

Simultaneous measurements of stem radius variation and sap flux density reveal synchronisation of water storage and transpiration dynamics in olive trees

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ABSTRACT

Continuous stem water relations, sap flux and radial variation, and soil moisture were monitored in rainfed and irrigated mature olive (*Olea europaea* L.) trees in field conditions in central Italy. A mathematical procedure was applied to describe plant–environment dependences in order to facilitate the identification of the correspondence between stem factors (sap flow and diameter variation) and environmental parameters (water availability and evaporative demand). A direct correspondence between the time series of the monitored parameters was observed in the two growing seasons. Soil water content was synchronous to stem diameter variation in irrigated trees, whereas they were asynchronous in rainfed conditions. On a daily basis, sap flux density showed an opposite trend with respect to patterns of vapour pressure deficit and evapotranspiration (ET_0) in spring, corresponded to the course of ET_0 in summer and lagged behind ET_0 in autumn. Maximum daily shrinkage was correlated with vapour pressure deficit ($R^2=0.50$, in rainfed; $R^2=0.51$, in irrigated plants), whereas it was not significantly related to ET_0 . Conversely, cumulative sap flow showed a good relationship with ET_0 ($R^2=0.60$, in rainfed; $R^2=0.51$, in irrigated plants) and scaled exponentially with maximum daily shrinkage ($R^2=0.56$, in rainfed; $R^2=0.61$, in irrigated plants), indicating consistent radial transfer of water between xylem and phloem. The proposed analytical approach highlights the importance of combining measured parameters and sensor outputs in order to determine adjustments of specific plant functionality traits, such as the dynamics of water status in trees, for modelling and practical uses. This study also indicates a different accounting of the effect of microclimatic variables on plant signals based on stem sensors. Copyright © 2014 John Wiley & Sons, Ltd.

KEY WORDS Mediterranean environment; *Olea europaea*; stem radius; sap flow

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INTRODUCTION

Drought stress limits tree growth worldwide, determining structure and function of many agricultural and forestry systems (Centritto *et al.*, 2011; McDowell *et al.*, 2011). The Mediterranean region, a ‘hot spot’ where aridity and water resource shortage are historical and recurring problems (Giorgi and Lionello, 2008), will likely be subjected to future lower summer precipitation and prolonged drought periods (Dai, 2010), creating condition where water shortage might become critical even for species adapted to low water requirements. In this region, agroecosystems are the main consumers of fresh water and, consequently, face the challenge of developing sustainable

approaches to water management (Ferreter *et al.*, 2011). Sagacious strategies in water saving require improved determination of whole-plant water relations. In this sense, a better knowledge on water transport in trees can provide practical information, through simultaneous measurements of whole tree water loss (e.g. Čermák and Nadezhdina, 1998; Tognetti *et al.*, 1998; Nadezhdina *et al.*, 2010; Marino *et al.*, 2014) and stem radius variation (e.g. Giovannelli *et al.*, 2007; Fernández and Cuevas, 2010).

Contemporaneous role of the tree trunk in long-distance water transport and storage functions has rarely been addressed (Tognetti *et al.*, 1996; Goldstein *et al.*, 1998; James *et al.*, 2003; De Pauw *et al.*, 2008). Trunk diameter variations and sap flow, automatically monitored through applied plant sensors, are advantageously considered as promising plant-based variables for irrigation scheduling, either alone or in combination with other plant or environmental parameters (Ferreter and Goldhamer, 2003;

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Moriana *et al.*, 2003; Jones, 2004; Naor, 2006; Cuevas *et al.*, 2010). To tackle the influence of climatic changes, the use of relative indicators, either determining at a certain stage of water stress the effects on plants or monitoring the course of a developing stress event, were suggested (Ferreira *et al.*, 1997; Goldhamer and Fereres, 2001; De Swaef *et al.*, 2009; Fernández *et al.*, 2011a).

Olea europaea L. is a prominent feature of present-day Mediterranean vegetation. Olive trees showed anisohydric control of plant water status, exhibiting a tight stomatal control over transpiration (Centritto *et al.*, 2005; Aganchich *et al.*, 2009), lowering midday potential during summer to maintain transpiration (Marino *et al.*, 2014), but insufficient to prevent loss of hydraulic conductance under the severe drought (Tognetti *et al.*, 2009). Stem water relations determined through dendrometers and sap flow sensors responded to variations in plant water status, soil moisture availability and evaporative demand (e.g. Tognetti *et al.*, 2004, 2005). Tognetti *et al.* (2009) observed that stem radial increment and sap flux of olive trees did not differ consistently between the rainfed and deficit irrigation treatments in a mild year. On the contrary, in a dry year, rainfed trees showed a small increase in maximum daily shrinkage (MDS) during drought periods compared with irrigated ones, despite the latter having higher transpiration. Because trees subjected to deficit irrigation acclimated somewhat functionally and structurally to long-term partial higher soil water availability, Tognetti *et al.* (2009) concluded that rainfed trees had more conservative water use than irrigated ones. Consequently, as the annual water use of olive trees may be regulated by long-term adjustments to limited seasonal water availability, the access to moist soil layers and trunk water sink may contribute significantly to the volume of water transpired. Therefore, the water uptake limitations in olive should lie in the conductance pathway from soil to foliage to air, though studies on the interplay between storage and transport functions in trunks of mature trees are scarce. De Pauw *et al.* (2008), applying a water flow and storage model to study stem water relations, provided new insights on shrinkage–swelling phenomena in trees. Recently, Cocozza *et al.* (2009, 2012) observed applying empirical links between stem radius variations and climate condition patterns that variation in rate and duration of daily stem shrinkage in response to low air temperature in winter occurred independently of the effects of water deficit suffered by poplar trees the previous summer, and the timing of transition from the dormant winter state to the active growth stage and till the slow expansion phase was distinguished in olive trees.

The rhythm of stem radius changes is mainly induced by water uptake (i.e. reversible changes) and wood growth (i.e. irreversible changes) (Zweifel *et al.*, 2001, 2010; Deslauriers and Morin, 2005; Intrigliolo and Castel, 2007). The synchronisation of sap flow pattern with stem radius

variation and environmental evaporative demand has been addressed simultaneously with environmental variables (De Swaef *et al.*, 2009; Fernández *et al.*, 2011b). The application of mathematical functions, performing quantitative solutions and sensitivity analysis (Baldochi, 1994), may be a useful tool to address the issue of synchronisation between plant signals and environmental variables. Our study was then conducted: (i) to derive mathematical functions for the synchronisation of stem water relations, obtained through mechanistic insights and environmental water availability and (ii) to reveal the usefulness of stress sensors on elucidating adaptation processes in a framework suitable for application in modelling schemes. The approach adopted in the present study relies on the strength of the signal, defined by the tree-to-tree variability due to the presence of a control treatment (irrigated vs rainfed), as a critical point to identify plant response to water availability. Trends of stem radius variation and sap flow were coupled with soil moisture and atmospheric data. Then, a detailed high-resolution analytical approach was applied on the recorded data to obtain analytical solutions for the seasonal synchronisation of stem water relations, i.e. defining the coupling processes of plant variables with soil water content and environmental evaporative demand, reference evapotranspiration (ET_0) and vapour pressure deficit (VPD) during the vegetative season.

MATERIALS AND METHODS

Study area and experimental plantation

The experiment was conducted at the Santa Paolina experimental farm of Trees and Timber Institute-National Research Council, located in Follonica, central Italy (42°55′ 58″N, 10°45′51″E, 17 m a.s.l.), on 10-year-old olive trees (*O. europaea* L., cv. Leccino) cultivated at single-trunk free canopy (Gucci and Cantini, 2000) at a spacing of 4 × 4 m. Trees have a single trunk and the main branches from 1.5 m above ground, and the canopy has spherical shape. The soil, which belongs to the Piane del Pecora system, is sandy-loam (sand 64.2%, silt 16.9% and clay 18.9%) and has a depth of about 3 m. Standard cultural practices in the region were followed. In the growing seasons preceding the experiment, all trees were equally irrigated to guarantee the uniformity of plant development with micro-sprayers. Two 360° micro-sprayers (with approximately 1.25 m spray radius) per tree was installed, with sprinkler heads located 30 cm from the trunk and approximately 0.4 m above the soil surface. Two water treatments (rainfed and irrigated control supplied with 100% of the crop ET_0) were applied from mid-May to late October during the growing seasons 2011 and 2012. To estimate total daily ET_0 , the canopy reference ET_0 was hourly calculated and then weekly averaged using the Penman–Monteith equation (Doorenbos and Pruitt, 1977; Allen *et al.*, 1998). Air temperature (T_{mean} , T_{max} and T_{min} , °C),

total rainfall (P , mm), wind speed (u , m s^{-1}), total radiation (R_s , $\text{MJ m}^{-2} \text{h}^{-1}$) and relative humidity (RH , %), were recorded every 15 min with a standard meteorological digital station placed at 100 m from the orchard. VPD (kPa) was calculated using the Goff–Gratch formulation for saturated water vapour pressure (Goff and Gratch, 1946). A crop coefficient of 0.5 and a coefficient of ground cover 0.8 were applied. Control trees received an average of 3900 dm^3 of water. Measurements of trunk sap flow and stem radius variation were carried out on three trees per treatment between January 2011 and December 2012.

Soil water content

Soil volumetric water content (hereafter referred to a soil water content, SWC, %) was continuously measured within the rainfed and irrigated areas using Terrasense SMT2 soil moisture sensors (model PS-0077-DD, Netsens s.r.l., Florence, Italy). Two sensors per treatment were used. The system consisted of two probes per sensor that measured two depth segments (0.10 and 0.30 m) in a single profile. Sensors were installed in the middle of the irrigation ray at an average distance of 90 cm from the trunk per treatment. Soil water content was acquired every 15 min with a Netsens communication platform based on a GPRS integrated main unit, a wireless units and LiveData® software for data storage and elaboration.

Dendrometer measurement

Stem radius variations were monitored using automatic point dendrometers on four individual trees. The used dendrometers measure the linear displacement of a sensing rod pressed against the bark. The operating principle of the linear variable transducer (AB Electronics Ltd., Romford, Essex, UK) that responds to stem radius variation is described elsewhere (Giovannelli *et al.*, 2007; Coccozza *et al.*, 2009). Trees were monitored with these high-resolution automated dendrometers installed on the trunk at 50 cm from the soil surface and shielded from direct sunlight and weather damage by aluminium foils. Data were recorded every 15 min and averaged hourly to calculate 'stem radius variation'. MDS was then computed as the difference between the maximum stem diameter (i.e. the stem radius value measured before sunrise) and the minimum stem diameter recorded during the irrigation/rain free days.

Sap flow measurement

Granier-type sensors (Granier, 1985) were inserted radially into 20 mm depth of the stem at the height of ~ 1.3 m in six plants (three per water treatment); averaged stem diameter at the level of sensor installation was 75 mm. A set of probes per tree was installed on the north side of the trunk to avoid the sun-exposed side. The sensors consisted of a

pair of copper-constant thermocouples vertically spaced; the upper probe was continuously heated through a heating wire supplied with a constant power source (120 mA). The temperature difference of the two probes was recorded to obtain the volume flux density of sap flow per plant (J_d , $\text{m}^3 \text{ s}^{-1} \text{ m}^{-2}$) (Granier, 1987; Huang *et al.*, 2009; Lemeur *et al.*, 2009). The temperature difference was estimated on a daily basis in order to avoid errors in the daily maximum and daily total flow calculations due to season and soil drying/rewetting cycles. Sap flow ($\text{dm}^3 \text{ h}^{-1}$) was measured continuously, as described in Marino *et al.* (2014). The hourly sap flow values were used to obtain the cumulative sum of sap flow (dm^3) measured in the daily time of MDS.

Analysis of seasonal patterns

The seasonal patterns of stem radius variation and sap flux density were analysed by studying periods of 15 days, evaluating the amplitude and frequency phase of stem radius variation according to Coccozza *et al.* (2012). To characterise seasonal stem radius variation over the year, the duration (days) of each phase was calculated considering the occurrence of environmental conditions (temperature, ET_0 and VPD) and the intensity of stem shrinkage, defined by the amplitude of daily stem radial oscillation. The growing season was classified in phases according to three criteria: (i) duration; (ii) environmental conditions that origin cycle phases; and (iii) net radius variation (stem radius variation or increment).

The seasonal course was classified and analysed starting with the identification of daily stem radial variation in each period, according to the classification of Tardif *et al.* (2001), allowing a division of the year into three periods: winter shrinkage, spring rehydration and summer transpiration. Seasonal climatic fluctuations were determined with the environmental data (air temperature, ET_0 and VPD), which define specific ranges of meteorological data and then observing the stem dynamics in relation to environmental conditions. The relationship between stem radius variation and environmental variables defined characteristic patterns of (i) a period of instability in winter, with strong episodes of swelling and shrinking of trunks; (ii) a short period of stability, with practically no stem radius increment; and (iii) a period of radial growth during spring and summer, with a steep and continuous increase of the stem radius. Data of stem radius in the growing season were related to ET_0 and VPD. The variable function coefficients allowed defining three stages, consequently to the degree of agreement of stem and ET_0 behaviour. The relationships were analysed separately for three 15-day time periods: at the beginning, April (day of year (DOY) 103–118), in the middle, July (DOY 182–197) and at the end, September–October (DOY 265–280), of the growing season.

Time series comparison

A procedure adapted from dendrochronology was adopted in order to compare raw diameter values by using the percentage agreement in the signs of the first differences of the two time series. This approach was applied to hourly stem radius variation and sap flow rate. The curves obtained by point dendrometers described the tree radial growth, showing increases and then decreases in width over time. Records of the growing period, spring and summer, were focused on the high-frequency signals of stem growth through the ‘detrending’ or ‘standardisation’ method, which removes the effects of tree growth from the time series, retaining the environmental variability, as widely applied in dendrochronology for tree-ring growth series (Cook and Kairlukstis, 1990). Considering an idealised series of radial increment measurements, that is n days in length, collected from a tree growing without disturbances, and the basis of allometry that affects the tree growth, it is usually the case that ‘raw’ radial increment series, such as ring-width series of tree rings, exhibit a decreasing trend with increasing seasonal course, such as age in tree ring. Therefore, the individual series were detrended using ARSTAN (Cook and Holmes, 1986), which was originally developed as a tool for cross-timing of tree-ring series. The curve detrending was conducted through the ‘first differences’ (option -1 of ARSTAN), effectively removing all low-frequency variance. It was used for the high-frequency variance of the hour-to-hour. Every tree series was detrended to produce an hourly-standardised curve for the single tree. Then, the standardised curve was statistically analysed with the time series analysis programme software package (Frank Rinn, Heidelberg, Germany), also originally developed for cross-timing of tree-ring series.

The degree to which the time series of different water treatments are correlated was estimated through cross-correlation method to evaluate intrinsic variability under the same environmental conditions. In dendrochronology, two main concepts have been used to express the quality of agreement between time series: Gleichläufigkeit (Glk) and/or t -values. Glk is a nonparametric test that measures the high-frequency coherence between tree-ring data and allows an estimation of common signals within age class subsamples (Esper *et al.*, 2001). Raw diameter values are compared statistically by the percentage agreement in the signs of the first differences of the two time series (the Glk) (Kaennel and Schweingruber, 1995). In this case, the Glk was a measure of the day-to-day agreement between the interval trends of two time series based upon the sign of agreement or the sum of the equal slope intervals as a percentage. With an overlap of 50 days, Glk becomes significant ($P < 0.05$) at 62% and highly significant ($P < 0.01$) at 67%. With an overlap of 10 days, Glk becomes significant ($P < 0.05$) at

76% and highly significant ($P < 0.01$) at 87% (Kaennel and Schweingruber, 1995). In this study, the analysed time series were mostly longer than 50 days, and the quality of agreement between time series was considered successful if the value of Glk was $>60\%$. The statistical significance of the Glk (GSL) was also computed. The TVBP, a student’s t -value modified by Baillie and Pilcher (1973) and further developed by Munro (1984), was used for investigating the significance of the best match identified. The TVBP is commonly used as a statistical tool for comparing and cross timing of time series, determining the degree of correlation between curves. This method eliminated low-frequency variations in the time series, as each value was divided by the corresponding 5 days moving average (Cocozza *et al.*, 2009, 2012).

Mathematical approach

The high sensitivity of the transducers required an accurate data analysis to allow a precise and correct elaboration. Stem radius variation, sap flow density, SWC series and ET_0 and VPD records were processed through the use of the derivative mathematical function as a support to the use of rough data. The derivative analysis was performed through OriginPro software package (OriginLab, Massachusetts, USA). The derivative of a function represents an infinitesimal change in the function with respect to one of its variables. For a function of a single real variable, the derivative at a point is equal to the slope of the tangent line to the graph of the function at that point. As the experimental data are a function of time, $f(t)$, the analysis was performed through time derivative $f'(t)$:

$$f'(t) = \frac{df(t)}{dt} = \lim_{\Delta t \rightarrow 0} \frac{f(t + \Delta t) - f(t)}{\Delta t},$$

where t corresponds to time and Δt is the time increment.

The derivative of the function at a chosen input value describes the best linear approximation with respect to time of the function near that input value. This analysis allowed the rate of variation of a function to be emphasised; when the derivative is positive, the input function is increasing, whereas the function is decreasing when the derivative is positive (Figure 1). Moreover, the higher value of the derivative is the change in the value of the function. In the present work, the magnitude of peaks of derivative curves was not considered, as it was not chosen to study the rate of change of the input function. The high sensitivity of the transducer produced high number of events (peaks, x -axis intersection) on the derivative curve. Therefore, in order to amplify the eventual differences between water treatments in the response to ET_0 and VPD, normalised derivatives were used. For each water treatment and selected period, the derivative curve was simply divided by the maximum absolute value in order to provide data ranging from -1 to 1 . The intersection of the derivative curve with the x -axis, i.e. the null value of the derivative, corresponds to an extreme of

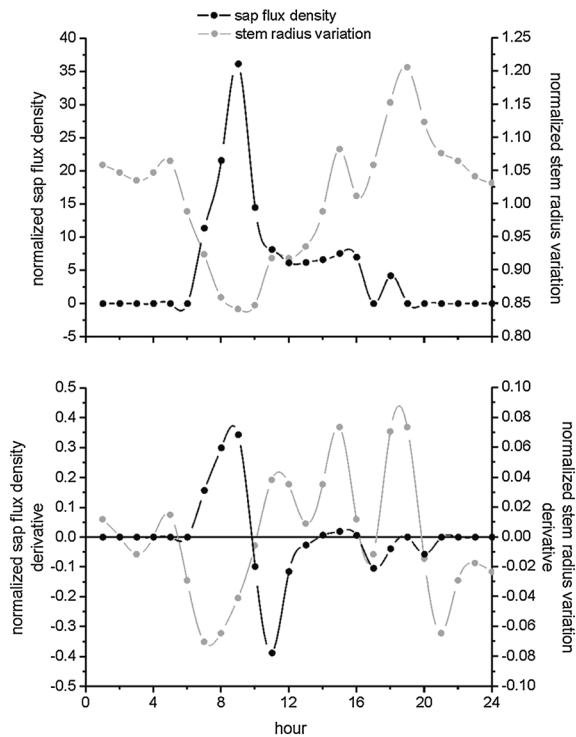


Figure 1. Example of a signal curve and its first-order derivative in the representative synchronisation of stem diameter variation and sap flux density.

the input function. A positive (negative) derivative that intersects the x -axis indicates a local maximum (minimum) of the input function.

Statistical analysis

Analysis of variance was used to test the equality of regression coefficients. In order to define the effect of environmental

variables on MDS and sap flow, the plant responses to water treatment were considered during the monitoring period, namely the irrigation period, from June to October. Cumulative sap flow was related to MDS by nonlinear regression, showing different relationship in irrigated and rainfed plants. MDS and cumulative sap flow were related to VPD and ET_0 , respectively, by linear regression. Relationships were carried out with the programme Origin-Pro8 (OriginLab Corporation, Northampton, UK). Statistical comparison was considered significant at $P=0.05$.

RESULTS

Meteorological data

The dynamics of environmental parameters showed the typical Mediterranean pattern, with relatively cold winter and, consequently, lowest values of temperature, VPD and ET_0 , and a hot and dry season, approximately from April to September, with the highest temperature, VPD and ET_0 values in the summer (Figure 2). The maximum thermal peaks recorded were 36.1 °C (DOY 234) and 36.5 °C (DOY 231) in 2011 and 2012, respectively. The VPD values ranged from 0.03 kPa (DOY 75) to 1.83 kPa (DOY 238) in 2011, and between 0.02 kPa (DOY 316) and 2.24 kPa (DOY 231) in 2012. The cumulative ET_0 reached 746.46 and 748.54 mm from DOY 135 (15 May) to DOY 304 (31 October) in 2011 (1127.59 mm on a yearly basis) and 2012 (1120.98 mm on a yearly basis), respectively.

Soil water content

While soil moisture were similar in rainfed and irrigated conditions over the winter months, rainfed trees were subjected to summer water deficit (data not shown). The

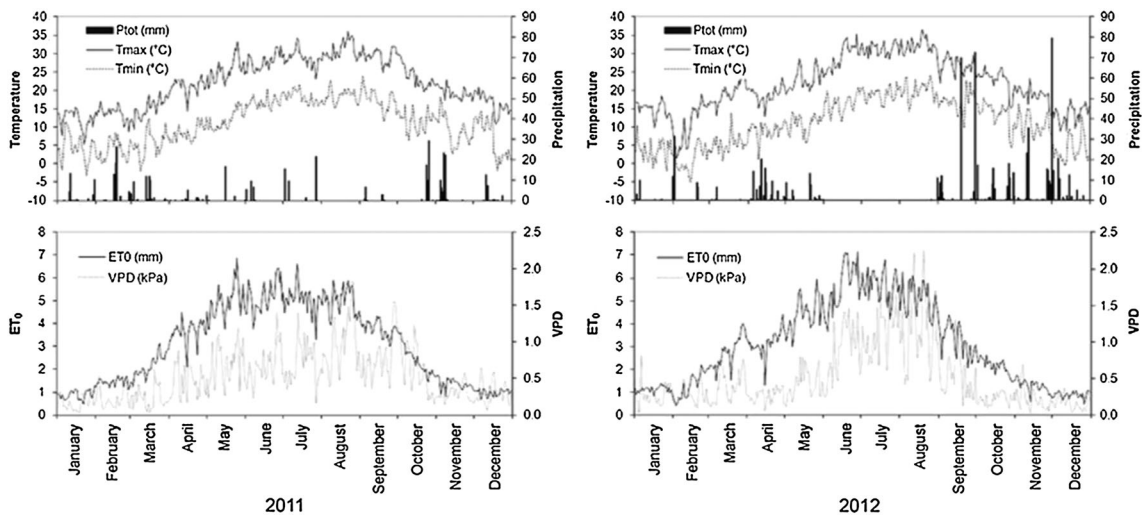


Figure 2. Daily values of maximum and minimum air temperature (T_{max} and T_{min}), reference evapotranspiration (ET_0) and vapour pressure deficit (VPD) in 2011 and 2012.

lowest SWC values were recorded in mid to late summer in both years, when SWC in rainfed conditions decreased below the threshold of $0.21 \text{ m}^3 \text{ m}^{-3}$, corresponding to the conventional wilting point for crop plants, -1.5 MPa . Comparatively, in well-water conditions, SWC was generally between the field capacity threshold (about $0.36 \text{ m}^3 \text{ m}^{-3}$) and 50% available moisture ($0.29 \text{ m}^3 \text{ m}^{-3}$). Furthermore, differences between water treatments in SWC at the top layer were somewhat recorded at the beginning of spring and in autumn. Nevertheless, no differences were observed between the two water treatments in SWC of deeper soil layers as a result of winter precipitation, recovering to values above the field capacity threshold.

Stem radius variation

Stem radius variation patterns indicated that the radial growth was defined by the occurrence of stem increment following reduced stem shrinkage events in combination with varying environmental conditions, namely the increase in transpiration rate coinciding with the end of winter and the start of spring (data not shown). In the early growing season, the increase of air temperature boosted the stem diameter increment, occurring from mid-March through mid-November in both years. Radial growth continued with the increase in VPD and ET_0 during summer.

Sap flow rate

The two edges of the growing season were indicated by maximum daily stem sap flux density values of $9.5 \text{ m}^3 \text{ m}^{-2} \text{ s}^{-1}$ reached in March and November. The daily course of sap flux density was significantly higher ($P < 0.001$) in irrigated than in rainfed plants over the summer period and at the onset of autumn. In June and July, sap flux density started increasing between 6:00 and 7:00 and peaked at about 9:00 to 10:00 local time in irrigated plants (data not shown). Afterwards, stem sap flux density dropped progressively to minimum values, which occurred at about 16:00. This depression was then followed by a second daily peak, reached at about 18:00, as temperature declined and relative

humidity increased in late afternoon. Finally, as light intensity further declined towards the end of the day, also stem sap flux density dropped until whole-plant transpiration approached zero. A less pronounced trend in sap flux density was recorded in August, in irrigated plants. Whereas at the beginning of autumn, stem sap flux density did not vary markedly after reaching the morning peak, indicating that there was no 'midday' drop in whole-plant transpiration in irrigated plants (data not shown). The daily maximum sap flux density recorded over the summer period in control ranged between 20 and $30 \text{ m}^3 \text{ m}^{-2} \text{ s}^{-1}$.

Time series comparison

Stem radius changes were detrended for growth before being used as an index of environmental stress in trees (Zweifel *et al.*, 2005). The time series of hourly stem radius variation showed a highly significant correlation between trees within each treatment. The daily courses of time series reflected the different diurnal variations in air temperature and relative humidity (and consequently in VPD) among the monitored seasons. A strong similarity between comparison coefficients was found for patterns of the time series of stem radius variation. Glk values were highly significant ranging between 60.0 and 68.4 ($P < 0.001$); likewise, GSL values were always highly significant ($P < 0.001$). The TVBP values also showed 100% degree of correlation between time series of dendrometer dataset. As a consequence, the three trees in each treatment were pooled together for the following analysis (Table I). This was not possible for the time series of sap flux trends. Sap flux trend showed high correlation in irrigated plants (Glk = 60%; GSL = $P < 0.001$; TVBP = 20.1), whereas sap flux trend did not show correlation between trees in rainfed conditions. Thus, one model tree per treatment was selected for record completeness and regular trend and used for the following analysis (Table I).

Correlations between sap flux density and stem radius variation with ET_0 and VPD shifted through the experiment (Table II). At the beginning (in April) and at the end of the

Table I. Statistics of day-to-day agreement between the interval trends of two time series of dendrometer and sap flux sensors.

Time series		Rainfed	Irrigated	Data analysis
Dendrometer	Glk	68.4	60.0	Data were pooled together per treatment for the analysis
	GSL	*	*	
	TVBP	100.0	100.0	
Sap flux	Glk	—	60	A model tree per treatment was selected for the analysis
	GSL	—	*	
	TVBP	—	20.1	

Glk, percent agreement in the signs of the first differences of the two time series; GSL, statistical significance of the Glk; TVBP, Student's *t* value modified by Baillie and Pilcher (1973) and Munro (1984).

*99.9%.

Table II. Relationships between J_d (sap flux density) and ET_0 and VPD, and between stem radius variation and ET_0 and VPD, recorded at the beginning (April), in the middle (July) and at the end (October) of the growing seasons 2011 and 2012.

		$y = J_d$						$y = \text{stem radius variation}$					
		$x = ET_0$			$x = VPD$			$x = ET_0$			$x = VPD$		
		a	b	R^2	a	b	R^2	a	b	R^2	a	b	R^2
April	Rainfed	2.84	7.31	0.23	1.17	6.24	0.35	—	—	ns	—	—	ns
	Irrigated	2.53	5.06	0.15	1.45	4.05	0.17	1.04	-0.13	0.14	1.04	-0.06	0.07
		<i>ns</i>	<i>ns</i>		<i>ns</i>	<i>ns</i>		<i>ns</i>	<i>ns</i>		<i>ns</i>	<i>ns</i>	
July	Rainfed	4.09	25.79	0.13	5.59	5.58	0.05	1.07	-0.31	0.31	1.09	-0.09	0.23
	Irrigated	8.36	64.20	0.60	5.03	18.48	0.41	1.03	-0.15	0.57	1.03	-0.04	0.42
		*	*		*	*		<i>ns</i>	<i>ns</i>		<i>ns</i>	<i>ns</i>	
October	Rainfed	5.17	12.32	0.24	4.56	5.72	0.25	1.02	-0.23	0.23	1.03	-0.08	0.13
	Irrigated	6.62	9.06	0.07	5.27	6.17	0.16	1.05	-0.43	0.52	1.05	-0.15	0.30
		*	<i>ns</i>		*	<i>ns</i>		<i>ns</i>	<i>ns</i>		<i>ns</i>	<i>ns</i>	

Regression parameters of linear functions ($y = a + b * x$) fitted to the data and their significance are reported.

* $p < 0.001$.

growing season (beginning of October), sap flow and dendrometer parameters were not correlated to environmental variables in rainfed and irrigated trees. During the middle of the growing season (July), sap flux density was correlated to ET_0 ($R^2 = 0.60$, $P < 0.001$) and VPD ($R^2 = 0.41$, $P < 0.001$) in irrigated trees, with the slope the regression consistently steeper in irrigated than rainfed trees; whereas, stem radius variation was negatively correlated to ET_0 ($R^2 = 0.57$, $P < 0.001$) and VPD ($R^2 = 0.42$, $P < 0.001$) in irrigated trees.

The correspondence of meteorological data with stem radius variation and sap flux density fluctuation during the vegetative seasons was analysed through normalised derivative function (Figures 3 and 4). For a function of a single real variable, the derivative at a point is equal to the slope of the tangent line to the graph of the function at that point. Therefore, the study of derivative suggested that the variation of the function with respect to $y = 0$ defined the change in curve behaviour. The adopted mathematical approach showed a direct correspondence between the normalised plant measurements (stem radius variation and sap flux density) and normalised SWC (measured parameters), VPD and ET_0 (estimated parameters) time series in the growing seasons (Figures 3 and 4).

A specular and opposite behaviour was observed in the trend of stem radius variation and sap flux density time series (Figure 3). The negative (or positive) values of stem radius variation corresponded to positive (or negative) values of derivative functions of sap flux density in both water treatments, as shown in representative periods in April and July in both years. Soil water content was directly correspondent to stem diameter variation in irrigated trees, whereas inversely in rainfed conditions (Figure 3). Whereas, a specular and opposite trend was observed also between sap flux density and SWC

exclusively in irrigated conditions (Figure 3). Figures 3 and 4 also showed the synchronisation of stem radius variation and sap flux density with VPD and ET_0 , respectively. Stem radius variation showed opposite trends to VPD and ET_0 in both water treatments (Figure 3). In April, the sap flux density showed an opposite trend with respect to daily patterns of VPD and ET_0 from 10:00 to 16:00. In July, sap flux density matched the increase of ET_0 from 8:00 to 10:00 in rainfed, from 7:00 to 11:00 in irrigated plants, and then sap flux density decreased, whereas ET_0 increased up to 14:00. In October, on a daily basis, sap flux density lagged behind ET_0 .

Diurnal patterns of sap flow showed lower range of values in rainfed than in irrigated plants ($P < 0.0001$) throughout the growing seasons (data not shown). Daytime cumulative sap flow was positively, exponentially correlated to MDS in both water treatments (R^2 equals to 0.61 and 0.56 in irrigated and rainfed plants, respectively) (Figure 5). The best fit was obtained between MDS and VPD, instead of MDS and ET_0 , using a linear function with R^2 of 0.51 and 0.50 ($P < 0.0001$) in irrigated and rainfed plants, respectively (Figure 5). Cumulative sap flow showed a significant relationship with ET_0 , with R^2 of 0.51 and 0.60 ($P < 0.0001$) in irrigated and rainfed plants, respectively (Figure 5).

DISCUSSION

Linking plant functions, as trunk growth (stem variation) and water uptake (sap flow), to whole plant water status is of great interest in both plant ecology and irrigation science. However, tree growth patterns and water storage cycles, and their link with climate condition trends, are difficult to detect with empirical treatment of stem radius variation records. This complicates the use of stem radius

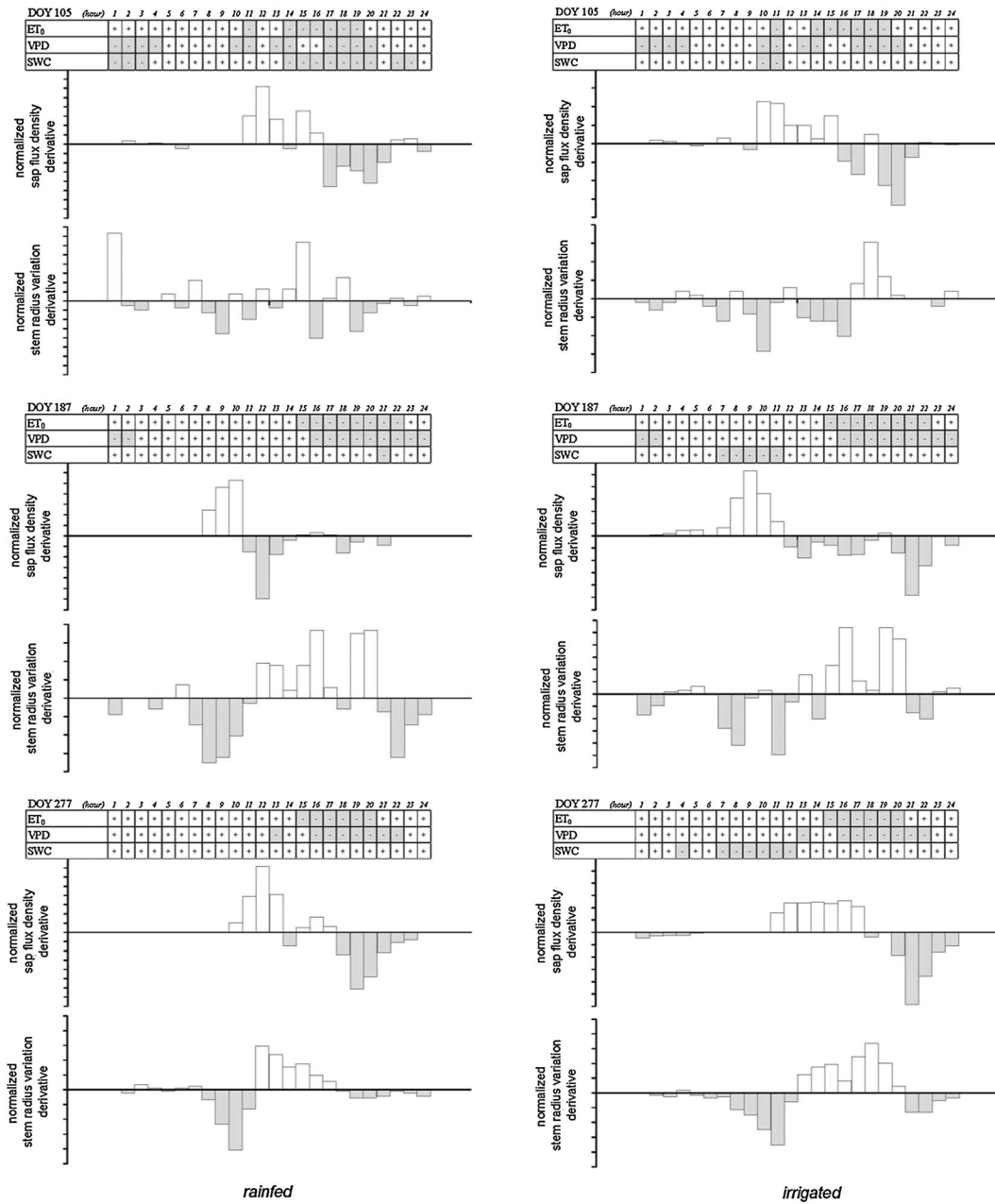


Figure 3. Normalised derivative values of ET_0 , VPD, SWC, sap flux density and stem diameter variation in representative periods at the beginning, April (DOY 105), in the middle, July (DOY 187), and at the end, October (DOY 277), of the growing season. Values of ET_0 , VPD and SWC are reported as sign of derivative ('+' positive and '-' negative values) in table; positive and negative values of derivative of sap flux density and stem diameter variation are presented on the graph.

changes as an index of environmental stress in trees (Zweifel *et al.*, 2005). To overcome these problems, our study aimed to synchronise stem radius variations and sap flux density fluctuations in relation to changes in SWC, VPD and ET_0 in olive trees through a mathematical approach. The correction factor in time series, to identify the correspondence of atmospheric and soil parameters patterns (temperature, VPD and ET_0 , and SWC) with stem diameter and sap flux daily fluctuations during the

vegetative seasons, was not necessary with the proposed mathematical approach, which was founded on a purely objective basis. This relation is commonly based on a misinterpretation of instrument sensitivity, which requires correction factors for the definition of plant parameters (Vandegheuchte and Steppe, 2012). Nevertheless, when a model fails the validation test, several options are available.

The application domain of the approach proposed in this study was validated on stem diameter variations of poplar

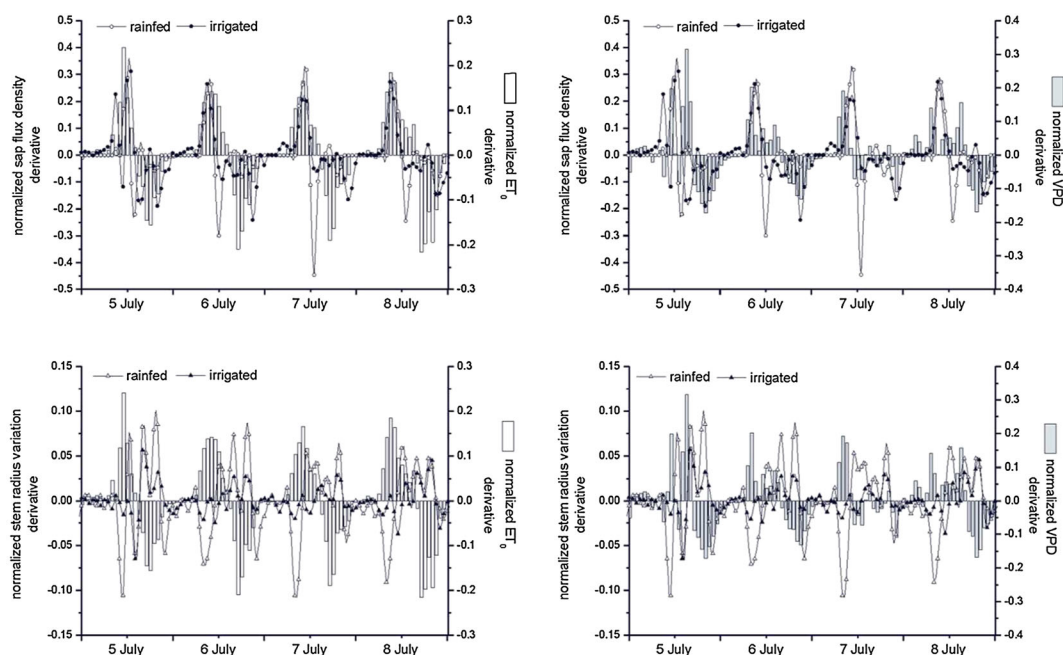


Figure 4. Normalised derivative values of sap flux density and stem diameter variation in synchronisation with SWC, VPD and ET_0 in July.

trees in a winter season (Cocoza *et al.*, 2009) and in olive trees over a whole year (Cocoza *et al.*, 2012). Representative periods at the beginning, in the middle and at the end of the season were selected following the main output of a companion study (Marino *et al.*, 2014), as each representative period had specific physiological traits at foliage level, in terms of gas exchange, spectral reflectance and water potential. From the analysis of the different parameter sets as a function of time and treatment, information regarding the overall seasonal behaviour of trunk water relations could be derived. In the representative periods, general conclusions about the differences between water treatments remain valid in both years, but significant changes in absolute values were observed during the seasons. Marino *et al.* (2014) observed that water stored in woody tissues was not sufficient to maintain transpiration in rainfed trees, and sap flow diurnal patterns showed a pronounced reduction throughout summer. This reflected soil water depletion without irrigation, which conversely was effective in countering water deficit in the irrigated trees.

The analysis of stem radius variation and sap flow density is commonly conducted following a descriptive procedure. At a daily timescale, hourly stem radius variation and sap flux density were related to each other via a loop that differs according to the whole plant water status. The combined use of stem diameter and sap flow fluctuations would provide complementary information sensitive to the whole-plant water status (Steppe *et al.*, 2008; Fernández and Cuevas, 2010; Fernández *et al.*, 2011b). The strength of the growth (stem diameter) and transpiration (sap flow) signal is due to stomatal regulation, which results in significant but contrasting relationships between sap flow rate and stem

diameter fluctuation depending on the intensity of water stress. Indeed, these relationships are affected by the stomatal response to stress and the xylem vulnerability to embolism of the tree species (Conejero *et al.*, 2007; Ortuño *et al.*, 2010). Indeed, there were significant differences between treatments in water potential and gas exchange (Marino *et al.*, 2014), as both parameters were significantly affected by time of the year and soil water availability. Gas exchange data showed also a typical maximum in the morning followed by a declining trend in both irrigated and rainfed plants, with the only exception of the values recorded in August that did not show any clear pattern.

Before sunrise, trunk diameter swelling was observed without significant sap flow, reflecting water redistribution inside the plant. From sunrise to afternoon, sap flow increased as stomata open and VPD increased (Marino *et al.*, 2014), followed by trunk diameter shrinkage, which reflected the movement of water from storage compartments (axial parenchyma and mature phloem) to the xylem following a radial water potential gradient. During the afternoon, trunk diameter swelling (refilling of storage tissues) was accompanied by a decrease of sap flow till next sunrise (as also showed by Tognetti *et al.*, 2009; Abdelfatah *et al.*, 2013). The diurnal fluctuations in trunk diameter and sap flow indicate the importance of modulating internal water storage and root water uptake to balance daily water use in olive trees. However, the release of water from sapwood during high evaporative demand may cause xylem embolism. Therefore, trees require the optimization of water flow through tissue compartments and a certain degree of coordination between capacitance,

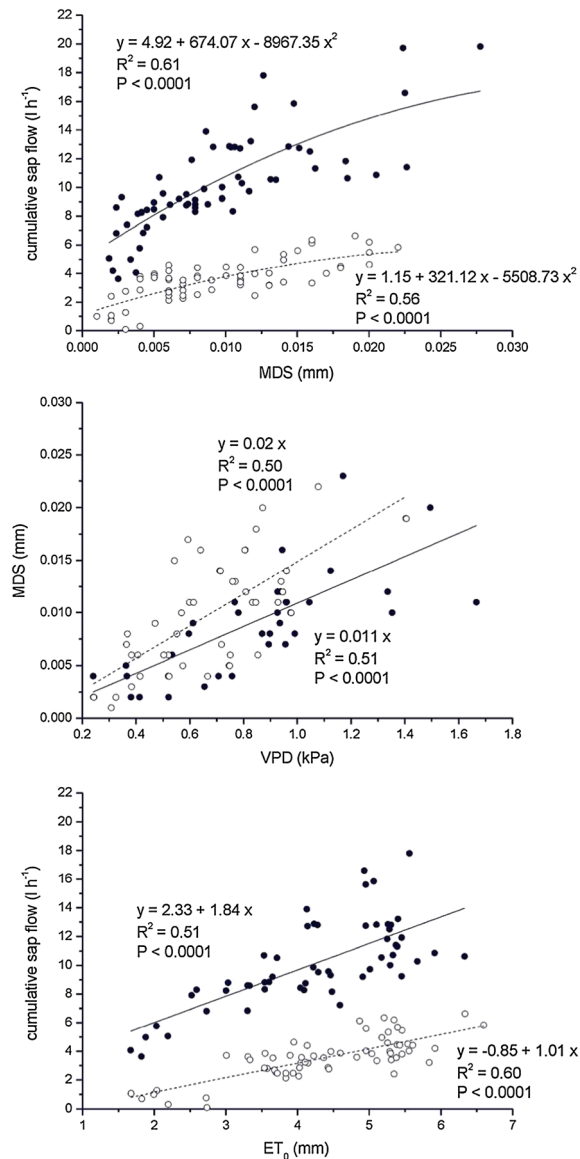


Figure 5. Relationships between maximum daily trunk shrinkage (MDS), cumulative sap flow, vapour pressure deficit (VPD) and evapotranspiration for the irrigated (black circle, solid line) and rainfed (white circle, dotted line) plants (data from June to October were shown). Slope and elevation of relationship are significantly different ($P < 0.001$).

vertical water flux in the xylem, and transpiration, radial water movement in the phloem (Meinzer *et al.*, 2009). Indeed, the radial resistance between xylem and bark can vary in a diurnal and seasonal basis, affecting the water flux between these two tissues (Steppe *et al.*, 2012), and correlations between parameters may change through the season. Sap flux density increased linearly in relation to VPD (Table II), confirming that there was no direct effect of VPD on stomatal control in irrigated plants. In contrast, when water was limiting, increases in VPD led to stomatal closure, thus reducing sap flow of rainfed plants (Table II). Stomatal closure in response to increasing VPD acts as an effective control to avoid excessive

water loss under drought and prevents leaf water potential from falling to dangerous levels (Centritto *et al.*, 2011).

Withdrawal of water from internal storage compartments can account for 10–50% daily water use in trees depending on species, ecosystem type and tree size (Goldstein *et al.*, 1998; Meinzer *et al.*, 2004; Scholz *et al.*, 2007, 2011). The use of stored water close to the site of transpiration reduces the apparent hydraulic resistance along the plant water transport pathway and can, therefore, buffer temporal changes in leaf water status, which in turn can reduce the extent of stomatal limitation to photosynthesis (Meinzer, 2002). Water storage as homeostatic mechanism is especially important in olive trees, because the daily water withdrawal from storage at times of peak transpiration (with later recharge) allows roots to take up water at moderate rates over a longer period and, thus, olive trees can meet their water needs irrespective of the erratic precipitation regime of Mediterranean climate. This species has a shallow root system, and water depletion of nonwetted areas between rows explored by roots might limit water use patterns during peak evaporative demand through hydraulic or chemical signals. The decrease of transpiration lagged behind the progressive reduction in stomatal conductance from early morning peak (Marino *et al.*, 2014). Some hysteresis in the relationship between sap flow and VPD or irradiance, as commonly observed in Mediterranean environments, could lay in the stomatal response to VPD and resistance to flow of water within the soil–plant continuum. This behaviour would suggest stomatal control of daily water use and isohydric responses in olive trees (Tognetti *et al.*, 2005).

The analysis showed different plant sensitivity in response to variation in SWC; the sensitivity was much higher when soil water availability was not limiting (irrigated plants), as the plant signals reacted quickly to environmental factors. However, the highest sensitivity was presented by sap flux density that responded promptly to SWC, with sap flux density increasing at decreasing SWC in irrigated plants. On the contrary, stem radius variation was asynchronous with SWC in rainfed plants: stem diameter increased when SWC decreased. Indeed, a marked decline in stomatal conductance and leaf water potential affected by soil water availability was found in August and, especially, September (Marino *et al.*, 2014). Soil water content determined the magnitude of stem radius variation with minimum evolution in June and September and higher in July and August, on a daily basis, when minimum peaks of SWC were reached (data not shown). Coccozza *et al.* (2012) observed that the stem diameter increment was linearly related with ET₀ and VPD and soil moisture deficit, considering the growth seasonal phases in the same olive tree plantation. The relationship between stem diameter variation and sap flow trend is complex because of daily stomatal regulation (Costa *et al.*, 2013). Indeed, at soil field capacity, both stem diameter and sap

flux density fluctuations reflected the evaporative demand. However, as SWC decreased, and lower xylem water potential and higher VPD developed, stomata gradually closed (Marino *et al.*, 2014), while stem diameter variation was still high. The diurnal pattern of sap flow rate and daily stem radius variation showed a steep morning variation leading to peaks in opposite direction, achieved in the central hours of the day (when VPD and global radiation were at their maximum), followed by a sustained gradual decrease through the afternoon. In general, sap flow and stem radius variation rates were poorly correlated on a daily basis, and a phase shift between these two time series was evident. On a whole-day basis, the rate of stem radius variation was associated to VPD, whereas sap flow rate was related to global radiation (Tognetti *et al.*, 2009).

A strong and clear dependency of stem radius variation and sap flux density on VPD and ET_0 was observed through the derivative function slope. Stem diameter showed opposite trends to VPD and ET_0 by derivative values, with small differences between irrigated and rainfed plants, when the stem diameter curve increased (positive derivative values) and VPD and ET_0 curves decreased (negative derivative values), and vice versa. On the other hand, the synchronisation of sap flux density with VPD and ET_0 showed correspondence in trends, showing the increasing (or the decreasing) slope of the function of coupled parameters. In the case of the synchronisation with VPD, the sap flux density derivative function was positive only for half of positive values of the VPD function in both water treatments in July; during the phase of increasing VPD, the sap flux density completed the daily increase and decrease phases. The synchronisation with ET_0 showed that the sap flux density function lagged behind ET_0 in both water treatments, in all representative periods. However, the synchronisation procedure highlighted the efficiency of adopted methodology for the main environmental variables that drive water movement through the plant (SWC, ET_0 and VPD). When air temperature and VPD were not limiting, plants opened their stomata in the early morning (Marino *et al.*, 2014). However, as air temperature and VPD increased concomitantly with lowering water potential, they induced stomatal closure, and sap flow decreased dramatically (Tognetti *et al.*, 2009; Abdelfatah *et al.*, 2013).

Differences in MDS and cumulative sap flow patterns between treatments were clear, though the relationship between MDS and cumulative sap flow was positive in both rainfed and irrigated trees (Figure 5). The correlation was similar between the two water treatments, but the analysis of the slopes suggests a strong influence of water treatments. The total daily withdrawal of stored water from the stem showed different sensitivity of MDS and cumulative sap flow to environmental variables, VPD and ET_0 , respectively (Figure 5), which might imply that the reservoir in stem portions was differently influenced. These findings are consistent with radial transfer of water between xylem and

phloem (Gall *et al.*, 2002), which can be interpreted in relation to phloem transport mechanisms (Wang *et al.*, 1997). Instead, the correspondence of MDS with VPD (Figure 5) suggests a strong dependency of MDS on evaporative demand. This explanation is in accordance with a stem radius reduction when VPD was high (Figure 4), indicating relatively low xylem water potential in the stem and implying a considerable flow of water from the roots to the trunk (Köcher *et al.*, 2013). Thus, varying water availability elicited different plant adaptations, as well as physiological adjustments or anatomical traits (e.g. xylem anatomy and vulnerability to embolism of current-year shoots) in olive trees (Köcher *et al.*, 2013; Torres-Ruiz *et al.*, 2013).

There was no unique relation valid for the whole season between plant water status and stem radius variation, though the proposed approach was applied in single solution for different periods of the growth season. Furthermore, the specific slope and intersection (with axis $y=0$) of the functions described the relationship between parameters in relation to water treatments in all representative periods of the vegetative season, as changes in the slopes of each parameter function.

In conclusion, the application of the derivative mathematical function allowed establishing the synchronisation of the daily courses of stem diameter and sap flow with those of water availability. The mathematical approach might be conveniently applied to examine time lags in term of water storage–transport capacities and associated environmental drivers to monitor the flow dynamics within a tree and to model plant water relations. More detailed and long-lasting experiments will add to contradictory results on indicators of water status often reported in literature for trees in the Mediterranean environment. Continuous monitoring by multisensors, such as dendrometer and sap flow probes, have the potential to detect important processes related to the short-term and long-term dynamics of plant water balance in tree trunks, while providing information on growth pattern, and thus on elastic properties of wood and plant sensitivity to drought. The approach highlights the importance to combine physiological and biometeorological parameters in order to describe and forecast water use dynamics in extensive olive tree plantations in the Mediterranean region.

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