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Early morning fluctuations in trunk diameter are highly sensitive to water stress in nectarine trees

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Abstract The sensitivity to water stress of different plant water status indicators was evaluated during two consecutive years in early nectarine trees grown in a semi-arid region. Measurements were made post-harvest and two irrigation treatments were applied: a control treatment (CTL), irrigated at 120 % of crop evapotranspiration demand to achieve non-limiting water conditions, and a deficit irrigation treatment, that applied around 37 % less water than CTL during late postharvest. The plant water status indicators evaluated were midday stem water potential (Ψ_{stem}) and indices derived from trunk diameter fluctuations: maximum daily shrinkage (MDS), trunk daily growth rate, early daily shrinkage measured between 0900 and 1200 hours solar time (EDS), and late daily shrinkage that occurred between 1200 hours solar time and the moment that minimum trunk diameter was reached (typically 1600 hours solar time). The most sensitive [highest ratio of signal intensity (SI) to noise] indices to water stress were Ψ_{stem} and EDS. The SI of EDS was greater than that of Ψ_{stem}, although with greater variability. EDS was a better index than MDS, with higher SI and similar variability. Although MDS was linearly related to Ψ_{stem} down to −1.5 MPa, it decreased thereafter with increasing water stress. In contrast, EDS was linearly related to Ψ_{stem}, although the slope of the regression decreased as the season progressed, as in the case of MDS. Further studies are needed to determine whether EDS is a sensitive index of water stress in a range of species.

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Introduction

Fruit orchards located in arid or semi-arid zones must deal with two main problems: water availability to obtain adequate production and, frequently, the poor quality of the water that is available. Consequently, producing high quality crops to maintain economic competitiveness becomes increasingly difficult. In this respect, irrigation scheduling based on plant water status is postulated as a promising tool for increasing water use efficiency since plant measurements include factors such as climate and soil water status (Jones 2004). For decades researchers have suggested that stem water potential (Ψ_{stem}) is a useful indicator in many species (Shackel et al. 1997). However, its main disadvantage is that it is a tedious measurement which cannot be automated and requires significant labor input (Naor and Cohen 2003; Ortuño et al. 2009). Advances in computing and electronics have made it possible to continuously record the trunk diameter fluctuations (TDF) first described by Kozlowsky and Winget (1964). From such data, Goldhamer and Fereres (2001) proposed a number of indices such as maximum (MXTD) and minimum trunk diameter (MMTD), maximum daily trunk shrinkage (MDS) and trunk growth rate (TGR) to characterize daily plant water status.

Since trees are part of the soil–plant–atmosphere continuum, plant water status measurements will depend not only on the soil water status but also on the environmental conditions (Fernández and Cuevas 2010; Ortuño et al. 2010), for which reason a reference value should be obtained in trees under non-limiting soil water conditions. The signal intensity of MDS (SI_{MDS}, obtained from trees exposed to water deficit and those from control, well watered trees) is a dimensionless variable where values greater than 1 indicate deficit irrigation and values equal to 1 indicate no water stress (Goldhamer and Fereres 2004). The SI_{MDS} relative to a non-stress control was tested for irrigation scheduling at various thresholds, previously calibrated by reference to the water stress level required according to the crop phenological period, increasing or decreasing the irrigation rate when SI_{MDS} exceeded or did not exceed, respectively, the SI_{MDS} threshold value (Fernández and Cuevas 2010). This type of irrigation scheduling has been studied in almond (Goldhamer and Fereres 2004; Pérez-Pastor et al. 2009; Puerto et al. 2013), citrus (García-Orellana et al. 2007; Velez et al. 2007; Ortuño et al. 2009), nectarine (De La Rosa et al. 2015) and peach (Conejero et al. 2007b) trees. In all these studies, maintaining the actual SI_{MDS} according to the pre-established threshold values presented serious problems, since rainfall promoted an excessive trunk growth in DI treatments and due to the loss of elasticity of the trunk tissues at the end of the growing season. For this reason, De La Rosa et al. (2015) proposed using both Ψ_{stem} and SI_{MDS} to improve this type of irrigation scheduling, thus avoiding excessive water stress levels.

The sensitivity of plant water stress indicators may be calculated by comparing SI_{MDS} and the coefficient of variation (CV—noise) as proposed by Goldhamer and Fereres (2001). The sensitivity of these indices to water stress, often compared with stem water potential (Ψ_{stem}—an indicator traditionally recognized as being very sensitive to water stress), has been repeatedly tested in different crops, as reviewed by Naor (2006) and Fernández and Cuevas (2010). Sometimes MDS was considered to show the greatest sensitivity to water stress, as in almond (Goldhamer and Fereres 2001), peach (Goldhamer et al. 1999; Remorini and Massai 2003), pomegranate (Galindo et al. 2013) and lemon (Ortuño et al. 2006) trees. Alternatively, Ψ_{stem} was more sensitive in apple (Naor and Cohen 2003), cherry (Abdelfatah et al. 2013), kaki (Badal et al. 2010), plum (Intrigliolo and Castel 2004) and pomegranate (Intrigliolo et al. 2011) trees. In contrast, TGR was generally less sensitive, and only responded to water stress in young trees (Moriana and Fereres 2002; Nortes et al. 2005) or at certain phenological stages of rapid trunk growth in adult trees (mandarin—Pagán et al. 2012; olive—Moriana et al. 2011 and plum—Intrigliolo and Castel 2004). The early detection of plant water stress is also important. Indeed, De la Rosa et al. (2014) found that Ψ_{stem} and MDS detected the water stress earlier than the gas exchange parameters in early nectarine trees under water deficit conditions.

Nevertheless, there are limitations to the use of MDS in irrigation scheduling, although signal intensity was similar or slightly higher for MDS than for Ψ_{stem}, the high CV of MDS (>15 %) compared to Ψ_{stem} (<10 %) suggesting that trunk diameter sensors should be installed on multiple trees to achieve robust results (Naor and Cohen 2003). Furthermore, other factors can affect MDS independently of soil water content and climatic water demand, such as tree age (Moriana and Fereres 2004), tree size (Intrigliolo and Castel 2006), the phenological period (Marsal et al. 2002; Fereres and Goldhamer 2003; Intrigliolo and Castel 2004; Conejero et al. 2007a; Egea et al. 2009; Pagán et al. 2012) and crop load (Moriana and Fereres 2004; Intrigliolo and Castel 2007; Conejero et al. 2010). Perhaps the most limiting factor is that MDS decreases when trees are submitted to severe water stress, rendering it unusable for scheduling irrigation during such periods (Ortuño et al. 2010), since its sensitivity decreases. Moreover, MDS decreased its sensitivity to water deficit according to the phenological stage, as seen in grapewine during post-veraison, and even during pre-veraison, when the water stress level was higher than −0.8 MPa (Intrigliolo and Castel 2007).

This work studies the sensitivity to water stress of different plant water status indicators, traditionally studied indicators and two new indices derived from TDF (early daily shrinkage, EDS, and late daily shrinkage, LDS, both of which varied according to the time of day that measurements were made) in early nectarine trees. Measurements were made during the post-harvest period, which includes 5 months of high water demand (from May to October) and accounts for 70 % of annual water inputs.

Materials and methods

Experimental site

The study was performed during two consecutive years (2009 and 2010) in a commercial orchard located in Murcia (38°8′N; 1°13′W). The experimental plot consisted of 2 ha of 7-year-old early nectarine trees cv 'Flanoba' grafted onto hybrid GF677 rootstock at a spacing of 5.5 m × 3.5 m. At the beginning of the experiment the trunk diameter of the trees and percentage of area shaded averaged 14.2 cm and 62.8 %, respectively, with no significant differences between treatments. The soil, with an average depth of 1.55 m, had a low-available potassium and phosphorus content, low organic matter and a clay-loam texture. The electrical conductivity (EC) of the irrigation water ranged from 1.5 to 2.5 dS m^{-1}, according to the source used (irrigation canal, well or a mix of both). Usual cultural practices (e.g. weed control, fertilization, pruning, fruit thinning and banding) were carried out by the technical department of the commercial orchard. The weather was typically Mediterranean, with hot, dry summers and mild, wet winters. Annual average temperatures were 24.1 and 22.7 °C

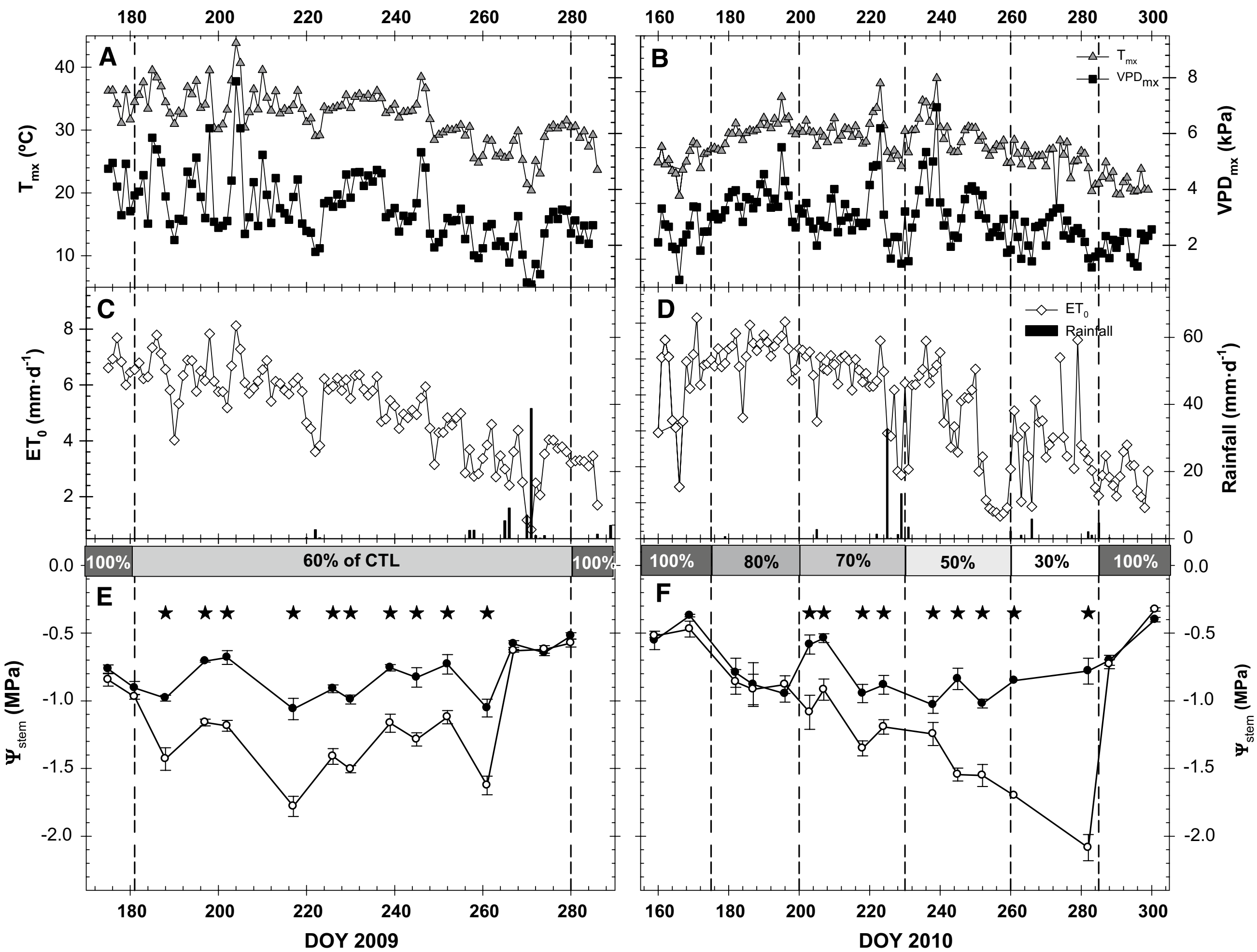

Fig. 1 Seasonal pattern of **a**, **b** maximum daily temperature (T_{mx}, *triangles*) and maximum daily vapor pressure deficit (VPD_{mx}, *squares*), **c**, **d** daily reference crop evapotranspiration (ET_0, *diamonds*) and rainfall (*bars*) and **e**, **f** stem water potential (Ψ_{stem}). Each *point* corresponds to daily average of 6 measurements per treatment for DI (*open circles*) and CTL (*filled circles*). *Error bars* denote ± SE. *Left* and *right panels* indicate data from 2009 and 2010, respectively. *Vertical dashed lines* separate periods with different irrigation rates in DI. *Asterisks* indicate significant differences between treatments at $p < 0.05$

for 2009 and 2010 respectively, with a maximum temperature in the summer of 2009 of 43.8 °C. Rainfall was mainly distributed between autumn and spring, amounting to 306 mm in 2009 and 330 mm in 2010 (data not shown). The reference crop evapotranspiration (ET_0) reached 1381 and 1258 mm in 2009 and 2010, respectively (Fig. 1c, d).

Irrigation treatments and measurements

A drip irrigation system was installed, with two lines per tree row spaced 1.2 m and 9.33 pressure-compensated emitters (1.6 l h^{-1}) per tree placed every 75 cm. Irrigation was scheduled weekly with a frequency that varied from 1 to 2 times per day in spring–summer to 2–5 irrigations per week for the rest of the year. The irrigation treatments applied were: (1) a control (CTL), irrigated at 120 % of crop evapotranspiration (ET_c) to maintain non-limiting soil water conditions; and (2) a water deficit treatment (DI), in which irrigation was less than the control during the postharvest period (which is considered non-critical for subsequent crop quality and yield). The DI treatment received 40 % less than the control continuously during the first year, from 20 to 70 % less (decreasing gradually) during the second. ET_c was determined as the product of reference crop evapotranspiration (ET_0), the crop coefficients (between 0.25 and 0.55) proposed by the Agricultural Information System of Murcia (www.siam.es) for this area, adjusted for tree size (Fereres and Goldhamer 1990), and an additional leaching fraction applied due to the salinity of the irrigation water used. During the period of water deficit, the DI treatment received 177 mm during the first year

(38 % less than CTL) and 167 mm during the second year (36 % less than CTL).

The experimental design consisted of three replicates per treatment, randomly distributed within the orchard. Each replicate had three adjacent tree rows and 15 trees per row. Measurements were taken in two trees per replicate of the central row, the other trees serving as borders.

Hourly meteorological data were measured from an automatic weather station located in the orchard. The variables measured were air temperature (T), relative humidity (RH), global solar radiation (G), wind speed 2 m above the soil surface (W), and rainfall (P). Daily ET_0 was calculated according to the FAO-56 Penman–Monteith equation (Allen et al. 1998) and hourly values of air vapor pressure deficit (VPD) from the T and RH. Maximum daily T and VPD were determined based on hourly values.

Soil volumetric water content (θ_v) was measured at 0.20 m depth with three multi-parameter soil sensor Hydra Probe II probes (Stevens Water Monitoring Systems, USA) per treatment, installed in the dripper line, 0.10 cm from the dripper and at 0.50 m from the trunk. Measurements were taken every 15 s, and 10 min means were recorded by a CR1000 data logger (Campbell Scientific, Inc., Logan, USA). Mean θ_v values were used to calculate the level of relative extractable water (REW, Granier 1987) using the following equation:

$$\mathrm{REW} = (R - R_{\mathrm{MIN}}) \times 100/(R_{\mathrm{MAX}} - R_{\mathrm{MIN}})$$

where R (%) is the actual soil water content, R_{MIN} (%) the minimum soil water content measured in dry conditions, and R_{MAX} (%) is the soil water content at field capacity. The values of R_{MIN} and R_{MAX} were 15 and 39 %, respectively.

Trunk diameter fluctuations were monitored in 6 trees per treatment (including those with Hydra Probes) using a set of linear variable displacement transducers (LVDT; Solartron Metrology, Bognor Regis, UK, model DF ± 2.5 mm, precision ± 10 μm) installed on the northern side of trunks, 30 cm above the ground and mounted on holders built of aluminium and invar (an alloy comprising 64 % Fe and 35 % Ni that has minimal thermal expansion). Measurements were taken every 30 s, and 10 min means were recorded by a CR10X data logger (Campbell Scientific, Inc., Logan, USA), connected to an AM16/32 multiplexer programmed to report mean values every 10 min. Several indices were derived from TDF following Goldhamer and Fereres (2001): maximum (MXTD) and minimum (MNTD) daily trunk diameter, maximum daily trunk shrinkage (MDS = MXTD − MNTD) and trunk daily growth rate (TGR, calculated as the difference between MXTD of two consecutive days). In addition, new indices based on TDF were determined: early daily trunk shrinkage (EDS) which took place between 0900 hours and midday solar time, and late daily trunk shrinkage (LDS), which occurred between midday and the moment that the minimum trunk diameter was reached (around 1600 hours solar time).

Midday (1200 hours solar time) stem water potential (Ψ_{stem}) was measured every 7–10 days in one leaf per tree from the inner part of the canopy that was enclosed within foil-covered plastic and aluminum envelopes at least 2 h before the measurement, in the same trees which were monitored by the LVDT sensors. Measurements were taken in a pressure chamber (Soil Moisture Equipment Corp. Model 3000) according to the procedure described by Hsiao (1990). Leaf conductance (g_s) was measured in one leaf per tree as in the case of Ψ_{stem}, using a portable gas exchange system CIRAS2 (PPSystem, Hitchin, Herfordshire, UK). Measurements were made on mature sun-exposed leaves under saturating light conditions (1500 μmol m^{-2} s^{-1}), leaf temperature ($T_{\mathrm{leaf}} \approx 30$ °C) and constant ambient CO_2 concentration ($C_a \approx 380$ μmol mol^{-1}). Daily variations in Ψ_{stem}, gas-exchange parameters and environmental conditions (air temperature and relative humidity) were measured from predawn to sunset at approximately 2 h intervals on 26th August, 2010 (summer)—a clear day representative of the postharvest period.

Sensitivity analysis for the different plant water stress indicators was carried out using the methodology proposed by Goldhamer and Fereres (2001). Signal intensity (SI) was calculated as the ratio between the deficit and control treatment average values, and sensitivity as the ratio between SI and the average coefficient of variation (noise) of the original variables during the water deficit period. In order to compare SI, CV and the sensitivity of the above mentioned indices, we only used data from those days when measurements for all the indicators were available. In addition, all measurements were always taken in the same trees. In this way, variables concerning the sampling day and type and size of the sample did not interfere with the study.

Statistical analysis

Relationships between plant water status indicators and meteorological variables were explored through linear and non-linear regression analyses. The coefficient of determination (r^2) was used to assess the goodness of fit of the associations among variables. Analysis of variance (ANOVA) was used to discriminate the main treatment effects. All analyses were performed using Statgraphics Plus for Windows Version 4.1.

Results

Soil water status

The control treatment showed average values of REW of between 0.6 and 0.73 (data not shown). These values were considerably less than 1 (the value considered to represent field capacity) as they were made 4 h after irrigation at midday, and water was rapidly depleted at the point of measurement (20 cm depth) due to the high root density. REW values of DI plants were significantly lower than in CTL plants, and gradually decreased during the water deficit period to reach the lowest value of 0.35.

Plant water status indicators

Ψ_{stem} varied between −0.4 and −1.06 MPa, according to climatic demand, in CTL over the 2 years of the study (Fig. 1e, f). The minimum values reached by DI were −1.78 and −2.08 MPa in 2009 and 2010, respectively. During the first year, DI values decreased rapidly compared to the control and maintained a constant difference of around 0.5 MPa (with a maximum of 0.7 MPa). During the second year, Ψ_{stem} varied according to the water deficit applied. When water deficit was mild (20 % less irrigation applied), DI values did not differ from control values, but more severe stress (30 % less irrigation) caused differences of around 0.4, and 1.2 MPa at the end of the growing season when irrigation was 70 % less.

MDS and EDS were apparently highly dependent on the meteorological variables studied (maximum daily temperature, T_{mx}, maximum daily air vapor pressure deficit, VPD_{mx} and ET_0) (However, TGR was not significantly correlated with any meteorological variable in the 2 years studied (data not shown).

During the experimental period, the mean MDS values were around 230 and 335 µm for CTL and DI, respectively, being significantly (45 %) higher in DI (Table 1).

Table 1 Mean values of the trunk diameter fluctuation parameters: maximum (MDS), early (EDS) and late (LDS) diameter shrinkage for the two irrigation treatments during the experimental period

Year	Treatment	MDS (µm)	EDS (µm)	LDS (µm)
2009	CTL	233 a	94 a	119 a
	DI	330 b	167 b	121 a
	ANOVA	<0.001	<0.001	ns (0.76)
2010	CTL	224 a	79 a	130 a
	DI	338 b	161 b	145 a
	ANOVA	<0.001	<0.001	ns (0.18)

Different letters within a column indicate significant differences according to ANOVA range test ($p < 0.05$)

In 2009, MDS values of DI were significantly higher from Day 187 (6 days after the beginning of water deficit) until Day 261 of the year. The rainfall (amounting to 61.1 mm) that occurred between Days 262 and 269 considerably diminished the differences in MDS between CTL and DI (Figs. 1c, 2a).

During the second year, the first significant difference in MDS values between treatments occurred at the end of a period during which a 20 % deficit was applied (Fig. 2b), a reduction that was not detected by Ψ_{stem} (Fig. 1f). Between Days 198 and 210 the largest differences between treatments (≈220 µm) occurred when VPD_{mx} was around 3 kPa, and 20–30 % less water was being applied to DI than to CTL. Rainfall (51.9 mm) between Days 225 and 232 decreased inter-treatment differences in Ψ_{stem}, while differences in MDS between treatments disappeared for 7 days. Between Days 250 and 260, differences were increased both in Ψ_{stem} and MDS during the 50 % deficit period. Afterwards, Ψ_{stem} differences continued to increase but MDS differences diminished and finally disappeared in spite of the lower irrigation and the increased soil moisture deficit (Figs. 1f, 2b).

During the experimental period, the mean values of EDS were around of 85 and 165 µm for CTL and DI, respectively, being significantly (95 %) higher in DI plants (Table 1). In 2009, EDS showed similar behavior to MDS (treatment differences in EDS started from the sixth day of deficit and ended with the rainfall Days 262–269) (Fig. 2a, c). In 2010, EDS showed the first significant difference between treatments on day 184, earlier than the other indices. Thereafter, treatment differences in EDS remained constant at around 80 and 100 µm for several weeks, except on the rainy days of mid-August when both CTL and DI had similar EDS values. Nevertheless, treatment differences remained and continued until the end of the water deficit period (Fig. 2d).

Treatment differences averaged 114 and 88 µm in 2009 and 100 and 75 µm in 2010, for MDS and EDS, respectively (Fig. 2a–d) and lasted slightly longer in the case of EDS during the second year.

Absolute LDS values were slightly higher than EDS values, except in DI plants, with no clear treatment differences (Table 1). In both years, the LDS of DI plants was significantly higher than that of CTL for only a small part of the water deficit period (21 out of 99 days in 2009, 35 out of 109 days in 2010) (data not shown), although when the whole season was considered there were no significant differences between treatments (Table 1).

Maximal values of TGR (near 100 µm day^{-1}) occurred in June and declined thereafter until growth stopped in late October, coinciding with the start of autumn. The TGR of CTL trees was generally higher than in DI throughout the period that water deficit was applied. However, significant

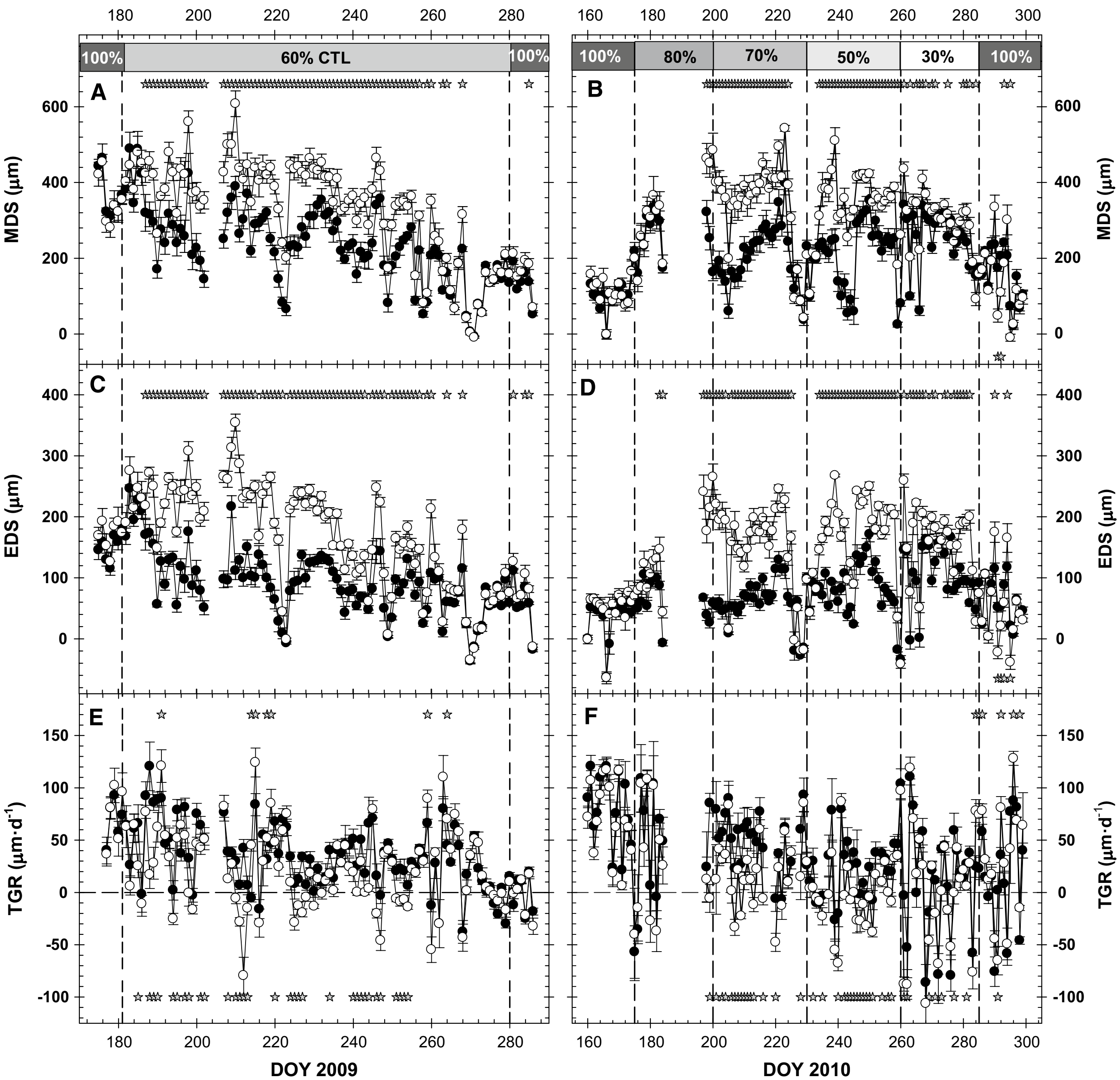

Fig. 2 Seasonal pattern of **a**, **b** maximum daily trunk shrinkage (MDS), **c**, **d** early daily trunk shrinkage (EDS), **e**, **f** trunk daily growth rate (TGR). Data are mean ± SE of 6 measurements for DI (*open circles*) and CTL (*filled circles*) plants. *Left* and *right panels* indicate data from 2009 and 2010, respectively. *Vertical dashed lines* separate periods with different irrigation rates in DI. *Asterisks* indicate significant differences between treatments at $p < 0.05$. The *top of the figure* indicates the water applied in DI as percentage of CTL. TDF measurements were interrupted due to malfunctioning of the sensors

treatment differences in TGR were only detected on 31 % of the days (averaged over both years of the study) that plants were exposed to water deficit (Fig. 2e, f).

Sensitivity of plant water status indicators

Signal intensity (SI, ratio of the deficit and control treatment value) of the plant water status indicators behaved very unevenly, depending on the water stress applied and the time of year considered (Table 2). During the water deficit period, $SI_{\Psi_{stem}}$, SI_{MDS} and SI_{EDS} averaged 1.4, 1.5 and 1.9 for 2009 and 1.5, 1.7 and 2.3 for 2010, respectively (Table 2).

In 2009 and 2010, SI_{EDS} was clearly greater than SI_{MDS} and $SI_{\Psi_{stem}}$. However, SI_{MDS} and $SI_{\Psi_{stem}}$ were similar throughout 2009, but in 2010 SI_{MDS} (1.4) was lower than

Table 2 Amount of irrigation water applied to the CTL and DI treatments, precipitation (*P*), signal intensity (SI), coefficient of variation (CV) and ratio between SI and CV for maximum (MDS) and early (EDS) daily trunk shrinkage and stem water potential (Ψ_{stem}) in each irrigation period

Year	Periods	Irrigation		*P* (mm)	SI			CV			SI CV^{-1}		
		CTL (mm)	DI (%)		MDS	EDS	Ψ_{stem}	MDS	EDS	Ψ_{stem}	MDS	EDS	Ψ_{stem}
2009	181–200	70	68	0	1.5	1.9	1.4	0.14	0.11	0.07	11.1	17.3	19.5
	201–230	99	54	3	1.7	2.3	1.6	0.16	0.15	0.07	10.9	15.8	23.9
	231–260	85	67	5	1.5	1.9	1.5	0.13	0.15	0.09	11.7	12.8	16.9
	261–280	30	62	62	1.0	1.2	1.2	0.20	0.25	0.08	5.2	4.7	14.9
	Season	284	62	70	1.5	1.9	1.4	0.16	0.17	0.08	9,5	11.3	19.0
2010	181–200	76	78	0	1.3	1.4	1.0	0.29	0.28	0.18	4.5	5.1	5.6
	201–230	79	72	51	1.9	2.9	1.5	0.21	0.27	0.13	8.7	11.0	11.5
	231–260	79	54	6	1.9	2.0	1.5	0.11	0.10	0.09	16.4	20.8	16.7
	261–280	26	32	7	1.4	2.8	2.7	0.14	0.12	0.08	9.7	23.7	33.7
	Season	260	64	64	1.7	2.3	1.5	0.18	0.19	0.12	9.5	12.2	12.5

Data are means of each period. The measurements used correspond to days on which are measured Ψ_{stem}. Each measurement corresponds to average of 6 sensors and measurements per treatment

$SI_{\Psi_{stem}}$ (2.7) and SI_{EDS} (2.8) when DI received 70 % less water than CTL (Table 2).

The CV shows that SWP had the lowest variability (0.10), while MDS and EDS showed medium but similar variability (0.18) and TGR had the highest variability (0.27). The greatest sensitivity was shown by Ψ_{stem} (19 and 12.5 for 2009 and 2010, respectively), while the sensitivity of EDS (11.3 and 12.2 for 2009 and 2010, respectively) was higher than that of MDS (9.5 and 9.5 for 2009 and 2010, respectively). Although Ψ_{stem} generally had the highest sensitivity throughout 2009 and most of 2010 (except for DOY 231–260), in 2010 EDS had similar sensitivity to Ψ_{stem} up to DOY 230 (Table 2).

The diurnal behavior of TDF hourly trunk shrinkage and meteorological variables were studied at three different times during 2010 (Fig. 3), as the water stress became more severe (Days 182, 207 and 282). TDF responded diurnally and seasonally to variations in soil moisture conditions and the evaporative demand of the atmosphere. The maximum hourly trunk shrinkage (≈50 μm h^{-1}) occurred slightly after midday in CTL, but earlier (by 2 and 3.5 h when water stress was moderate or severe, respectively) in DI plants (Fig. 3g–i) and with a greater magnitude (≈100 μm h^{-1}).

Relationships with Ψ_{stem}

Ψ_{stem} was well-correlated with the different indices derived from TDF. The coefficients of determination improved when three postharvest periods (rather than the whole year) were considered (June, July–August and September–October), defined according to the deficit irrigation strategies and the atmospheric variables, comprising data from the 2 years of the study (Fig. 4).

MDS and Ψ_{stem} showed a different pattern as postharvest progressed, since a Ψ_{stem} of −0.9 MPa corresponded to MDS values of 375 μm in June, 250 μm in July–August and 225 μm in September–October (data not shown). MDS was linearly related to Ψ_{stem} up to June, when Ψ_{stem} ranged from −0.3 to −0.9 MPa. In the periods July–August and September–October, the best fits were non-linear regressions in Ψ_{stem} values of between −0.6 and −1.8 and −0.3 and −2.1 MPa, respectively.

EDS was linearly related to Ψ_{stem} (although the slope decreased as the season progressed) with coefficients of determination similar to those of MDS (Fig. 4b), which were not improved by fitting non-linear regressions.

Discussion

In early nectarine trees, both traditional (Ψ_{stem} and MDS) and the newly proposed (EDS) indices of plant water status responded sensitively both to the continuous moderate deficit in the first year and the gradual deficit (from mild to severe) of the second year imposed postharvest. Control trees were under non-limiting soil water conditions (data not shown), with Ψ_{stem} values characteristic of well-watered trees (Shackel et al. 1997). These indices were dependent on meteorological variables, with closer relationships for MDS, EDS and LDS (data nos shown). Recently, De la Rosa et al. (2013) showed that MDS is strongly correlated with VPD_{mx} and T_{mx}, in well irrigated early nectarine trees.

EDS generally showed higher SI than the other indices during the 2 years of the study (Table 2), even when applying 70 % less water (at the end of 2010) (Table 2). A decrease has frequently been observed in SI_{MDS} at the end

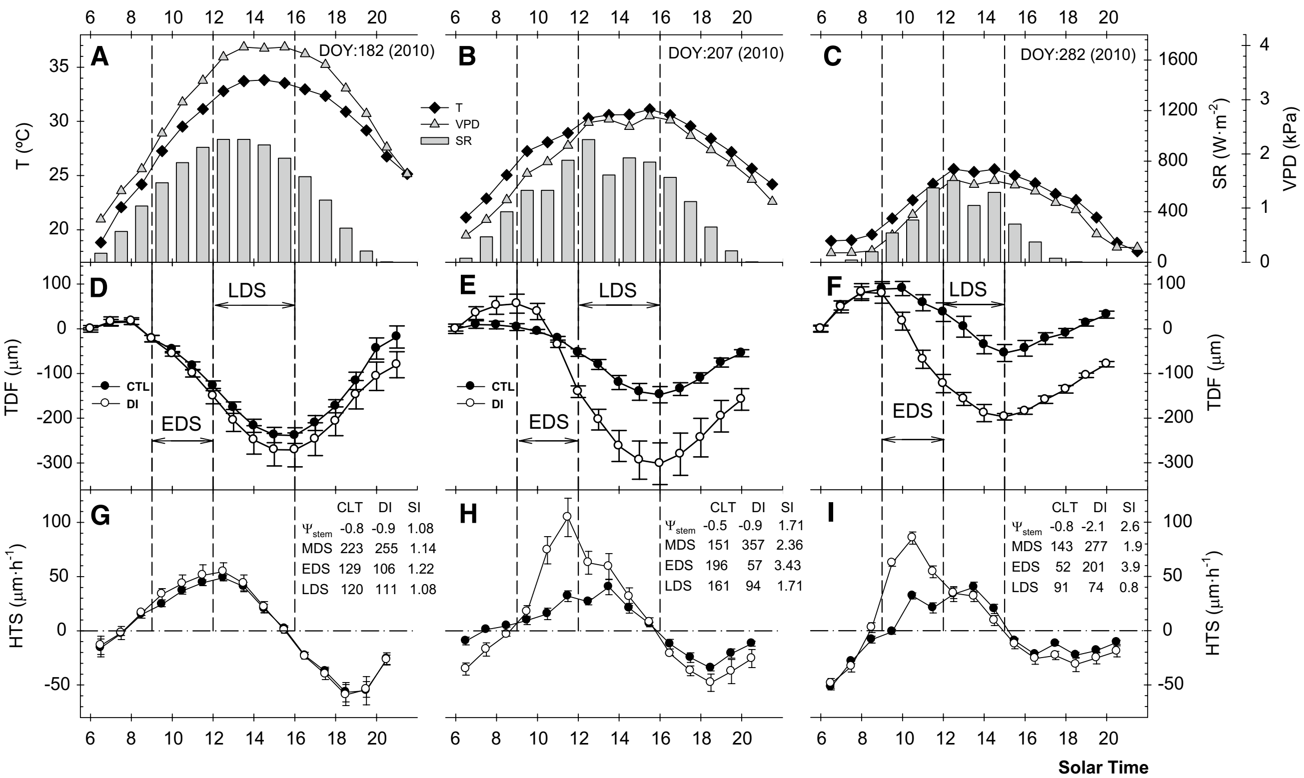

Fig. 3 Time courses of **a** temperature (*T*, *diamonds*), vapor pressure deficit (VPD, *triangles*) and solar radiation (SR, *bars*), **b** trunk diameter fluctuation (TDF) and **c** hourly trunk shrinkage (HTS) on days of the year 182 (*left*), 207 (*center*) and 282 (*right*) of 2010 for DI (*open circles*) and CTL (*filled circles*). Data are mean ± SE of 6 measurements (*EDS* early daily trunk shrinkage, *LDS* late daily trunk shrinkage)

of the season, probably as a result of a decrease in the tissue elasticity of the bark, decreased foliar mass or a lower water demand (Fereres and Goldhamer 2003; De la Rosa et al. 2014).

Before midday (the period of time for which EDS is calculated), leaf conductance of CTL and DI were similar until 1000 hours as indicated on DOY 238 in 2010 (Fig. 5d). However, the lower soil water content (SWC) of the DI treatment decreased Ψ_{stem} and produced the greatest degree of daily trunk shrinkage in DI trees (as in Figs. 3g–i, 5c) since increasing amounts of stem water reserves would have been recruited to sustain leaf transpiration as water stress progressed, as mentioned by Remorini and Massai (2003). These authors found that in the middle part of the day, stomatal regulation maintains leaf water potential of peach, whereas large differences were still evident for Ψ_{stem}. Thus similar trends for TDF and Ψ_{stem} between irrigated and non-irrigated trees were found, as in our study (Figs. 3, 5).

As the soil dried and/or as evaporative demand increased during the morning, the early stomatal closure of deficit-irrigated trees limited transpiration around mid-morning, since stomata are a particularly sensitive early indicator of water deficit, as previously argued (Jones 2004). In contrast, control trees showed higher stomatal conductance during most of the rest of day (Fig. 5d). Plants experiencing water stress show a more limited duration of the maximum stomatal opening than those that are well watered (Henson et al. 1982; Ruiz-Sánchez et al. 2007; Egea et al. 2011; Romero et al. 2012). Early stomatal closure is promoted by synergistic effects of the diurnal increase in VPD and limited soil water availability (Angelopoulos et al. 1996; Chaves et al. 2002).

Although DI trees showed decreased stomatal conductance, their hourly trunk shrinkage reached maximum values just before midday, which is earlier than in CTL (Fig. 5c), depending on the Ψ_{stem} of DI trees (Fig. 3). Likewise, $\Delta\Psi_{stem}$ only showed differences between treatments before midday (Fig. 5f). After midday the hourly trunk shrinkage values of the two treatments matched each other. Thus, EDS showed the highest SI values during most of the experiment (Table 2). Moreover, incomplete overnight stem rehydration can influence trunk shrinkage the following day (Zweifel et al. 2000). Indeed, as the 2010 season progressed, low soil water availability prevented complete recovery of trunk diameter during the night, promoting an

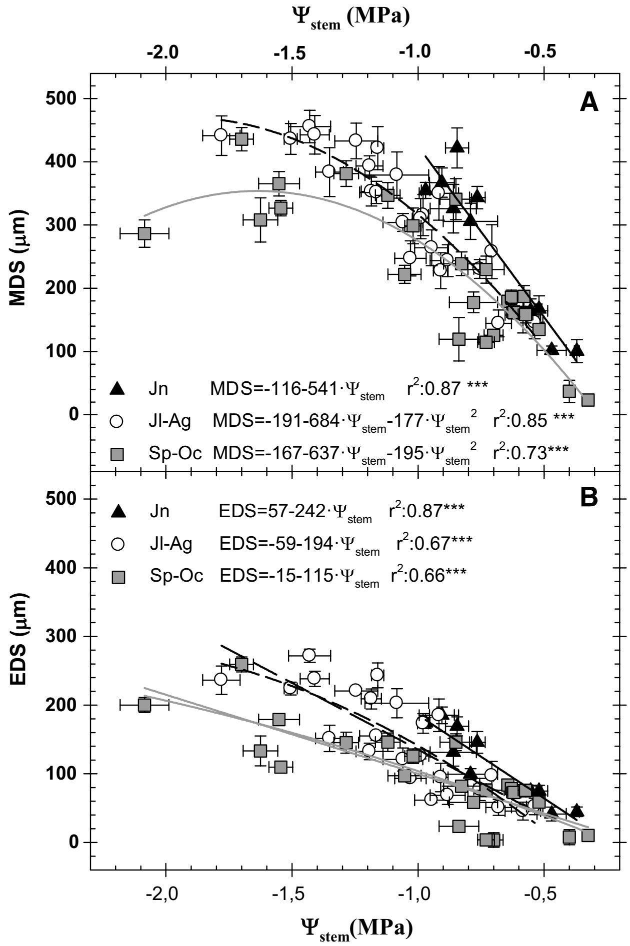

Fig. 4 Relationship between stem water potential (Ψ_{stem}) and **a** maximum daily trunk shrinkage (MDS) and **b** early daily trunk shrinkage (EDS) for three different postharvest periods in the 2 years of the study: June (*triangles*), July–August (*circles*) and September–October (*squares*). Each *point* corresponds to daily average of 6 sensors and measurements per treatment. Bidirectional *error bars* denote ± SE

earlier maximum of hourly trunk shrinkage the following day in DI trees (Fig. 3).

When the sensitivity (SI ratio and CV) was analyzed, Ψ_{stem} was generally the most sensitive index to water stress (Table 2), as indicated by many authors in different crops (McCutchan and Shackel 1992). Among the TDF-derived parameters, EDS had the highest sensitivity, although slightly lower than Ψ_{stem}. However, during most of 2010 EDS had similar or higher values of sensitivity than Ψ_{stem}, only being lower at the end of the year, coinciding with severe water stress. Interestingly, the sensitivity of EDS increased as the water stress increased (Table 2), similarly to that observed for Ψ_{stem}, an index considered to detect the accumulative effects of water deficit (Intrigliolo and Castel 2006). In contrast, MDS decreased with the water stress level (Ortuño et al. 2010), as previously detected under

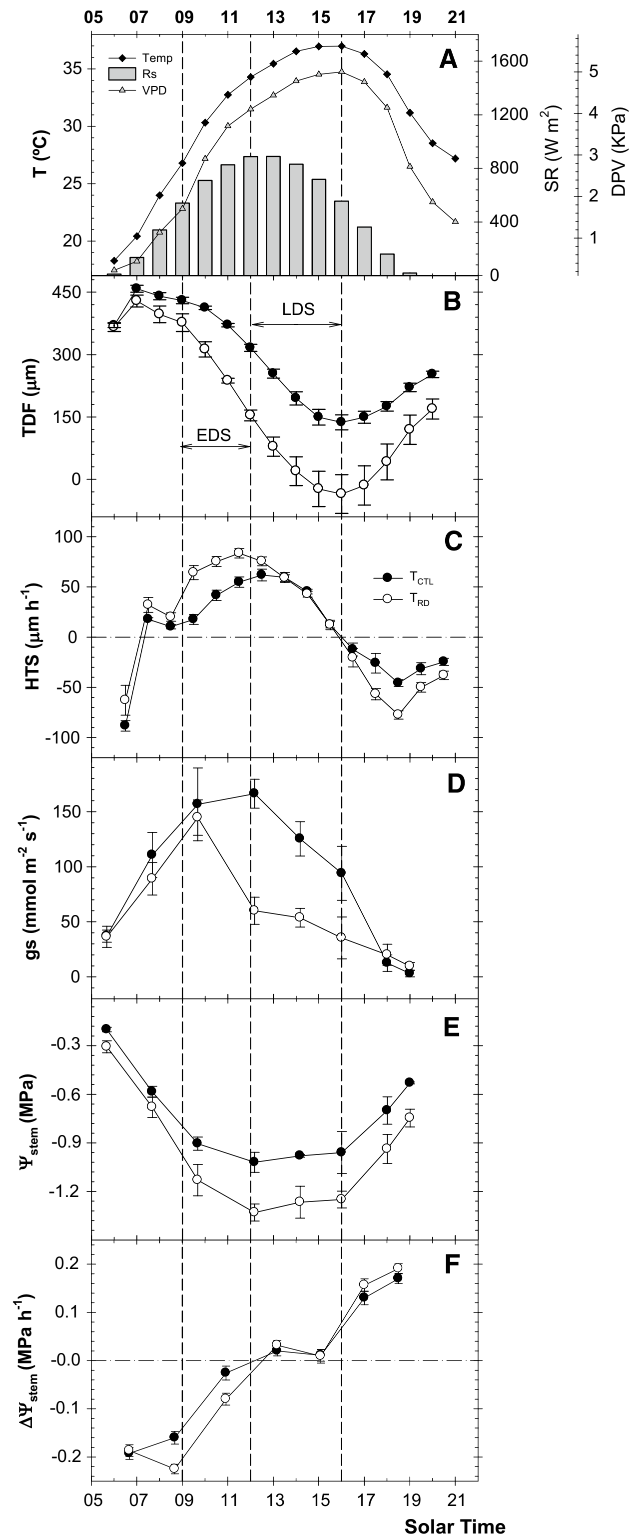

Fig. 5 Time courses of **a** temperature (T, *diamonds*), vapor pressure deficit (VPD, *triangles*) and solar radiation (SR, *bars*), **b** trunk diameter fluctuation (TDF), **c** hourly trunk shrinkage (HTS), **d** stomatal conductance (g_s), **e** stem water potential (Ψ_{stem}), **f** slope of the stem water potential ($\Delta\Psi_{stem}$) on 26 August 2010 (DOY 238) for DI (*open circles*) and CTL (*filled circles*). Data are mean ± SE of 6 measurements (*EDS* early daily trunk shrinkage, *LDS* late daily trunk shrinkage)

severe water stress, probably due to restricted tree transpiration (Hinckley and Bruckerhoff 1975).

Similar (or higher) disparities of CV in mature almond (Goldhamer and Fereres 2001), grapevine (Intrigliolo and Castel 2007) and pomegranate (Intrigliolo et al. 2011), with >30 % for MDS and <10 % for Ψ_{stem}, indicate the higher sensitivity of Ψ_{stem} to water deficit. High variability (CV) in MDS has been attributed to trunk irregularities (Intrigliolo et al. 2011) and the variable resistance to water flow (between the bark and the trunk xylem) between trees (Naor et al. 2006). In contrast, in lemon (Ortuño et al. 2006) and peach (Remorini and Massai 2003) trees, MDS was more sensitive than Ψ_{stem} for detecting differences in plant water status of deficit irrigated trees compared with well-watered trees, since the CV of MDS was around 15 %, and only slightly higher than that of Ψ_{stem}.

TGR showed lower inter-treatment differences than the other TDF-derived parameters (Fig. 2g, h). The low sensitivity of TGR would probably be due to a high CV and its greater dependence (than other indicators) on crop phenology, as previously mentioned (Egea et al. 2009; Ortuño et al. 2010).

The relationships between TDF-derived parameters and Ψ_{stem} during different postharvest periods (June, from July to August and September to October) were closer than in the annual data set (Fig. 4). Ortuño et al. (2006) argued that the main factor controlling MDS is xylem water potential. However, as the season came to an end (September–October), the slope of the MDS or EDS versus Ψ_{stem} regression decreased, as described in peach (Marsal et al. 2002), plum (Intrigliolo and Castel 2004) and pomegranate (Intrigliolo et al. 2011) trees, due to the different fruit growth rates during the growing season. Although this does not explain the data here (Fig. 4) as fruit had already been removed, differences in slope of the relationships between MDS or EDS and Ψ_{stem} are probably due to the loss of trunk tissue elasticity (Gènard et al. 2001; Intrigliolo and Castel 2004) and increased xylem cavitation as the season was ending (Kozlowsky 1976).

Curvilinear relationships between MDS and Ψ_{stem} were also observed (Fig. 4a, c). In several crops, MDS values decreased as water stress levels increased due to the depletion of water stored in the trunk (Hughet et al. 1992; Ortuño et al. 2010), the decrease in transpiration (Hinckley and Bruckerhoff 1975) and/or the decreased conductance of water from the bark to the xylem at a certain water potential. Before midday, the trunk contraction in DI trees increased proportionally with the water stress, and so $\Delta\Psi_{stem}$ and hourly trunk shrinkage behaved similarly during the period that EDS was calculated (Fig. 5c, f), which was reflected in a closer linear relationship between both variables during the three postharvest periods studied (data not shown). However, during most of the post-midday period, the DI trunk shrinkage was similar to that of CTL. This could mean that the curvilinear relationships between MDS and Ψ_{stem} are due to the shrinkage of the trunk after midday, which is affected by stomatal closure, as mentioned above.

Conclusions

Although trunk-derived indices readily detect water stress, high tree-to-tree variability may limit the development of robust, reliable indices. With moderate variability (CV < 15 %), MDS and EDS were seen to be less sensitive indices than Ψ_{stem} in this work, although their signal intensity was generally greater than that of Ψ_{stem}. Among the indices derived from TDF, EDS was more sensitive than the standard indices (MDS and TGR) and has practical advantages related to ease of calculation (requiring data acquisition at known times each day). EDS might facilitate the continuous and necessary knowledge of the plant water status when a more efficient irrigation scheduling is required in commercial orchards located in areas with limited available water resources. Consequently, EDS seems a promising index for irrigation scheduling in early nectarine trees, and possibly in other Mediterranean species that show similar diurnal patterns of stomatal behavior. Further studies are needed to determine whether EDS can be used as a sensitive water stress index in a greater range of species.

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