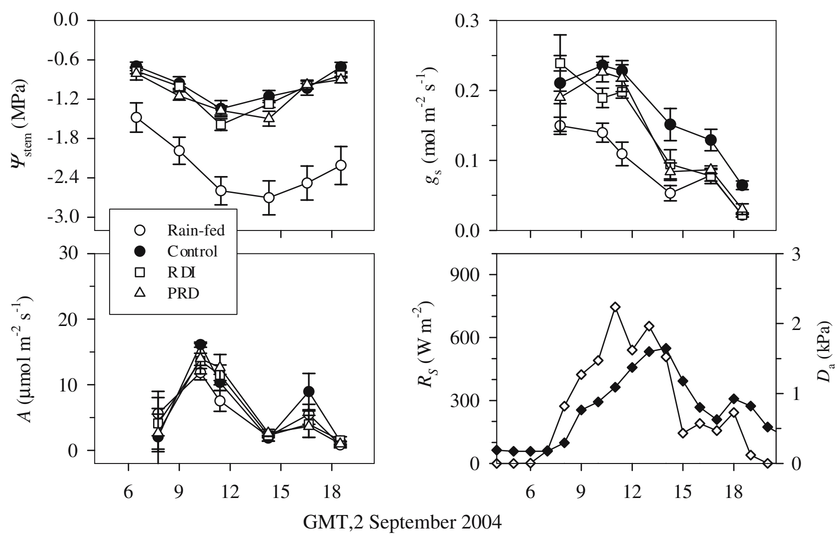

Fig. 5 As in Fig. 4, except that the measurements were made on 2 September 2004

observed, except for the minimum daily values measured in September (Table 1). In 2004, measurements in June and July show no differences between treatments in predawn Ψ_{stem}. In July, we measured at midday greater values of Ψ_{stem} in the Control trees than in the rest of the treatments. In September the measurements were made on the second day of the month, so the deficit irrigation treatments were not affected by the recovery of irrigation, since IA values were not 100% of ET_c until September 6, DOY 251 (Fig. 2). This month we found significant differences ($P<0.05$) in Ψ_{stem} between the unirrigated and the irrigated treatments, both at predawn and midday. No differences, however, were found between the Control

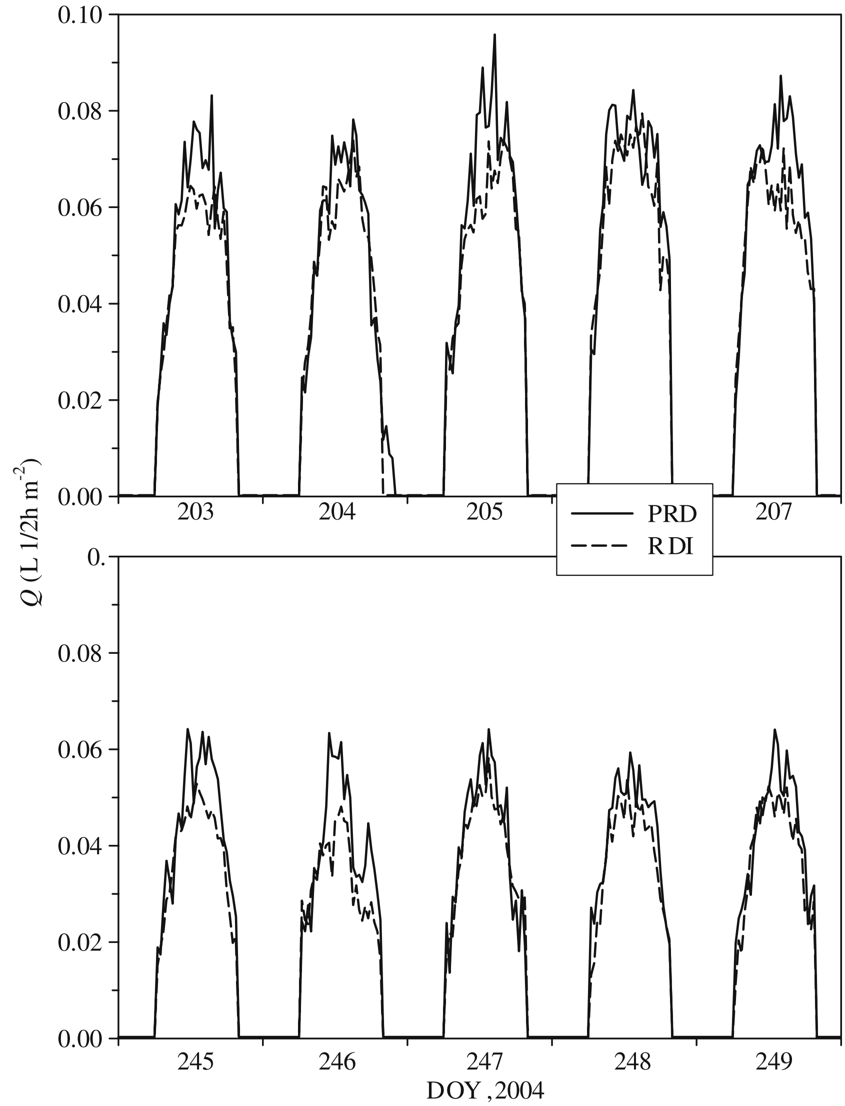

Fig. 6 Diurnal time course of sap flow per unit leaf area (Q) calculated from the sap flow measurements made in the trunk of representative trees of the treatments RDI and PRD at the end of July and at the beginning of September 2004. Data represent the average of the 3 sets of probes installed in one RDI tree and that of the 2 sets of probes installed in one PRD tree. See text for details on the treatments. DOY = day of year (DOY 245 = September 3)

and the deficit irrigation treatments. Both in 2003 and 2004, the values of predawn Ψ_{stem} measured in the Rain-fed trees were usually below −0.50 MPa (Table 1), a value considered by many as a threshold for water stress in olive (Fernández and Moreno 1999). This threshold value was reported for leaf water potential (Ψ_{leaf}), but at predawn $\Psi_{stem} \approx \Psi_{leaf}$. In general, the recorded Ψ_{stem} values were lower in 2004 than in 2003. This agrees with the lowest REW values measured in 2004 (Fig. 3).

Table 2 shows data on the seasonal evolution of the daily maximum values of g_s and A measured in trees of the four studied treatments, during the experimental seasons of 2003 and 2004. We found no differences in g_s between treatments in 2003. In July 2004 we found some differences between treatments, and in September the g_s values were significantly lower ($P < 0.05$) in the unirrigated trees than in the irrigated ones. No differences were found between irrigated treatments, at this time of

Table 2 Daily maximum values of stomatal conductance (g_s) and net CO_2 assimilation rate (A) measured in trees of the four studied treatments throughout the irrigation seasons of 2003 and 2004

Month	Treatment	g_s (mol m^{-2} s^{-1})		A (μmol m^{-2} s^{-1})	
		2003	2004	2003	2004
May	Rain-fed	0.193a		23.3a	
	Control	0.223a		25.3a	
	RDI	0.202a		18.7a	
	PRD	0.237a		20.5a	
June	Rain-fed	0.169a	0.251a	15.0b	18.3a
	Control	0.163a	0.260a	16.0b	19.5a
	RDI	0.144a	0.239a	9.6a	18.6a
	PRD	0.191a	0.261a	8.9a	18.6a
July	Rain-fed	0.218a	0.223ab	17.1a	14.6ab
	Control	0.247a	0.242b	16.8a	16.0b
	RDI	0.215a	0.183a	17.5a	11.6a
	PRD	0.188a	0.241b	15.7a	15.3b
August	Rain-fed	0.164a		13.8a	
	Control	0.195a		14.4a	
	RDI	0.135a		12.4a	
	PRD	0.168a		14.5a	
September	Rain-fed	0.190a	0.140a	18.3ab	11.8a
	Control	0.230a	0.236b	20.6b	16.1a
	RDI	0.202a	0.189ab	16.7a	13.6a
	PRD	0.227a	0.226b	17.8ab	14.0a

In 2003, measurements were made in the Rain-fed and Control treatments in one day of each month, and in the RDI and PRD treatments one or two days after. In 2004, all the treatments were measured on the same day. Data shown are the average of six sampled leaves. See text both for details on the measurements and definition of treatments. Means followed by a common letter are not significantly different at the 5% level

the year. Results on A show some differences between treatments in 2003. In June the A values recorded in the Rain-fed and Control trees were greater than those from the RDI and PRD trees. These differences, however, might be partly due to differences in PAR between the two measurement days: the average value of PAR during the measurement of maximum A was 1207 μmol m^{-2} s^{-1} in June 12, the day in which A was measured in the Rain-fed and Control treatments, and 304 μmol m^{-2} s^{-1} in June 11, the day in which A was measured in the deficit irrigation treatments. In September 2003, at the end of the irrigation season, the greatest A values were recorded in the Control trees, and no significant differences ($P < 0.05$) were observed between the other three treatments. In 2004, the greatest values of A were always recorded in Control trees. In July we found greater A values in the PRD than in the RDI trees. In September, however, we found no differences between treatments. Weather conditions in September 2, the measurement day, likely affected the results.

Figures 4 and 5 show the diurnal time courses of Ψ_{stem}, g_s and A values recorded at the end of the experimental seasons of 2003 and 2004, respectively. Also shown are the time courses of R_s and vapour pressure deficit of the air (D_a, kPa), the two main weather variables influencing plant water status and leaf gas exchange, for each measurement day. Data on Ψ_{stem} confirms results shown in Tables 1 and 2: the Ψ_{stem} values were closer to zero in the Control trees than in the Rain-fed trees; the values in the deficit irrigation treatments were somewhere in between, and no consistent differences between RDI and PRD were observed. In September 2004 (Fig. 5) the differences in Ψ_{stem} between irrigated treatments were smaller than in September 2003 (Fig. 4). This could partially be due to the fact that 2 September 2004 was a partially cloudy day with relative low atmospheric demand, while 2&4 September 2003 were both hot and clear sky days. The Ψ_{stem} values recorded in the Rain-fed treatment were markedly lower in September 2004 than in September 2003, despite the small difference in θ between the two

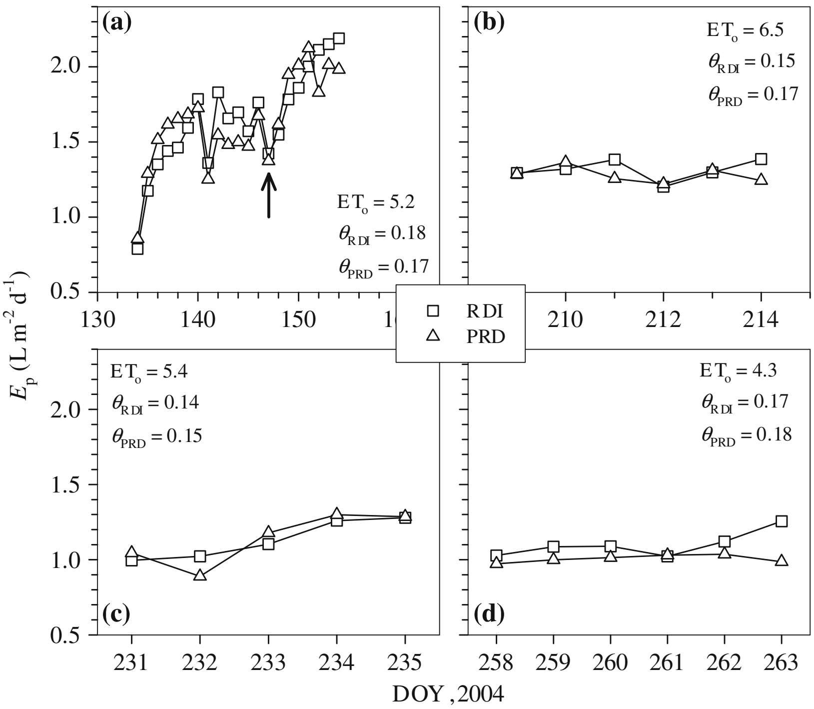

Fig. 7 Values of daily transpiration per unit of leaf area (one side) (E_p) estimated from the sap flow measurements made in one PRD and one RDI tree, at mid May (**a**), end of July (**b**), end of August (**c**) and mid September (**d**) 2004. The arrow in figure (**a**) shows the beginning of the irrigation treatments. Average data for each of the measurements periods on reference evapotranspiration (ET$_o$, mm) and volumetric water content (θ, m^3 m^{-3}) in the soil of both trees are also shown. See text for description of the treatments. DOY=day of year

dates (0.11 m^3 m^{-3} in 2003 and 0.10 m^3 m^{-3} in 2004). On 2 September 2003, significant differences ($P < 0.05$) in g_s were recorded between the Rain-fed and the Control treatments, except at sunset, when the stomata were nearly fully closed (Fig. 4). The g_s values recorded in the RDI and PRD trees were in between those of the Control and Rain-fed trees for most of the day, and no clear differences between both deficit irrigation treatments were observed. On 2 September 2004 (Fig. 5), the meteorological conditions were likely responsible, at least in part, for the peak g_s values having being recorded later on the day than in September 2003 (Fig. 4). The fact that the g_s values were much lower in September 2004 than at about the same time of 2003 could be explained by differences in the trees water status, as shown by the Ψ_{stem} values. Once again, the g_s values of the trees under deficit were in between those of the Rain-fed and Control trees, and no differences between RDI and PRD were observed for most of the day. The daily courses of the sap flow rates measured throughout the irrigation season of 2004 in representative trees of both deficit irrigation treatments (Fig. 6), agree with the lack of differences in g_s between those treatments. The A values recorded in the four studied treatments (Figs. 4, 5) showed the same tendency than the g_s values: A was significantly lower ($P < 0.05$) in the Rain-fed trees than in the Control trees. The values of the two deficit irrigation treatments fell between the Rain-fed and Control treatments. Differences between treatments were smaller in 2004 than in 2003, probably due to the lower R_s registered in September 2004.

In Fig. 7 we show the daily water consumption per unit of leaf area, estimated from sap flow measurements in a representative tree of the PRD and RDI treatments, at different periods along the experimental period of 2004. Also shown in the figure are the average values of ET$_o$ and θ for each period and treatment. Figure 7a shows a clear response of E_p to the beginning of irrigation in May 26, day of year (DOY) 147. Soon after the increase of θ by irrigation

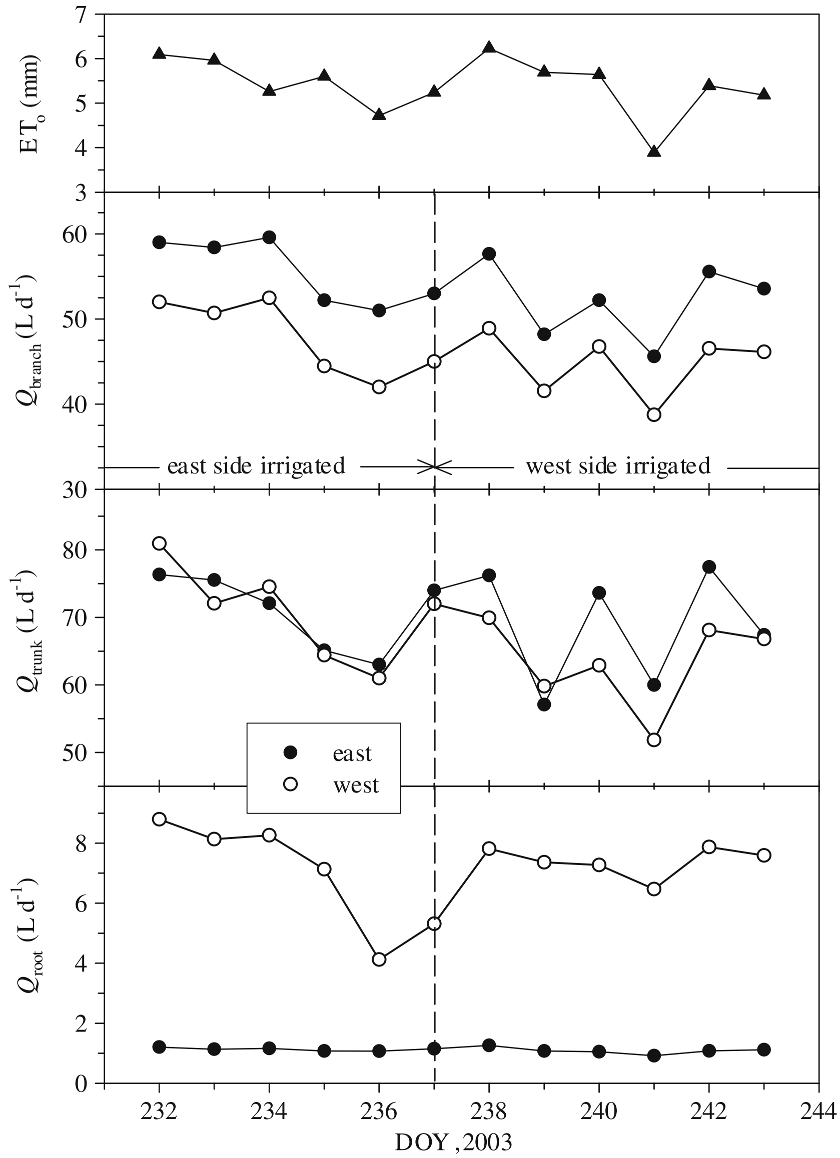

Fig. 8 Daily sap flow estimated from heat-pulse measurements made in two main roots (Q_{root}) of a tree of the PRD treatment, each growing in one of the two sides, east and west, of the rootzone affected by the alternate irrigation. Measurements, made at the end of August 2003, correspond to a few days before and after changing irrigation from the east to the west side. Also shown are the daily sap flow estimated from the readings of the heat-pulse probe installed at each side of the base of the trunk (Q_{trunk}), and those recorded at the two main branches of the tree (Q_{branch}), which were also oriented one to the east and the other to the west. Values of reference evapotranspiration (ET_o) for the measurement days are also plotted. DOY=day of year (DOY 232=August 20)

(at this time of the year even the deficit irrigation treatments were irrigated to 100% of ET_c) and due to the atmospheric demand typical of that time of the year, high enough to enhance transpiration but not as high as to favour stomatal closure, E_p peaked to values over 2.0 l m^{-2} day^{-1}. At the end of July (Fig. 7b) and August (Fig. 7c) irrigation was reduced to match the requirements of the imposed deficit irrigation treatments, which could explain the drop on E_p to values between 1 and 1.5 l m^{-2} day^{-1}. In mid September (Fig. 7d) the experimental trees were again irrigated to 100% of ET_c, but the low atmospheric demand made

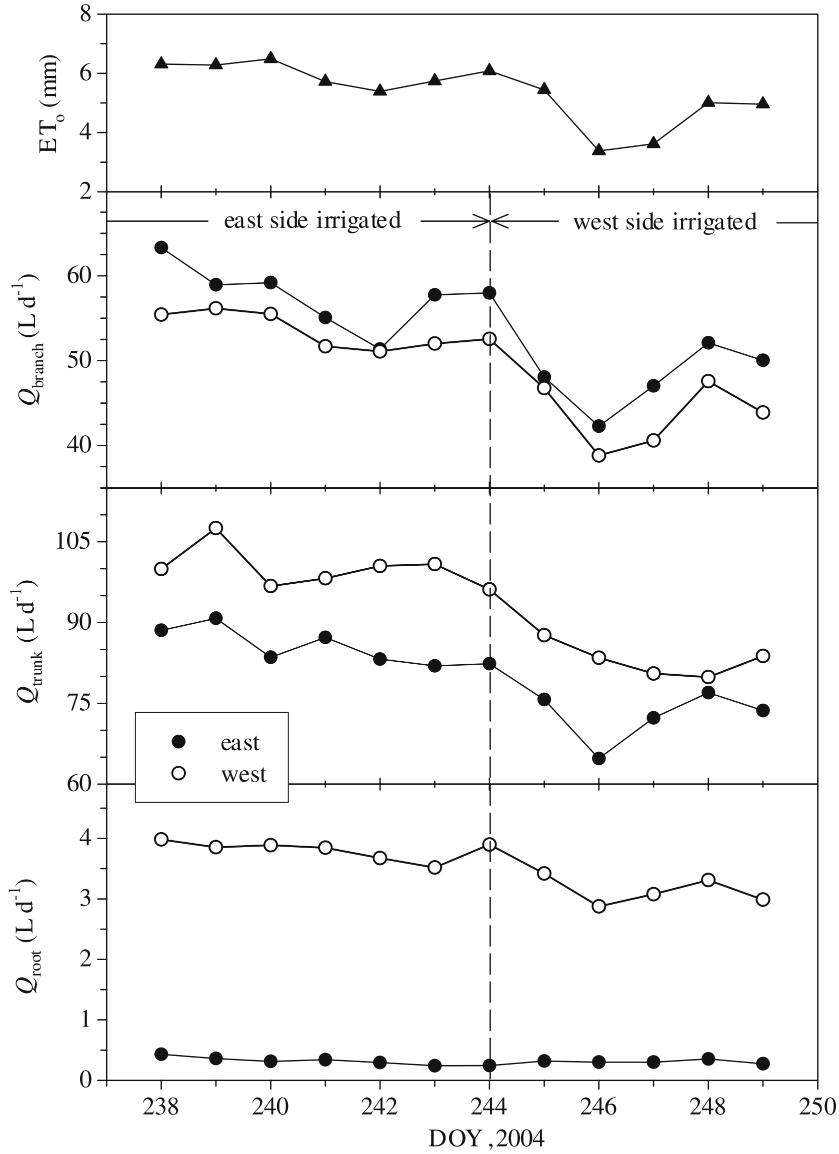

Fig. 9 As in Fig. 8, but for the measurements made at the end of August and beginning of September 2004

the E_p values to remain around 1 l m^{-2} day^{-1}. In addition, the LA of the trees was at its maximum at this time of the year (the growing period ended at the end of July), which contributed to the observed lower transpiration per unit of leaf area. In any case, the key result from this figure is that no differences in E_p between the two trees under deficit irrigation were found, for most of the experimental days.

Figures 8 and 9 show that switching irrigation in the PRD trees, from one half of the rootzone to the other half, did not have any influence on the sap flow recorded in any of the explored conductive organs. Data shown in these figures were recorded at the end of the irrigation seasons, and correspond to a single tree. The other two trees instrumented in 2004 showed the same tendency. Also shown in the figures are the daily ET$_o$ values calculated for the measurement periods. The corresponding REW values are shown in Fig. 3. We were expecting some change in the recorded sap flow values with the alternate irrigation, at least in Q_{root}, but Figs. 8 and 9 show that the Q values mimicked the atmospheric demand rather than the change of irrigation from one side of the rootzone to the other. As for the influence of switching irrigation on θ, in 2003, when irrigation was applied to the other side every 2 weeks, soil water measurements made around the period shown in Fig. 8 show that θ decreased in the drying side from 0.19 to 0.17 $m^3\ m^{-3}$. In 2004, when irrigation was applied to the other side every 3 weeks, measurements made around the period shown in Fig. 9 show that θ decreased from 0.17 to 0.14 $m^3\ m^{-3}$.

Discussion

The small and random differences found in Ψ_{stem}, g_s and A, provide no clear evidence of PRD causing a positive effect on the olive tree performance, as compared to RDI (Tables 1 and 2; Figs. 4, 5). Benefits of the PRD approach were reported in the early work made in grapevine (Dry et al. 1996, 2000a, b, 2001; Dry and Loveys 1999; Loveys et al. 2000; Stoll et al. 2000), but in those experiments PRD was compared to full irrigation treatments, and not to deficit irrigation treatments. Dos Santos et al. (2003) and de Souza et al. (2003, 2005) had a PRD and a traditional deficit irrigation treatment in grapevines, both corresponding to an irrigation of 50% of ET_c. De Souza et al. (2003) observed less negative values of Ψ_{leaf} in PRD than in the deficit irrigation affecting both sides of the vine. They found lower values of g_s in the PRD vines than in vines under other deficit irrigation treatment, at the end of the season only, as well as in measurements made under controlled conditions of CO_2, light and temperature, and observed no differences in A between both deficit treatments. In a companion study, dos Santos et al. (2003) found that PRD reduced leaf area associated with lateral shoots, canopy wideness and shoot weight. All the differences between treatments reported by de Souza et al. (2003) and dos Santos et al. (2003) were subtle, and the authors advise more research before recommending PRD at the commercial level. The work made by de Souza et al. (2005) in the same vineyard confirms above results.

Kang et al. (2002) studied the influence of PRD in pear trees. Apart from the peculiarities of their PRD treatment (water was applied once every 3 weeks by pond irrigation), the authors mention that groundwater contribution possibly influenced their results. Additionally, they compared PRD to full irrigation but not to a deficit irrigation treatment. Therefore, their results, and those from further experiments they did in the same orchard (Kang et al. 2003a, b) are little illustrating of possible differences between PRD and a regulated or conventional deficit irrigation treatment. Goldhamer et al. (2002), however, used typical PRD treatments and companions RDI treatments in daily-irrigated pear trees. Both PRD and RDI trees received 50% of ET_c during stage 2. They measured the daily time course of Ψ_{stem} at the end of this stage, and found less negative values in PRD1 than in RDI1, from 6:00 to 9:00 am. No differences, however, were found in g_s. In addition, they did not detect a reduction in trunk growth as measured with linear variable displacement transducers, which supports the assumption that there was not a PRD effect. They also found no differences between the PRD and RDI trees neither in fruit growth patterns nor in individual fruit weights. The authors concluded that their experiment did not support the occurrence of PRD-related root signalling. However, and based on the Ψ_{stem} results, they recommend more research specific for fruit trees.

In mature olive trees, Wahbi et al. (2005) and Centritto et al. (2005) observed that in olive trees irrigated with 50% of ET_c by PRD, Ψ_{leaf} was significantly lower than in control trees irrigated with 100% of ET_c on the two sides; the PRD trees closed their stomata earlier in the day than the control trees, and both the relative water content and photosynthetic capacity of the leaves were maintained in the PRD trees. Our results show that the reduction in Ψ_{stem} observed in our PRD treatment, as compared to the Control treatment, was similar to the RDI treatment, except for the midday minimum recorded on 4 September 2003 (Table 1). Figure 4, however, shows that the recorded Ψ_{stem} values were similar in both deficit irrigation treatments for most of the day, except at 14:00 hours, when the daily minimum was recorded. We also observed a decrease in g_s in our PRD trees as compared to our Control trees (Table 2, Figs. 4, 5), but a similar decrease, or even greater sometimes, was recorded in the RDI trees. The values of A decreased parallel to the decrease on irrigation (Table 2, Figs. 4, 5): the greater A values were usually recorded in the Control trees, and the lower ones in the Rain-fed trees; the values in the RDI and PRD trees were somewhere in between, and there were no differences between these treatments, except in July

2004, when we recorded a greater daily maximum in PRD than in RDI (Table 2). This exception does not allow us to support the assumption of *A* being favoured in PRD as compared to RDI. Centritto et al. (2005) measured g_s and *A* both in ambient conditions and in controlled conditions (PPFD of 1400 μmol m^{-2} s^{-1}, leaf temperature fixed to 25 °C, relative humidity in the range of 45–55%). In ambient conditions, g_s and *A* were significantly lower in PRD than in the control treatment in which trees were irrigated with 100% of ET_c on the two sides; in controlled conditions there was a parallel significant increase in g_s and *A* in all treatments, in comparison to their respective values obtained in ambient conditions. They also reported that gas exchange studies of stomatal vs. non-stomatal limitations to *A* based on measurements made at ambient CO_2 concentration, could lead to significant underestimation of diffusional limitations.

De Souza et al. (2003, 2005) remarked that point measurements under field conditions such as those made with a porometer may not reveal stomatal control as effectively as other more integrated measurements such as stem sap flow or leaf carbon isotope composition. Sap flow measurements made by the Souza et al. (2003) supported their results on stomatal closure, in the sense that they recorded lower sap flow rates in PRD vines than in vines under deficit irrigation affecting both sides, which suggests a stronger reduction on g_s in the PRD treatment. The sap flow values recorded in our experimental trees show a similar transpiration dynamics in both the PRD and the RDI trees, and no indications of greater sap flow rates in RDI than in PRD. Figure 6, in fact, shows even slightly greater sap flow rates per unit leaf area (*Q*) in the PRD trees than in the RDI trees. This, however, could be due to errors in the estimation of either LA or actual sap flow rates. In any case, our sap flow measurements, which reflect water use over a long term, agree with our gas exchange measurements, in the sense that both show no evidence of g_s being more reduced in PRD trees than in RDI. The daily water consumption, also estimated from the sap flow measurements, was similar in the trees of our two deficit irrigation treatments for most of the days, throughout the irrigation period (Fig. 7). The trees respond clearly and immediately to water supplied by irrigation, with significant increases in E_p (Fig. 7a) on the days after the start of the irrigation season. This quick response of the root water uptake and E_p to water supply is well known in olive (Fernández and Moreno 1999; Fernández et al. 2001). Later in the season E_p was more influenced by the atmospheric demand and the soil water status than by the type of deficit irrigation treatment (Figs. 7b–d). The recorded values of E_p agree with what it is known for olive, except for those at the beginning of the irrigation season, which are greater than those previously reported. Likely the favourable weather and soil water status at that time of the year, in addition to the low LA per tree after the winter pruning, were responsible for the high E_p values recorded on those days. In a previous work we carried out in the same orchard (Fernández and Moreno 1999), sap flow measurements made in well-irrigated trees later in the season showed a peak E_p value of 1.65 l m^{-2} day^{-1}, on a day with maximum values of R_s and D_a of 850 W m^{-2} and 3 kPa, respectively. This agrees with data recorded in potted olive plants by Natali et al. (1991), who reported a maximum E_p value of 1.7 l m^{-2} day^{-1}. In our previous work we rarely observed E_p values greater than 1.20 l m^{-2} day^{-1}, which agree with data shown in Figs. 7b, c, d.

Alternating irrigation in our PRD trees did not cause a change in either the water taken up by main roots at each side of the trees, or in the sap flow in both trunk locations and main branches of each side (Figs. 8, 9). When we got the results of 2003 (Fig. 8) this lack of response surprised us, since Fernández et al. (2001) reported, from measurements made in the same orchard, that roots of the same characteristics as those monitored in this work were able to absorb water immediately after wetting, and root activity quickly shifted to the regions were the soil had been wetted. We thought that perhaps the lack of response shown in Fig. 8 was due to the relatively high amount of water still remaining in the soil of the drying part at the end of the 2 weeks without irrigation. This was one of the reasons we decided to alternate irrigation every 3 weeks in 2004. The results of that year, however, showed the same (Fig. 9), despite the lower values of θ in the dry side just before switching irrigation, as compared to those measured in 2003. Kang et al. (2003b) measured sap flows in main roots and in the trunk of pear trees under different irrigation treatments, including PRD. They observed a quick increase in water uptake in roots of the drying side after rewatering; their monitored roots had a bigger diameter than ours (100.4 mm and 64.3 mm diameter roots in the west and east side of the vine), and their PRD treatment consisted of alternating pond irrigation between the two sides of the trees once every 3 weeks, which caused sudden and dramatic changes in θ, from about 0.25 to 0.40 $m^3 m^{-3}$. In the work by Fernández et al. (2001), $\theta = 0.13$ $m^3 m^{-3}$ before rewatering. Loveys et al. (2000) observed that switching irrigation every 14 days was appropriate for grapevine, but they also commented on results with other woody species showing that this frequency could be delayed. Big trees such as the olive tree, capable to explore great volumes of soil—the volume of the wet bulbs in the Control treatment amounts to up to 10 m^3 (Fernández et al. 2003)—may have a different response to PRD than species with smaller and shallower root systems, such as grapevine. Wahbi et al. (2005) found no significant differences between alternating irrigation in olive every 2 or 4 weeks.

In previous work made in our experimental orchard, Fernández et al. (2003) showed that in trees irrigated with 100% ET_c by localised irrigation, E_p was markedly curtailed, as compared to the values recorded when the whole rootzone was wetted. Their results suggest that the water lost by transpiration was restricted due to a portion of the roots having being left in drying soil—localised irrigation wets just part of the rootzone—and that there is no need to alternate irrigation for achieving this effect. This hypothesis is supported by the findings of Wartinger et al. (1990) in almond, a species of a similar habitat. They observed control of stomata closure by ABA in young trees growing in big plastic lysimeters in which different soil drying treatments were imposed to the whole root system. They concluded that the hormone is produced in fine roots in drying soil, and that this phenomenon occurs as long as soil water content is high enough to avoid damage to the fine root system. They stated that ''it is the integration of water status over the entire soil profile, or at least a major part of it, that determines root activity and thus ABA production by roots''. It seems, therefore, that for some species including olive, no additional advantages on controlling water use are achieved by PRD as compared to RDI.

Conclusions

We have observed no improvement on the measured variables in mature olive trees under PRD as compared to RDI. Our data on stomatal conductance show that water lost by transpiration was restricted in the trees of both deficit irrigation treatments, as compared to the full irrigated treatment. These data, as well as those from the sap flow measurements, show that the reduction on transpiration was similar in the PRD trees than in the RDI trees. The switching of irrigation in PRD had no influence either in the water taken up by main roots at each side of the trees, or in the sap flow in both trunk locations and main branches of each side. Results from this work, and from previous work we did in the same orchard (Fernández et al. 2003), suggest that roots left in drying soil when a localised irrigation system is used might be responsible for the mentioned reduction on transpiration, and that there is no need to alternate irrigation for achieving this effect. Despite the fact that we did not evaluate the influence of PRD on either growth or on yield, our results suggest that similar benefits are to be achieved in olive orchards with RDI and PRD. Taking into account that an irrigation system suitable for the PRD approach is more expensive and difficult to manage, we see no agronomical advantages on PRD as compared to RDI.

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