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Abstract: Stem diameter variations result from the fluctuation of environmental factors, mostly temperature trend and water availability. To test the causal effects of seasonal course on stem radius variation, an analytical solution was applied to the synchronization of radial fluctuations and environmental parameters, whose baseline is largely unexplored.
Stem radius variations were continuously monitored during two consecutive years in four field-grown olive tree cultivars (Canino, Cipressino, Leccino, Maurino) in an experimental farm in central Italy, between November 2004 and October 2006, using automatic point dendrometers.
Stem diameter patterns showed intense shrinkage events suddenly when air temperature dropped below 0 °C during winter. The growing season was described by patterns of air temperature, reference evapotranspiration, cumulative degree-days, vapour pressure deficit and soil moisture deficit, and correlated to patterns in stem radius variations. Three phases of tree-ring formation were evidenced: development induction state, active growth stage and, slow expansion phase.
The derivative analysis approach applied on point dendrometer records was conveniently used to define the sensitivity of stem radius variations to environmental conditions in olive trees, which may complement the monitoring the progression of radial growth in Mediterranean regions under climate change scenarios.

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Agricultural and Forest Meteorology **- manuscript submission**

Dear Editor,

We have the pleasure to submit the manuscript entitled **“A detailed high-resolution analytical approach to study the correspondence between tree-ring formation and seasonal course in a Mediterranean environment**”, by Claudia Cocozza, Alessio Giovannelli, Bruno Lasserre, Claudio Cantini, Fabio Lombardi and Roberto Tognetti. We believe that the manuscript falls within the guidelines of *Agricultural and Forest Meteorology*.

Motivation of the work:

The analysis of stem radius variations with environmental parameters is useful to comprehend the dynamics of tree development and plant water status throughout seasons. Knowledge of the dynamics of stem development at a short time scale is required for a better understanding of the phenomenon of tree growth. Stem radius variations in trees may be addressed by using an analytical solution to seasonal synchronization of stem phenology and environmental parameters. Studies on stem development focus essentially on the stem growth, whereas there is basically poor information about the intra-annual stem phenology. The importance of this study relies on studying stem phenology through an original approach that provides new and thorough insights on tree adaptation to changing environmental conditions. Data will be conveniently implemented in phenological modelling, towards predicting the response of woody plants to global warming in threatened Mediterranean-type ecosystems.

***Highlights**

Stem diameter patterns showed shrinkage events when temperature dropped below 0 °C.
The growing season correlated to patterns in stem radius variations.
Tree growth was described by patterns of evaporative demand and plant phenology.
A derivative analysis approach was applied on point dendrometer records.
The sensitivity of stem radius variations to environmental conditions was defined.

A detailed high-resolution analytical approach to study the correspondence between tree-ring formation and seasonal course in a Mediterranean environment

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Running title: Climate influence on tree-ring formation

Abstract

Stem diameter variations result from the fluctuation of environmental factors, mostly temperature trend and water availability. To test the causal effects of seasonal course on stem radius variation, an analytical solution was applied to the synchronization of radial fluctuations and environmental parameters, whose baseline is largely unexplored.

Stem radius variations were continuously monitored during two consecutive years in four field-grown olive tree cultivars (Canino, Cipressino, Leccino, Maurino) in an experimental farm in central Italy, between November 2004 and October 2006, using automatic point dendrometers.

Stem diameter patterns showed intense shrinkage events suddenly when air temperature dropped below 0 °C during winter. The growing season was described by patterns of air temperature, reference evapotranspiration, cumulative degree-days, vapour pressure deficit and soil moisture deficit, and correlated to patterns in stem radius variations. Three phases of tree-ring formation were evidenced: development induction state, active growth stage and, slow expansion phase.

The derivative analysis approach applied on point dendrometer records was conveniently used to define the sensitivity of stem radius variations to environmental conditions in olive trees, which may complement the monitoring the progression of radial growth in Mediterranean regions under climate change scenarios.

Key words: olive tree; point dendrometers; radial growth; seasonal course; stem radius variations.

1. Introduction

The length of the growing season is one of the main determinants of tree growth (Lupi et al., 2010). Although many studies have shown that temperature increase is responsible for important changes in the timing of some biological events, the relationship between variation of stem growth and duration of growing season remains an intriguing issue given the potential impact of climate change on plant phenology (Chuine et al., 1998; Galán et al., 2005; Geßler et al., 2007; García-Mozo et al., 2010). Several authors have used dendrometers to define the intra-annual dynamic of woody ring formation in order to understand the growth-climate relationship (e.g., Downes et al., 1999; Deslauriers et al., 2003; Giovannelli et al., 2007). The relationships among averaged wood properties, tree growth rates and environmental variables, however, tend to vary widely (Downes et al., 1999). This is largely because wood properties are the cumulative result of constantly varying developmental processes, with the result that determining the causal relationships between cambium phenology and xylem formation becomes crucial to comprehend the complex dynamics of tree growth. Radius variation phases and rates of stem growth during the season have been monitored in cold environments (e.g., Turcotte et al., 2009), while reference relationships or baselines to interpret the values of stem growth and environmental variables have to be developed for Mediterranean woody plants.

The rhythm of stem radius changes induced by water uptake and wood growth contributes to stem radius dynamics (Zweifel et al., 2001; Deslauriers and Morin, 2005; Intrigliolo and Castel, 2007; Zweifel et al., 2010). The activation of plant growth in spring and dormancy in winter has been mainly related to temperature (Heide and Prestud, 2005; Rossi et al., 2006; Cocozza et al., 2009), though spring hydration determined through dendrometers may be readily confused with the onset of stem growth (e.g., Deslauriers et al., 2007a; Turcotte et al., 2009). The complexity of the interaction between environmental conditions and growth dynamics is indicated by the varying degree of temporal correspondences between stem radius variations and specific climate variables. The synchronization of stem radius dynamics with environmental parameters at a short time scale is required for predicting cambial activity and may be achieved through high-resolution dendrometers.

The olive tree, Olea europaea L., is a Mediterranean tree important for its high potential of adaptation to harsh environments. Many different olive genotypes are cultivated worldwide and are characterized by high degree of morphological and biological variations (Rugini and Lavee, 1992). Phenological models revealed temperature as the best external variable to predict flowering time in olive tree cultivars (Osborne et al., 2000; Galán et al., 2005), demonstrating the potential of olive tree flowering as a measurement of the biological impacts of climatic warming in the Mediterranean region. Photoperiod might also have an influence on the timing of olive tree flowering (De Melo-Abreu et al., 2004), and using temperature as input variable and photoperiod as the threshold date to start temperature accumulation resulted in higher phenological model validity (García-Mozo et al., 2008). Differences in tree growth are expected to result in different xylem features in distinct olive tree cultivars. The forecasting of tree-ring properties in olive trees can be improved by understanding the intra-annual stem radius variations, which will be useful to predict the risk of climate change on species growing in Mediterranean environments.

In olive trees, stem diameter dynamics has been used to derive indices of water stress (Cuevas et al., 2010), as being useful for precise irrigation scheduling in commercial plantations (Fernández and Cuevas, 2010). Reference values are obtained by relating stem diameter measurements and plant water relations under non-limiting growth conditions with the evaporative demand of the atmosphere (Goldhamer and Fereres, 2001; Fereres and Goldhamer, 2003; Ortuño et al., 2006a, 2006b). Moreno et al. (2006) found that maximum daily shrinkage (MDS) at trunk level reflected changes in the evaporative demand, with daily mean vapour pressure deficit (VPD) and midday air temperature, therefore continuous recording of MDS offers the promising possibility for sagacious irrigation scheduling in olive tree plantations. Tognetti et al. (2009) studied 16-year-old olive trees, grown under different water treatments for 14 years in an experimental site plantation in southern Italy, and found that plants growing under rainfed conditions showed a small increase in MDS during drought periods, pointing to increasing water conservation and acclimation potential with progressively decreasing water availability.

Empirical links between stem diameter variations and climate condition patterns could be used to derive iterative models for wood properties as a function of environmental signals and physiological processes. The application of mathematical functions is, however, preferable to perform quantitative solutions and sensitivity analysis (Baldocchi, 1994). It was hypothesized that seasonal changes in climate conditions, exerting a dominant control over cambium phenology, and stem radius variations would be synchronized through a mathematical approach that consider the non linearity of biological system. A detailed high-resolution analytical approach to describe the correspondence between tree-ring formation and climate variables was applied, defining the duration of growth phases and coupling processes of stem diameter with minimum temperature (T_{min}) and reference evapotranspiration (ET_0) throughout the seasons in four olive tree cultivars. In particular, the study was aimed at: (1) assessing the use of non-invasive methods with high resolution for the characterization of stem radius variations; (2) monitoring the progression of radial growth for the determination of intra-annual phases in tree-ring formation; (3) identifying the effect of environmental factors on stem radius variations through analytical processes.

2. Materials and Methods

2.1 Study area and experimental plantation

The experiment was conducted during the years 2004-2006 at the Santa Paolina experimental farm of CNR- IVALSA, located in Follonica (GR), Toscana, central Italy (42°55'58'' N, 10°45'51'' E, 17 m a.s.l.), using olive trees of four cultivars (Canino, Cipressino, Leccino and Maurino) cultivated at free vase system at a spacing of 4x4 m. The cultivars were chosen because of their different growing habit, vigour, frost resistance and water consumption. The olive orchard is on a sandy-loam soil with natural cover crop and no tillage traditionally managed again the main olive pests. The plants were not pruned during the three-years period of the experiment so that the canopy was set free to grow naturally without any modification. During the growing season preceding the experiment, all trees have been equally irrigated with a trickle system to guarantee the uniformity of plant development. The monitoring was conducted on rainfed olive trees, and started when plants were three years old. The experimental design was a complete randomised block, replicated four times, with subplot for micro-morphometric analysis.

2.2 Meteorological data

Climate data were recorded every 15 minutes with a standard meteorological digital station placed at 100 m from the orchard (quality-controlled data were supplied by Regione Toscana). The variables measured were air temperature (T_{mean}, T_{max} and T_{min}, °C), total rainfall (P, mm), and relative humidity (Rh, %). The maximum temperature was 34.6 °C in July 2006 and minimum temperature was -6.6 °C in January 2006. Vapour pressure deficit (VPD, kPa) was calculated from hourly values of T_{mean} and Rh. Climate of the area is typical Mediterranean with hot summer and relatively cold winter (Fig. 1), and hourly reference evapotranspiration (ET_0) was calculated following Hargreaves-Samani (Allen et al., 1998). Soil moisture deficit (SMD, mm) was calculated as the difference between cumulative ET and cumulative rainfall, with SMD < 0 set to zero.

For each period, cumulative degree-days (CDD) were determined by the single sine method from daily maximum and minimum temperature in the growth season using the method of Zalom et al. (1983). The number of degree-days above a particular temperature threshold provides a sum of (growing) degree-days over a period. The calculation was made using the simplest method, with a low temperature threshold of 10 °C and high temperature of 30 °C.

2.3 Stem data collection

Stem radius variations were monitored between October 2004 and October 2006 using automatic point dendrometers (Label et al., 2000) on four individual trees per each olive tree cultivar. The dendrometers measure the linear displacement of a sensing rod pressed against the bark. The operating principle is based on the use of a linear variable transducer (AB Electronics Ltd., Romford, Essex, UK) that responds to stem radius variation with an average sensitivity of 2 ± 0.01 mm V^{-1} (linearity of ± 2%, linear expansion coefficient of 16 μmm^{-1} $°C^{-1}$). As the stem expands and contracts, the rod transmits the signal to the transducer. The variable potential is digitised by an analogical-to-digital converter (PCI-1710 pg, Advanthech, Taiwan) connected to a PC-based data recording system. Trees were monitored with 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. Raw data were recorded every 15 min, and hourly and daily averages were then calculated. To minimize temperature effects, the stem radius measurements were corrected with a control measurement derived from point dendrometers installed on a quartz tube.

2.4 Time series comparison

The hourly values of stem radius of four cultivars, measured using automatic point dendrometers, were statistically analysed with the Time Series Analysis Programme (TSAP) software package (Frank Rinn, Heidelberg, Germany), which was originally developed as a tool for cross-timing of tree-ring series. In dendrochronology two main concepts have been used to express the quality of agreement between time series: *Gleichläufigkeit* (Glk) and/or *t*-values. Raw diameter values were cross-dated 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 is a measure of the day-to-day agreement between the interval trends of two chronologies 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 eliminates low-frequency variations in the time series, as each value is divided by the corresponding 5 days moving average.

2.5 Stem radius variation

The analysis of seasonal patterns was conducted by studying periods of 10 days, considering the amplitude and frequency phase. To characterize seasonal stem radius variation over the year, the duration (days) of each phase was calculated considering the occurrence of environmental conditions (T_{min}, ET_0 and VPD) and the intensity of stem shrinkage. Each season was classified according to three criteria: (i) duration, (ii) environmental conditions that origin cycle phases and (iii) net radius variation (stem variation or increment) (Table 1).

Two phases of the diurnal cycle of stem radius variation were defined, according to Downes et al. (1999): 'shrinkage' is the decrease in stem size from a local maximum to a local minimum of the same event (i.e., the period during which the stem radius decreased in the growing season); 'recovery' is the increase in stem radius from a previous minimum until a successive maximum (i.e., the portion of the cycle during which the stem radius increased until reaching the position observed at the local maximum before stem shrinkage started).

Stem radial fluctuations (i.e., stem radius shrinkage in winter and stem diameter increment, SDI, in the growing season) correspond to circadian variation calculated as the difference between the maximum point of stem shrinkage and the onset of this event. The diurnal thermal minimum and thermal excursion (variation) were recorded for every stem shrinkage event. The amplitude of the stem shrinkage was calculated considering the variation between the beginning and the end of the shrinkage phase. The daily mean approach gave results more similar to the stem cycle than the daily maximum (Deslauriers et al., 2007a).

The seasonal course was classified according to Tardif et al. (2001), allowing a division of the year into three periods: winter shrinkage, spring rehydration and summer transpiration. Seasonal climatic changes were determined with the raw meteorological data (air temperature, ET_0, VPD, SMD), which define specific ranges of climatic values, and, then, observing the stem dynamics in relation to environmental conditions (Fig. 1). Data of stem radius in the growing season were related to ET_0 (VPD and SMD, data not shown). The variable function coefficients allowed defining three stages, consequently to the degree of agreement of stem and ET_0 behaviour. Moreover, each stage was characterized by duration in days and CDD (Table 1).

2.6 Mathematical approach

The first exploration was on the seasonal rhythm of stem radius variation. The data analysis was done on a tree-by-tree basis, and then averaged by cultivar. The relationship between climate data and stem radius variation using a mathematical approach was tested. Although a general pattern was described based on graphical analyses of the time series, useful tools to clearly define the seasonal patterns of radius variation are still lacking.

Rough data collected in winter season were first analysed following Cocozza et al. (2009). Whereas, records of the vegetation period, spring and summer, were focused on the high-frequency signals of stem growth through the "detrending" or "standardization" method, which removes the effects of tree growth from the time series, enabling to focus on the climatic fluctuations. Detrended values of stem diameter series for each cultivar were obtained by fitting a smooth mathematical growth function. To remove the effect of growth trends in the series, individual series were standardized, by fitting a negative exponential curve to the measured data series and dividing observed by expected values. Therefore, seasonal stem radius series did not contain growth patterns. The fitting procedure assumes that most of the individual growth trend was due to the biological growth trend (Cook et al., 1990).

However, the pronounced noise signal, due to the sensitivity of the transducer, did not allow an accurate analysis of data. As a consequence, stem variation, air temperature and VPD records were processed through the use of the derivative approach as a support to the use of rough data. The derivative analysis was done 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)*:

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

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 emphasized; when the derivative is found to be positive, the input function is increasing, when it is negative the function is decreasing. Moreover, the higher value of the derivative the faster 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. In fact, due to the sensitivity of the transducer, the data present a permanent noise, which means, on the derivative curve, a high number of events (peaks, x-axis intersection), without correspondence with the scope of the present study. In order to amplify the eventual differences between cultivars in the response to air temperature and VPD, normalized derivatives were used. For each olive cultivar and each considered season 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 the input function. A positive (negative) derivative that intersects the x-axis indicates a local maximum (minimum) of the input function.

2.7 Pointer day analysis

Pointer days were analysed with a dendrochronological approach (Neuwirth et al., 2007), in order to show daily growth patterns as affected sudden changes in environmental conditions (e.g., Schweingruber et al., 1990). All raw daily stem diameter measurement series were transformed into high-frequency time series of pointer values using a two-step approach. Ratios between the raw daily measurements for single cultivar series and their 13-day moving average were calculated according to Cropper (1979). Cropper-values were then normalized to have a mean of zero and a standard deviation of one over the season, which all cultivar have in. The resultant data highlight inter-daily growth anomalies. The time series of normalized Cropper-values, allowed for the interpretation of daily standard deviation units of site- and species-specific growth characteristics. In addition to the intensity of the growth anomalies, Cropper-values defined three classes of positive and negative growth deviations: “weak” for values > 1, “strong” for values > 1.28, and “extreme” for values > 1.645. Growth deviations with Cropper-values between -1 and 1 are named as “normal”. These thresholds correspond to the probability density function of the standardized normal distribution.

3. Results

3.1 Seasonal climatic patterns

The dynamics of environmental data showed the typical pattern, with the lowest values of temperature, VPD and ET_0 during the winter months, and highest values in the rest of year (Fig. 1). The study of daily temperatures showed succession of negative minimum thermal peaks in winter, when minimum temperatures ranged between -5.6 and 12.3 °C in 2004-2005 season, with the lowest value in March, and between -6.6 and 11.1°C in 2005-2006 season, with the lowest value in January. The negative thermal peaks of minimum diurnal air temperature, prompting stem shrinkage, were recorded immediately below 0 °C (Fig. 2). The growing seasons were characterized by mean air temperature ranging between 3.7 and 26.0 °C in 2005 and between 8.8 and 27.0 °C in 2006, with the highest maximum temperatures of 34.1 °C and 34.6 °C in July of both years.

Daily mean VPD values increased from the beginning of the measurement period, reaching maximum values in July, and then gradually decreased, from DOY (day of year) 210 in 2005 and DOY 197 in 2006 (Fig. 1). The VPD ranged from 0.01 to 1.92 kPa in 2004, from 0.03 to 1.58 kPa in 2005 and from 0.03 to 1.94 kPa in 2006.

Values of SMD increased from a baseline reached in DOY 74 (2005) and 84 (2006) to a maximum value in DOY 245 (2005) and 251 (2006) (Fig. 1). Daily mean ET_0 increased up to 6.25 and 6.48 mm in 2005 and 2006, respectively (DOY 209 and 195), decreasing thereafter, whereas cumulative values in ET_0 reduced the slope of increasing rate (Fig. 1).

In 2005, stage I was equally long in Canino, Cipressino and Leccino, whereas it was 56 days with 172 °C CDD in Maurino. Stage I had similar CDD in Canino, Cipressino and Leccino. Stage II differed in period length between cultivars: Cipressino > Canino > Leccino > Maurino, showing CDD in Cipressino > Canino > Leccino and Maurino. Stage III was similar in Leccino and Maurino, which showed higher CDD than Canino and Cipressino. In 2006, stage I varied in period length from shorter in Maurino to longer in Leccino; CDD decreased from Leccino > Cipressino > Canino > Maurino. Stage II protracted in Maurino > Cipressino > Canino > Leccino; with similar CDD in Cipressino, Leccino and Maurino. Stage III was longer in Canino than other cultivars; Cipressino, Leccino and Maurino showed similar values. Thus, stage III had identical CDD in the four cultivars, per year, being defined by the end and the beginning of winter season.

3.2 Stem radius variations

The diurnal stem radius variation showed a highly significant correlation between trees within each cultivar (Table 2). A strong similarity between cross timing coefficients was found for patterns of the time series of stem behaviour (Glk was significant, $P < 0.01$; TVBP > 74% degree of correlation between curves). As a consequence, the four trees per cultivar were pooled together for the following analysis. Moreover, differences in sensitivity to environmental variables between cultivars were not observed, showing stem radius variations in agreement with seasonal climatic cycles, with Glk > 83 in the inter-cultivar comparison of stem diameter time series of each year.

The seasonal trend in stem radius variations of Canino, Cipressino, Leccino and Maurino cultivars went with the cyclic phenological patterns. Stem shrinkage in winter reflected a direct sensitivity to low temperature, while cambium phenology followed the seasonal curse (Fig. 3). At the beginning of the monitoring period (19 October 2004) the mean diameter was 9.99, 8.30, 10.39 and 13.40 mm, while at the end of experiment (26 October 2006) was 27.86, 26.25, 25.34 and 31.01 mm in Leccino, Cipressino, Maurino and Canino, respectively. However, dynamics of intra-annual stem radius variation were induced by air temperature (Figs. 1; 2; 4), VPD, SMD and ET_0 (Figs. 1; 5).

Stem radius dynamics were not characterized by a correspondence between marked SDI in the growing season and high stem shrinkage in winter (Fig. 3).

In winter, from early December to mid March, the stem radius variations did not show evidences of irreversible variation (Figs. 2; 3). The effects of T_{min} resulted in winter shrinkage of 101 and 106 days in length, respectively, for 2004-2005 and 2005-2006 (Table 1). Stem shrinkage occurred in coincidence of minimum temperatures during winter, which, at the end of the season was completely reversible. Stem shrinkage events showed different amplitude ranges, up to 0.34 mm in 2004-2005 and 0.54 mm in 2005-2006 (Table 1). Stem shrinkage, suddenly appeared when T_{min} dropped below 0 °C (Fig. 2). In 2004-2005, 11 negative thermal cycles were recorded, in the range of minimum air temperature between -0.3 and -5.6 °C; whereas, in winter 2005-2006, 10 negative thermal cycles were between -0.7 and -6.6 °C.

A correspondence of minimum thermal peak and maximum stem shrinkage was observed through normalized derivative function (Fig. 4), highlighting the coincidence of reduction in air temperature and stem shrinkage in winter. The study of derivative suggested that the variation of the function with respect to y = 0 defined the change in curve behaviour, concurrently for stem radius variation and minimum air temperature in the four 4 cultivars (Fig. 4).

3.3 Stem diameter increment

The onset of growth was defined by the occurrence of reduced stem shrinkage, in combination with varying environmental conditions, namely induction of transpiration cycles and increase of air temperature (Fig. 1). In the growing season, the increase of air temperature boosted SDI values (Figs. 1 and 5), SDI enduring from mid March through mid November in both years of study. In the 2005 growing season SDI values were higher than in the following year, with different incremental threshold between cultivars. Indeed, in 2005, SDI was 12.88 mm in Canino, 10.91 mm in Cipressino, 11.64 mm in Leccino and 8.12 mm in Maurino; whereas, in 2006, SDI was 4.27 mm in Canino, 6.84 mm in Cipressino, 5.84 mm in Leccino and 6.26 mm in Maurino.

The stem growth continued with the increase in SMD and cumulative ET_0 during summer (Fig. 1). The present study showed a direct correspondence between the normalized and detrended stem radius and ET_0 time series in the growing season (Fig. 5). A specular and opposite behaviour was evident in the two curves (SDI and ET_0 time series). The negative (or positive) values of stem diameter corresponded to positive (or negative) values of derivative functions of ET_0 in the four cultivars, during spring and summer, in both years of monitoring.

The SDI showed statistically significant linear relationships with ET_0 (Fig. 6), and VPD and SMD (data not shown), considering the three seasonal stages. Data fitting was built starting with the identification of seasonal periods in daily radial activity, according to the classification of Tardif *et al.* (2001). The relationship between SDI and environmental variables defined characteristic patterns of (i) a period of instability in winter, with strong episodes of swelling and shrinking (Figs. 2; 3); (ii) a short period of stability, with practically no radius increment; (iii) a period of growth during spring and summer, with a steep and continuous increase of the stem radius (Fig. 6). In general, the four cultivars responded in synchrony, although small differences between trees were observed in the onset and end of each stage (Table 1). The stage I of growth was set at the beginning of the season from mid March to mid April (Table 1), being characterized by slight shrinkage events with SDI below 1 mm (Fig. 6). The stage II was set from mid April to early July, except for Canino in 2006 and Cipressino in 2005 for which the end of their stage II was set in mid June and end July, respectively. The stage II was defined by an important inflexion of stem radial increment, up to 5 mm in both years, with small differences between cultivars, and by a positive and significant correlation with ET_0 (Fig. 6). The stage III of growth was set from early July to mid November, expect for Canino in 2006 and Cipressino in 2005, as mentioned before. In 2006, the end of the stage III was set in late October, in coincidence of the stop of monitoring with dendrometers. The stage III was characterized by SDI up to 9 mm in 2005 and up to 2 mm in 2006, showing a negative correlation with ET_0 (Fig. 6).

3.4 Pointer days

All cultivars showed positive growth anomalies defined in the range of normal growth patterns (Neuwirth et al., 2007), following Cropper-values that were below the threshold of 1, regardless of the season (spring or summer) or year (2005 or 2006) in the four studied olive tree cultivars. Significant pointer days induced by remarkable environmental conditions were not observed.

4. Discussion

The study was aimed at monitoring the progression of radial growth and synchronizing the relationship between stem radial variations and climate variables in four olive tree cultivars, through a mathematical approach. Stem radius variation, generally, is defined by stem water content and wood growth, including bark and the degradation of dead phloem cells (http://prometheuswiki.publish.csiro.au/tiki-index.php, 2011). The methodology for analysing the output from high-resolution dendrometers made stem radius dynamics to be mathematically resolved. A detailed description was provided of seasonal phases in olive trees, defining shrinkage cycles during winter and growth stages during the growing season. This information may be conveniently used in the agronomic management of commercial olive tree plantation and in the sensitive monitoring of varying ecological circumstances, and extended to species with indeterminate growth habits and in climate with erratic patterns (Sprugel et al., 1991).

Minimum air temperature induced winter shrinkage, while VPD, SMD and ET_0 patterns were pioneering in the definition of the onset of moderate induction process in early spring and intrinsic stem growth later in the season. Seasonal course of local climate was regular, considering long term records for the area, which represented a regular signal explaining the relationship between environmental conditions and cambial activity. Indeed, air temperature, ET_0, VPD and SMD provided information of critical environmental values at many stages of plant development (Heide and Prestud, 2005; Badeck et al., 2004), useful to expand the application of point dendrometers and stem radius variations in stress physiology of woody plants.

4.1 Stem radius shrinkage during winter

Air temperature showed a weaving and cyclic course during the winter season, with negative thermal excursions. The nighttime shrinkage and daytime swelling of the stem are primarily dependent on temperature (Zweifel and Häsler, 2000; Turcotte et al., 2009). Stem shrinkage events occurred when temperatures suddenly dropped below 0 °C, in all cultivars showing highly similar time series and significant response to low temperatures. Indeed, the analysis of correspondence between stem shrinkage and air temperature did not reveal different sensitivity to freezing air temperature amongst cultivars, which showed similar shrinkage and swelling of stem during dormancy. In alpine conifers, a sharp stem radius changes in winter (frost shrinkage and thaw expansion) are caused by changes of the turgor in the elastic bark cells (cambium, phloem, and parenchyma) in the same way as the diurnal radius fluctuations in summer (Zweifel and Häsler, 2000). However, only small fluctuations in wood size are reported at moderate temperatures (Dobbs and Scott, 1971; Molz and Klepper, 1973; Siau, 1984).

When temperatures fall below the freezing point of sap, the reduction in the bark cell volume associated with the loss of intracellular water produces tissue shrinkage (Améglio et al., 2001), which produces the contraction phase. The swelling of the stem, as a result of hydrating cells, creates the expansion phase, which restores the tree to a physiologically active state specifying the range of stem size that allows water transport in the xylem and gas exchange of the canopy (Zweifel and Häsler, 2000). The stem radial swelling after winter shrinkage is also modulated by tissue elasticity (Améglio et al., 2001). Zweifel and Häsler (2000) suggested that the morphological structure of the xylem plays an important role in efficient radial water transport during freezing periods. Améglio et al. (2001) found that the magnitude of stem shrinkage in response to freezing temperatures is proportional to stem diameter. The onset of wood formation corresponds to the rise in air and soil temperature. However, the analysis of stem radius variation and its coordination with seasonal climatic trend needs additional functional and structural insights (Cocozza et al., 2009).

Wider stem shrinkage-recovery phases were observed in winter 2005-2006 than in previous year, in all cultivars. The two winter seasons were characterized by similar minimum temperature peaks, -5.6 °C and -6.6 °C in the first and second monitoring year, respectively. However, the number and the amplitude of thermal excursion events, as wave span between maximum and minimum temperature peaks, shaped differences in stem shrinkage cycles between the two winter seasons. Indeed, winter 2005-2006 showed wide thermal fluctuations tallied by stem radius variations, while limited thermal excursion events in winter 2004-2005 corresponded to relatively narrow stem radius variations. It may be hypothesized that the amplitude of thermal fluctuations defines the correspondence of radial variations with temperature peaks.

The derivative approach was useful for a clearer definition and description of stem radius variations related to climatic data. No tissue damage under low temperatures was detected, and each stem shrinkage event was followed by recovery, as shown by derivative functions with negative values (stem shrinkage phase) followed by positive values (stem recovery phase). Therefore, stem radius variations were entirely reversible under freeze–thaw cycles, suggesting acclimation of these olive tree genotypes to local environmental conditions. A general correspondence of stem shrinkage peaks, namely radius sensitivity, with low winter temperatures was, therefore, confirmed for this Mediterranean species, suggesting that point dendrometers could be consistently used to define sensitivity thresholds of stem radius variations to low air temperatures.

Stem shrinkage in olive trees did not show a genotype-specific thermal threshold. By contrast, Cocozza et al. (2009) identified specific thermal threshold in poplar clones. Comparison between effects of low temperature in poplar clones vs. olive tree cultivars might be inappropriate, as well as between the two experimental sites, which differ in temperature and precipitation patterns. Indeed, olive tree is well known for its hard, heavy and dense wood, which contrasts with that of poplar. However, these observations confirm the need to provide site- and plant-specific indications to define the short-term response of stem sensitivity to environmental conditions, necessary for predicting the long-term impact of climate change on tree growth. Dormancy release in olive trees is mainly due to chilling, with a weak-compensating effect by combination of maximum and minimum temperatures (De Melo-Abreu et al., 2004). The application of linear variable transducer sensors was a useful and non-invasive tool to test cold acclimation of olive trees in field conditions, which was confirmed a species with low chilling requirement for stem dormancy release (Rallo and Martin, 1991).

4.2 Radial fluctuation patterns in the growing season

The monitoring of stem radius variations showed regular growth trends in the four olive tree cultivars. The relation of SDI with environmental variables might be conveniently bounded to define cambium phenology and season lengthening. The increase of air temperature in spring triggered the induction phase of growth, temperature being important for its effect on the initiation of vegetation period (Orlandi et al., 2010). Nevertheless, air temperature and stem radius time series did not show a clear coincidence, as observed in winter season. During the growing season, instead, VPD, SMD and ET_0 influenced the radial growth phases. In other experiments, air temperature was found to be unrelated to growth rate of olive trees (Cuevas et al., 2010). Indeed, SDI indicates the timing of xylogenesis (e.g., Deslauriers et al., 2003); at the present study site, SDI was recorded from March to December, in 2005, and from March to October, in 2006. Evidences of threshold temperatures for xylogenesis have been found for trees at their altitudinal limit (Rossi et al., 2007). Different dynamics of SDI emerged between years, with higher SDI values in 2005 than 2006, suggesting inter-annual dynamics of tree-ring formation due to variable xylem production and specific thermal limits. Canino showed the highest SDI, probably related to absolute higher growth rates than others cultivars. Cumulative degree-days based on temperature thresholds were quite similar for 2005 and 2006, at the site study. Heat units were used to quantify phenological phases of stem growth, which progressed as a function of air temperature from the end of winter (phase of stem shrinkage). The different CDD required by each cultivar probably defines genotype-specific heat needs to evolve in the succeeding stage of stem growth, namely phenological phase.

The increase in ET_0 during the growing season drove stem shrinkage, as evidenced by the opposite derivative values. The decrease in stem radius derivative function matched the increase in ET_0 derivative function, in spring and summer, depicting cambial activity. The relationship between SDI and ET_0 may be explained by the association between MDS and daily tree transpiration (Moreno et al., 2006). Michelakis (1997) showed that MDS in olive trees was highly correlated to evaporation rate. Herzog *et al.* (1995) and Deslauriers et al. (2007b) observed that transpiration rate and VPD influence MDS in alpine conifers, the correlations being dependent also on the duration of stem radius and contraction phases. Impacts of changing environmental conditions on timing and duration of the growing season have been assessed by long-term plant phenological observations (Rutishauser et al., 2007), which may be further refined by monitoring stem radius variations. In olive trees, stem physiological parameters determined through dendrometers and sap flow sensors respond to variations in plant water status, soil moisture availability and evaporative demand (e.g., Tognetti et al., 2004, 2005). However, MDS has been found to be relatively more sensitive to seasonal water availability than plant transpiration rate (Remorini and Massai, 2003; Ortuño et al., 2006a, b; Conejero et al., 2007), affecting plant water status albeit supplied in modest amount (Tognetti et al., 2007). Indeed, trunk growth may not provide an independent measure of plant water status (Intrigliolo and Castel, 2007), particularly in alternate-bearing species such as the olive tree (Tognetti et al., 2009), which observed a small increase in MDS during drought periods, while unclear differences were recorded between different irrigation treatments.

The regression analysis indicated a linear relation between SDI and ET_0, defining three definite stem developmental stages within the growing season. The stage I probably corresponded to the induction signal, recording the increase of air temperature essential for meristem reactivation and for shifting to successive stages. Stem radius increased from one morning to the next in the stage II, following high evaporative demand. The stage III was defined by SDI decreasing with increasing evaporative demand. Values of SDI were high in the stage III for 2005 and in the stage II for 2006, although similar ET_0 ranges characterized the two growing seasons. By contrast, low SDI values were observed in the stage II for 2005 and in the stage III for 2006. Therefore, the range of SDI values could not be indicative of consecutive growth stages. Distinct patterns of development characterize these olive tree cultivars, and consequently their phenology. This information may be implemented in the definition of specific growth stage requirements in orchard management practices (Sanz-Cortés et al., 2002). The four cultivars differed in the duration of the three stem developmental stages, although, the statistical analysis did not support differences in cultivar sensitivity to environmental conditions.

5. Conclusion

In conclusion, this study provides a simple mechanistic model describing stem radius variations and complements the analysis of data matrix obtained using continuous high-resolution dendrometers (Deslauriers et al., 2007a, b; Giovannelli et al., 2007). On this model species for Mediterranean-type environments, we distinguished the timing of transition from the dormant winter state to the active growth stage and till the slow expansion phase (see Cherubini et al., 2003), saving living tissues from cold and drought damages. The approach provides new insights of shrinkage-swelling phenomena in Mediterranean environments, related to dehydration and hydration cycles, which are difficult to detect with stem radius variation alone. The ability to switch quickly between inactive to active stages would enable the olive tree to restart physiological processes and to cope with erratic climatic conditions of the Mediterranean region. The use of stem radius variation to extrapolate supplementary information on how trees use water and to schedule irrigation in modern tree plantations (e.g., Moriana and Fereres, 2002; Conejero et al., 2010; Egea et al., 2010) and to determine the timing of growth initiation (e.g., Downes et al., 1999; Deslauriers et al., 2003; Turcotte et al., 2009), however, requires expert interpretation (Fernández and Cuevas, 2010). Despite a long history of research into the physiological pathways that underlie plant phenology, we are still learning how multiple environmental influences interact with endogenous cues to predict biological events. By incorporating information on standardized stem radius oscillation, phenological observations would better contribute to explain how trees respond to global warming (Orlandi et al., 2010). The analysis of raw data and derivative values allowed an increase in the sensitivity of the investigative approaches applied to describe the response of olive tree cultivars to environmental conditions, which may complement the monitoring of the progression of radial growth and phenological stages in threatened Mediterranean ecosystems (García-Mozo et al., 2010).

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References

Allen, R.G., Pereira, L.S., Raes, D., Smith, M., 1998. Crop Evapotranspiration. Guidelines for Computing Crop Water Requirements. FAO Irrigation and Drainage Paper 56, Rome, p. 290.

Améglio, T., Cochard, H., Ewers, W.F., 2001. Stem diameter variations and cold hardiness in walnut trees. J. Exp. Bot. 52, 2135–2142.

Badeck, F.W., Bondeau, A.B.K., Doktor, D., Lucht, W., Schaber, J., Sitch, S., 2004. Response of spring phenology to climate change. New Phytol. 162, 295–309.

Baillie, M.G.L., Pilcher, J.R., 1973. A simple cross-dating program for tree-ring research. Tree-Ring Bull. 33, 7–14.

Baldocchi, D., 1994. An analytical solution for coupled leaf photosynthesis and stomata conductance models. Tree Physiol. 14, 1069–1079.

Cherubini, P., Gartner, B.L., Tognetti, R., Bräker, O.U., Schoch, W., Innes, J., 2003. Identification, measurement and interpretation of tree rings in woody species from Mediterranean climates. Biol. Rev. 78, 119-148.

Chuine, I., Cour, P., Rousseau, D.D., 1998. Fitting models predicting dates of flowering of temperate-zone trees using simulated annealing. Plant Cell Environ. 21, 455–466.

Cocozza, C., Lasserre, B., Giovannelli, A., Castro, G., Fragnelli, G., Tognetti, R., 2009. Low temperature induces different cold sensitivity in two poplar clones (*Populus* x *canadensis* Mönch ‘I-214’ and *P. deltoides* Marsh. ‘Dvina’). J. Exp. Bot. 60, 3655–3664.

Conejero, W., Alarćon, J.J., García-Orellana, Y., Nicolás, E., Torrecillas, A., 2007. Evaluation of sap flow and trunk diameter sensors for irrigation scheduling in early maturing peach trees. Tree Physiol. 27, 1753–1759.

Conejero, W., Ortuño, M.F., Mellisho, C.D., Torrecillas, A., 2010. Influence of crop load on maximum daily trunk shrinkage reference equations for irrigation scheduling of early maturing peach trees. Agric. Water Manage. 97, 333–338.

Cook, E.R., Briffa, K., Shiyatov, S., Mazepa, V., 1990. Tree-ring standardization and growth trend estimation. In: Cook, E.R., Kairiukstis, L.A. (Eds.), Methods of Dendrochronology. Applications in the Environmental Sciences. Kluwer Academic Publishers, Dordrecht, pp. 104-123.

Cropper, J.P., 1979. Tree-ring skeleton plotting by computer. Tree-Ring Bull. 39, 47-59.

Cuevas, M.V., Torres-Ruiz, J.M., Álvarez, R., Jiménez, M.D., Cuerva, J., Fernández, J.E., 2010. Assessment of trunk diameter variation derived indices as water stress indicators in mature olive trees. Agric. Water Manage. 97, 1293–1302.

De Melo-Abreu, J.P., Barranco, D., Cordeiro, A.M., Tous, J., Rogado, B.M., Villalobos, F.J., 2004. Modelling olive flowering date using chilling for dormancy release and thermal time. Agric. For. Meteorol. 125, 117–127.

Deslauriers, A., Morin, H., Urbinati, C., Carrer, M., 2003. Daily weather response of balsam fir (*Abies balsamea* (L.) Mill.) stem radius increment from dendrometer analysis in the boreal forests of Quebec (Canada). Trees 17, 477–484.

Deslauriers, A., Morin, H., 2005. Intra-annual tracheid production in balsam fir stems and the effect of meteorological variables. Trees 19, 402–408.

Deslauriers, A., Rossi, S., Anfodillo, T., 2007a. Dendrometer and intra-annual tree growth: What kind of information can be inferred? Dendrochronologia 25, 113–124.

Deslauriers, A., Anfodillo, T., Rossi, S., Carraro, V., 2007b. Using simple causal modeling to understand how water and temperature affect daily stem radial variation in trees. Tree Physiol. 27, 1125–1136.

Dobbs, R.C., Scott, D.R.M., 1971. Distribution of diurnal fluctuations in stem circumference of Douglas-fir. Can. J. For. Res. 1, 80-83.

Downes, G., Beadle, C., Worledge, D., 1999. Daily stem growth patterns in irrigated *Eucalyptus globules* and *E. nitens* in relation to climate. Trees 14, 102-111.

Egea, G., Nortes, P.A., González-Real, M.M., Baille, A., Domingo, R., 2010. Agronomic response and water productivity of almond trees under contrasted deficit irrigation regimes. Agric. Water Manage. 97, 171–181.

Fereres, E., Goldhamer, D.A., 2003. Suitability of stem diameter variations and water potential as indicators for irrigation scheduling of almond trees. J. Hort. Sci. Biotech. 78, 139–144.

Fernández, J.E., Cuevas, M.V., 2010. Irrigation scheduling from stem diameter variations: A review. Agric. For. Meteorol. 150, 135–151.

Galán, C., García –Mozo, H., Vázquez, L., Ruiz, L., Díaz de la Guardia, C., Trigo, M.M., 2005. Heat requirement for the onset of the *Olea europaea* L. pollen season in several sites in Andalusia and the effect of the expected future climate change. Int. J. Biometeorol. 49, 184–188.

García-Mozo, H., Mestre, A., Galán, C., 2010. Phenological trends in southern Spain: A response to climate change. Agric. For. Meteorol. 150, 575–580.

García-Mozo, H., Orlandi, F., Galán, C., Fornaciari, M., Romano, B., Ruiz, L., Diaz de la Guardia, C., Trigo, M.M., Chuine, I., 2008. Olive flowering phenology variation between different cultivars in Spain and Italy: modeling analysis. Theor. Appl. Climatol. 95, 385–395.

Geßler, A., Keitel, C., Kreuzwieser, J., Matyssek, R., Seiler, W., Rennenberg, H., 2007. Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. Trees 21, 1–11

Giovannelli, A., Deslauriers, A., Fragnelli, G., Scaletti, L., Castro, G., Rossi, S., Crivellaro, A., 2007. Evaluation of drought response of two poplar clones (*Populus* x *canadensis* Mönch 'I-214' and *P. deltoides* Marsh. 'Dvina') through high resolution analysis of stem growth. J. Exp. Bot. 58, 2673–2683.

Goldhamer, D.A., Fereres, E., 2001. Irrigation scheduling protocols using continuously recorded trunk diameter measurements. Irri. Sci. 20, 115–125.

Heide, O.M., Prestud, A.K., 2005. Low temperature, but not photoperiod, controls growth cessation and dormancy induction and release in apple and pear. Tree Physiol. 25, 109–114.

Herzog, K.M., Häsler, R., Thum, R., 1995. Diurnal changes in the radius of a subalpine Norway spruce stem: their relation to the sap flow and their use to estimate transpiration. Trees 10, 94–101.

Intrigliolo, D.S., Castel, J.R., 2007. Crop load affects maximum daily trunk shrinkage of plum trees. Tree Physiol. 27, 89–96.

Kaennel, M., Schweingruber, F.H., 1995. Multilingual glossary of dendrochronology. Swiss Federal Institute for Forest, Snow and Landscape Research. Paul Haupt, Bern.

Label, P., Beritognolo, I., Burtin, P., Dehon, L., Couée, I., Breton, C., Charpentier, J.P., Jay-Allemand, C., 2000. Cambial activity and xylem differentiation in walnut (*Juglans* sp). In: Savidge, R.A., Barnett, J.R., Napier, R. (Eds.), Cell and Molecular Biology of Wood Formation. BIOS Scientific Publishers, Oxford, pp. 209–221.

Lupi, C., Morin, H., Deslauriers, A., Rossi, S., 2010. Xylem phenology and wood production: resolving the chicken-or-egg dilemma. Plant Cell Environ. 33, 1721–1730.

Michelakis, N., 1997. Daily stem radius variations as indicators to optimise olive tree irrigation scheduling. Acta Hort. 449, 297–304.

Molz, F.J., Klepper, B., 1973. On the mechanism of water-stress-induced stem deformation. Agron. J. 65, 304-306.

Moreno, F., Conejero, W., Martín-Palomo, M.J., Girón, I.F., Torrecillas, A., 2006. Maximum daily trunk shrinkage reference values for irrigation scheduling in olive trees. Agric. Water Manage. 84, 290 – 294

Moriana, A., Fereres, E., 2002. Plant indicators for scheduling irrigation of young olive trees. Irri. Sci. 21, 83–90.

Munro, M.A.R., 1984. An improved algorithm for crossdating tree-ring series. Tree-Ring Bull. 44, 17–27.

Neuwirth, B., Schweingruber, F.H., Winiger, M., 2007. Spatial patterns of central European pointer years from 1901 to 1971. Dendrochronologia 24, 79–89.

Orlandi, F., Sgromo, C., Bonofiglio, T., Ruga, L., Romano, B., Fornaciari, M., 2010. Yield modelling in a Mediterranean species utilizing cause–effect relationships between temperature forcing and biological processes. Sci. Hort. 123, 412-417.

Ortuño, M.F., García-Orellana, Y., Conejero, W., Ruiz-Sánchez, M.C., Alarcón, J.J., Torrecillas, A., 2006a. Stem and leaf water potentials, gas exchange, sap flow and trunk diameter fluctuations for detecting water stress in lemon trees. Trees 20, 1–8.

Ortuño, M.F., García-Orellana, Y., Conejero, W., Ruiz-Sánchez, M.C., Mounzer, O., Alarcón, J.J., Torrecillas, A., 2006b. Relationships between climatic variables and sap flow, stem water potential and maximum daily trunk shrinkage in lemon trees. Plant Soil 279, 229–242.

Osborne, C.P., Chuine, I., Viner, D., Woodward, F.I., 2000. Olive phenology as a sensitive indicator of future climatic warming in the Mediterranean. Plant Cell Environ. 23, 701–710.

Rallo, L., Martin, G.C., 1991. The role of chilling in releasing Olive floral buds from dormancy. J. Amer. Soc. Hort. Sci. 116, 1058-1062.

Remorini, D., Massai, R., 2003. Comparison of water status indicators for young peach trees. Irri. Sci. 22, 39-46.

Rossi, S., Deslauriers, A., Anfodillo, T., Morin, H., Saracino, A., Motta, R., Borghetti, M., 2006. Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length. New Phytol. 170, 301–310.

Rossi, S., Deslauriers, A., Anfodillo, T., Carraro, V., 2007. Evidence of threshold temperatures for the xylogenesis in conifers in high altitudes. Oecologia 152, 1-12.

Rugini, E., Lavee, S., 1992. Olive. In: Hammerschlag, F.A., Litz, R.E., (Eds.), Biotechnology of Perennial Fruit Crops. CAB International, Wallingford, pp. 371–382.

Rutishauser, T., Luterbacher, J., Jeanneret, F., Pfister, C., Wanner, H., 2007. A phenology-based reconstruction of interannual changes in past spring seasons. J. Geophys. Res. 112, 1-15.

Sanz-Cortés, F., Martínez-Calvo, J., Badenes, M.L., Bleiholder, H., Hack, H., Llacer, G., Meier, U., 2002. Phenological growth stages of olive trees (*Olea europea*). Ann. Appl. Biol. 140, 151-157.

Schweingruber, F.H., Eckstein, D., Serre-Bachet, F., Bräker, O.U., 1990. Identification, presentation and interpretation of event years and pointer years in dendrochronology. Dendrochronologia 8, 9-38.

Siau, J.F., 1984. Transport Processes in Wood. Springer, Berlin, p.142.

Sprugel, D.G., Hinckley, T.M., Schaap, W., 1991. The Theory and Practice of Branch Autonomy. Annu. Rev. Ecol. Syst. 22, 309-334.

Tardif, J., Flannigan, M., Bergeron, Y., 2001. An analysis of the daily radial activity of 7 boreal tree species, northwestern Quebec. Environ. Monit. Assess. 67, 141–160.

Tognetti, R., d'Andria, R., Morelli, G., Calandrelli, D., Fragnito, F., 2004. Irrigation effects on daily and seasonal variations of trunk sap flow and leaf water relations in olive trees. Plant Soil 263, 249–264.

Tognetti, R., d'Andria, R., Morelli, G., Alvino, A., 2005. The effect of deficit irrigation on seasonal variations of plant water use in *Olea europaea* L. Plant Soil 273, 139–155.

Tognetti, R., d'Andria, R., Sacchi, R., Lavini, A., Morelli, G., Alvino, A., 2007. Deficit irrigation affects seasonal changes in leaf physiology and oil quality of *Olea europaea* (cultivars Frantoio and Leccino). Ann. Appl. Biol. 150, 169–186.

Tognetti, R., Giovannelli, A., Lavini, A., Morelli, G., Fragnito, F., d'Andria, R., 2009. Assessing environmental controls over conductances through the soil–plant– atmosphere continuum in an experimental olive tree plantation of southern Italy. Agric. For. Meteorol. 149, 1229–1243.

Turcotte, A., Morin, H., Krause, C., Deslauriers, A., Thibeault-Martel, M., 2009. The timing of spring rehydration and its relation with the onset of wood formation in black spruce. Agric. For. Meteorol. 149, 1403–1409.

Zalom, F.G., Goodell, P.B., Wilson, L.T., Barnett, W.W., Bentley, W.J., 1983. Degree-Days: The Calculation and Use of Heat Units in Pest Management. University of California, Division of Agriculture and Natural Resources, Leaflet 21373.

Zweifel, R., Häsler, R., 2000. Frost-induced reversible shrinkage of bark of mature subalpine conifers. Agric. For. Meteorol. 102, 213-222.

Zweifel, R., Item, H., Häsler, R., 2001. Link between diurnal stem radius changes and tree water relations. Tree Physiol. 21, 869–877.

Zweifel, R., Eugster, W., Etzold, S., Dobbertin, M., Buchmann, N., Häsler, R., 2010. Link between continuous stem radius changes and net ecosystem productivity of a subalpine Norway spruce forest in the Swiss Alps. New Phytol. 187, 819–830.

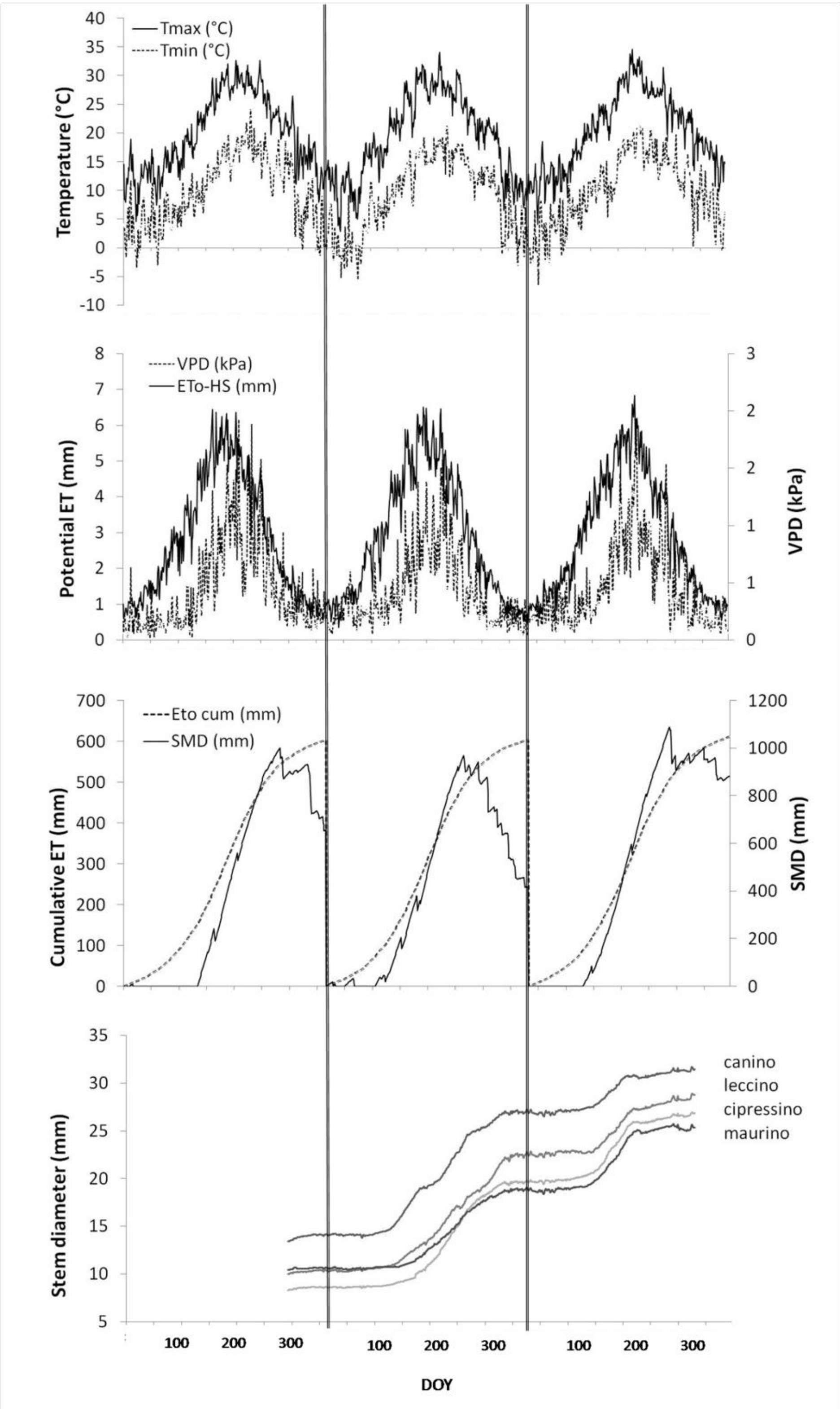

Fig. 1 - Daily values of maximum and minimum air temperature (T_{max} and T_{min}), reference evapotranspiration (ET_0), vapour pressure deficit (VPD), cumulative evapotranspiration, soil moisture deficit (SMD), and stem diameter of four cultivars of olive tree during 2004, 2005 and 2006 at the study site.

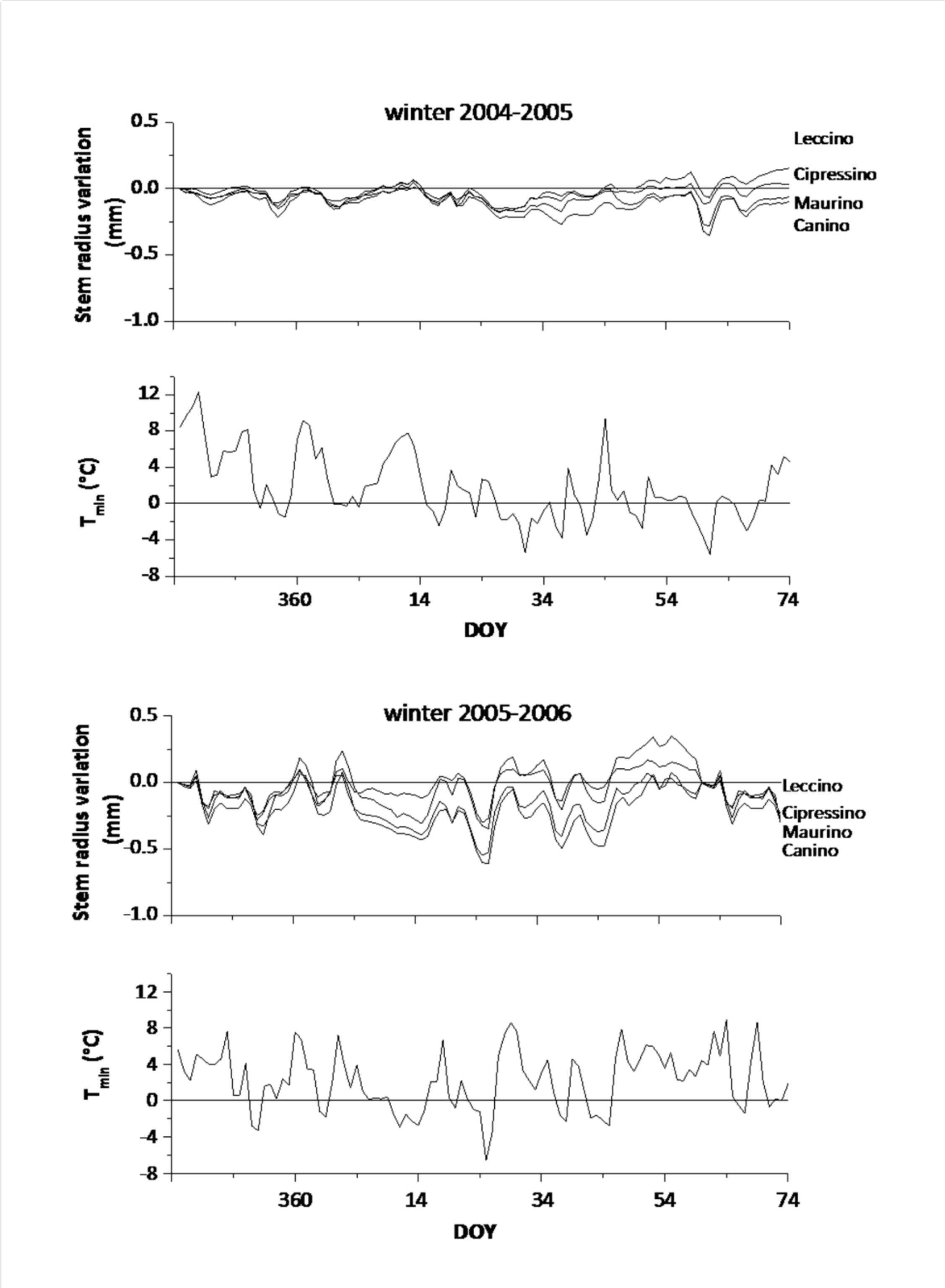

Fig. 2 – Daily values of minimum air temperature (T_{min}, dashed line) and stem diameter variation of four cultivars of olive tree (continuous lines) during the two winter seasons.

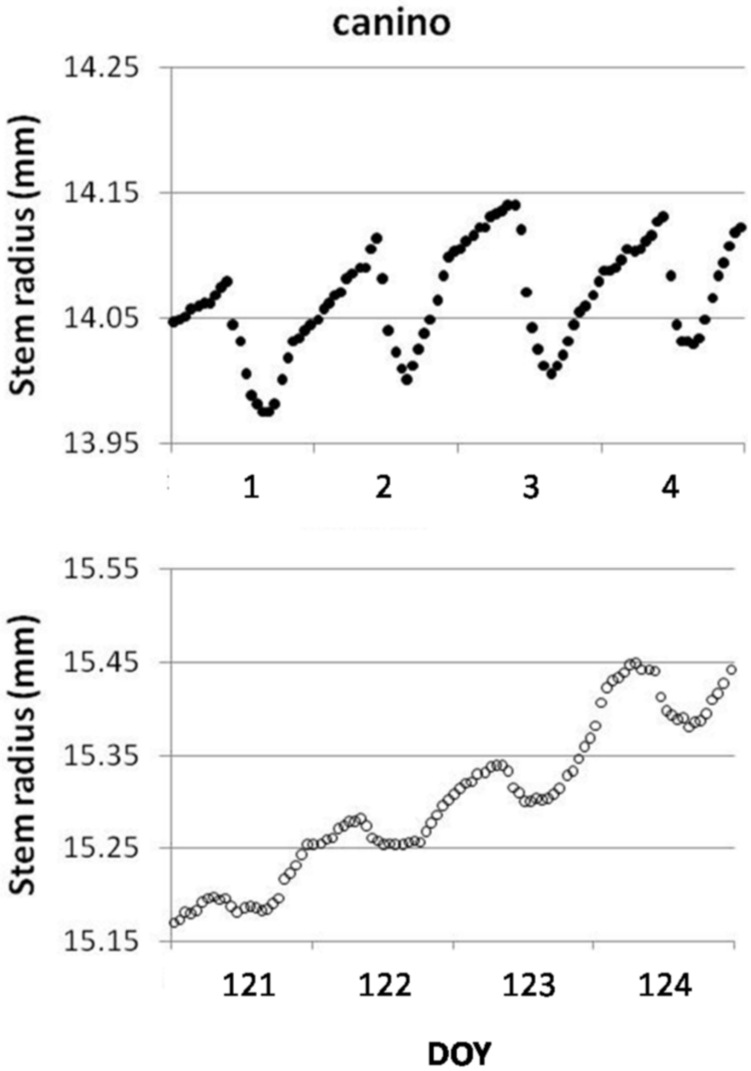

Fig. 3 – Typical stem radius variation in dormant (black circles) and growing (white circles) seasons (details for 2005) in Canino (all genotypes showed similar behaviour).

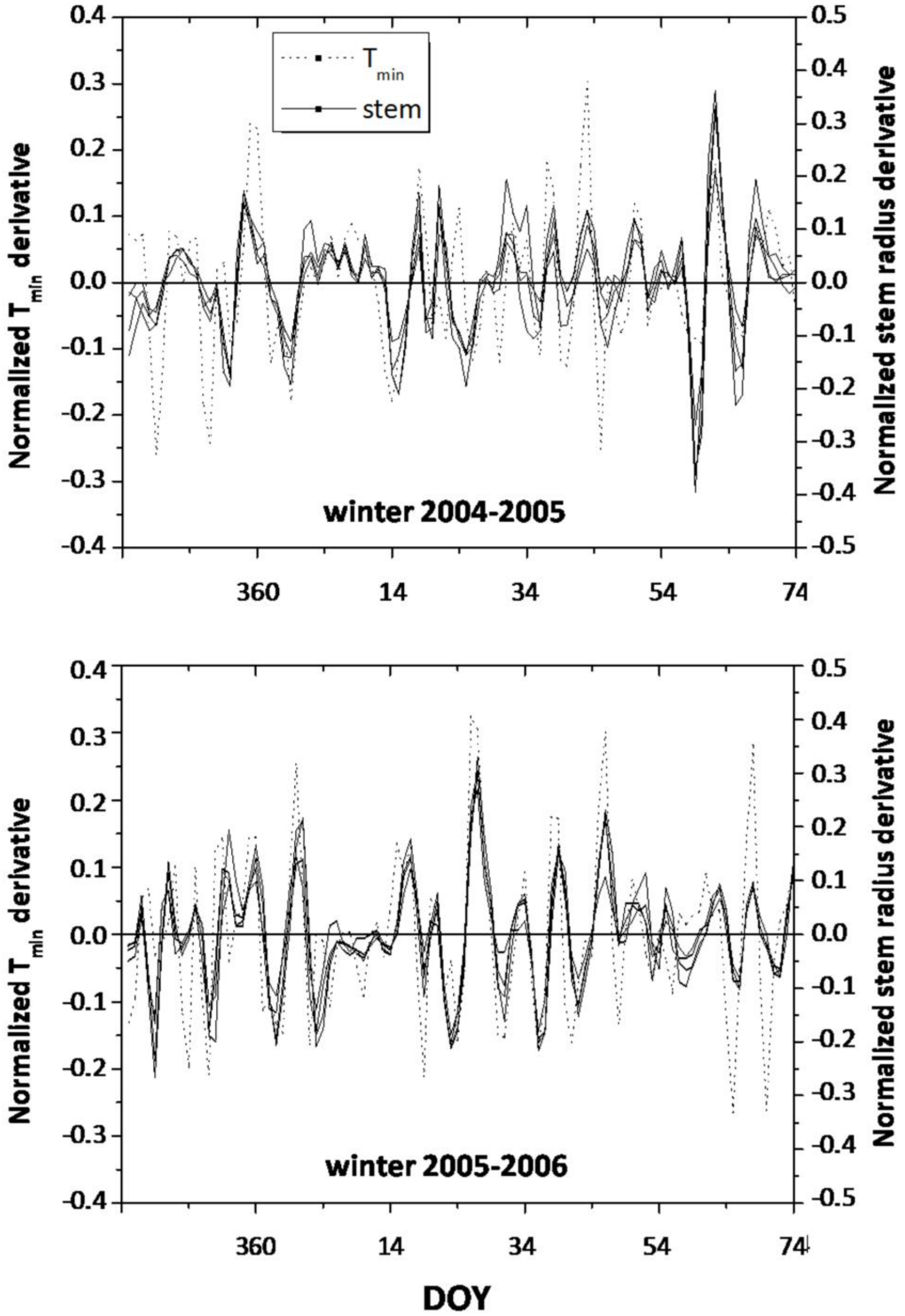

Fig. 4 – Normalized derivatives of stem radius for four cultivars of olive tree (continuous lines), and minimum air temperature (dotted line) in the two winter seasons. The standardization was carried out using the equivalent derivative of stem radius and minimum air temperature, and relative value range between –1 and 1.

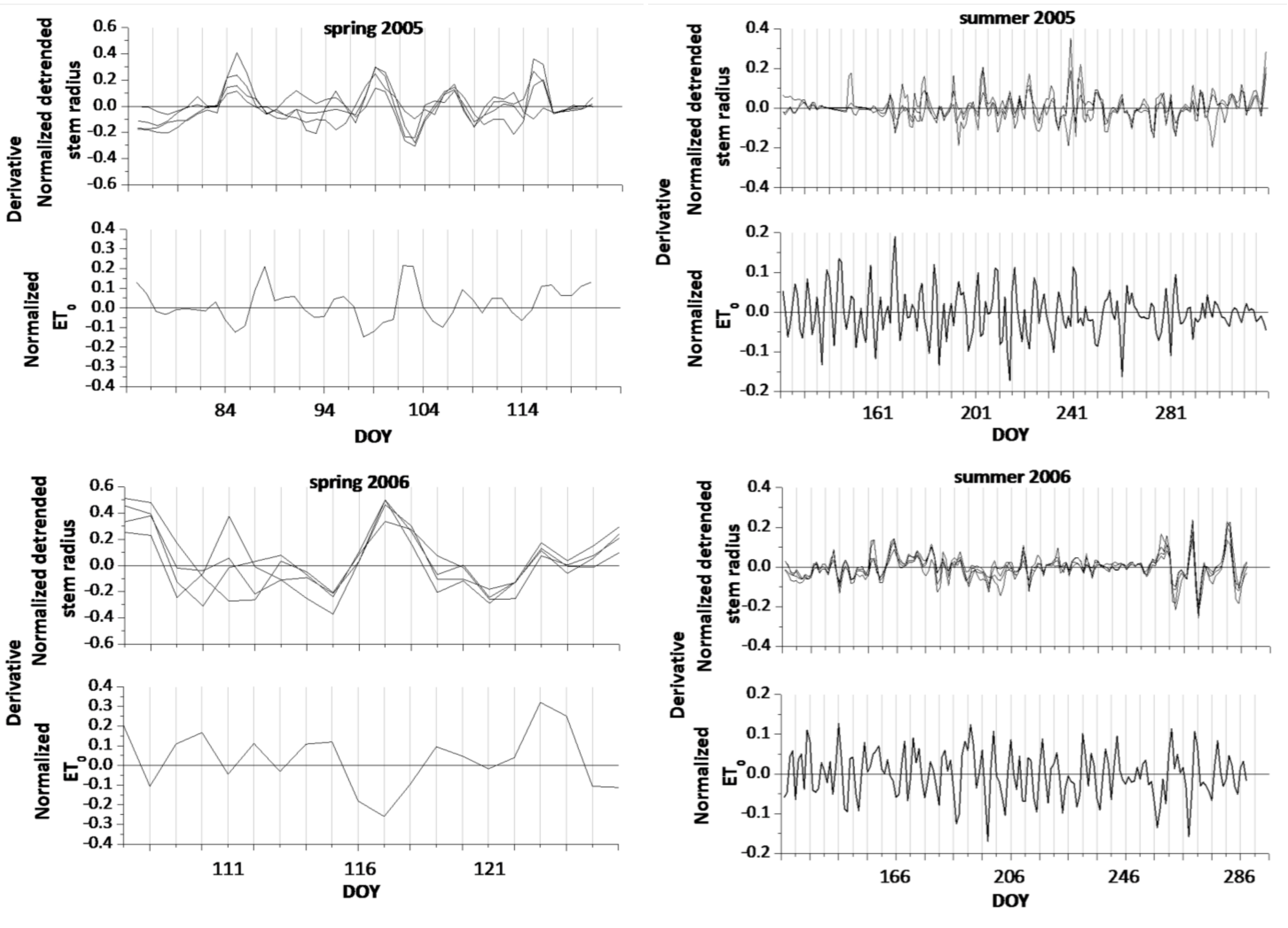

Fig. 5 – Normalized detrended derivative values of stem radius for four olive tree cultivars (continuous lines) and ET_0 in two growing seasons. The standardization was carried out using the equivalent derivative of stem radius and minimum air temperature, and relative value range between –1 and 1.

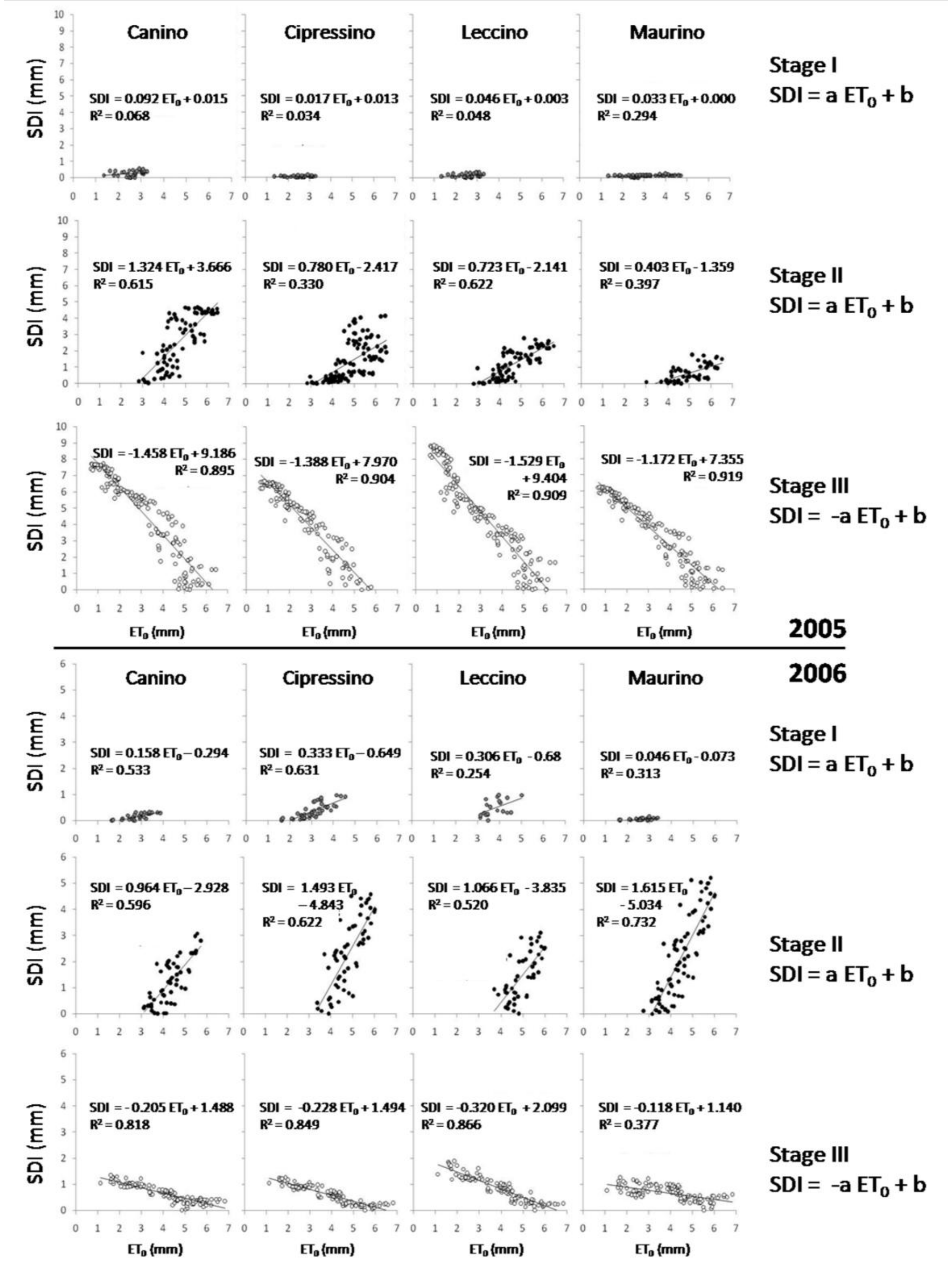

Fig. 6 – Relationship between SDI and ET_0 during the growing season 2005 and 2006. The three consecutive growth stages, defined by the relation between SDI and ET_0, are reported. Each point represents a single day.

Table 1 – Timing (DOY) and duration (days) of seasonal course, thermal range (T_{min} range), shrinkage amplitude (shrinkage range), stem diameter increment (SDI), and cumulative degree day (CDD) were reported per each cultivar in the two years of monitoring.

cultivar		dormant season 2004-2005	dormant season 2005-2006	growing season 2005			growing season 2006		
				stage I	stage II	stage III	stage I	stage II	stage III
Canino	DOY	341 - 75	340 - 80	76 - 110	111 - 187	188 - 339	81 - 111	112 - 165	166 - 299
	days	101	106	35	77	152	31	54	134
	T_{min} range (°C)	12.3 – -5.6	11.1 – -6.6	2.4 - 11.7	5.2 - 19.4	4.6 - 21.5	2.8 - 11.1	5.2 - 15.4	8.4 - 21.5
	shrinkage range (mm)	0.05 - 0.34	0.10 - 0.50						
	CDD (°C)			76.6	730.0	2011.8	73.4	416.9	1949.7
	SDI (mm)				12.88			4.27	
Cipressino	DOY	341 - 75	340 - 80	76 - 110	111 - 210	211 - 339	81 - 125	126 - 182	183 - 299
	days	101	106	35	100	129	45	57	117
	T_{min} range (°C)	12.3 – -5.6	11.1 – -6.6	2.4 - 11.7	5.2 - 19.6	4.6 - 21.5	2.8 - 12.0	5.2 - 19.1	8.4 - 21.5
	shrinkage range (mm)	0.02 - 0.16	0.04 - 0.38						
	CDD (°C)			76.6	1012.1	2011.8	146.7	620.1	1949.7
	SDI (mm)				10.91			6.84	
Leccino	DOY	341 - 75	340 - 80	76 - 110	111 - 182	183 - 339	81 - 136	137 - 182	183 - 299
	days	101	106	35	72	157	56	46	117
	T_{min} range (°C)	12.3 – -5.6	11.1 – -6.6	2.4 - 11.7	5.2 - 19.4	4.6 - 21.5	7.6 - 12.4	5.2 - 19.1	8.4 - 21.5
	shrinkage range (mm)	0.04 - 0.20	0.12 - 0.54						
	CDD (°C)			76.6	669.3	2011.8	210.7	620.1	1949.7
	SDI (mm)				11.64			5.84	
Maurino	DOY	341 - 75	340 - 80	76 - 131	132 - 182	183 - 339	81 - 105	106 - 182	183 - 299
	days	101	106	56	51	157	25	77	117
	T_{min} range (°C)	12.3 – -5.6	11.1 – -6.6	2.4 - 11.8	7.1 - 19.4	4.6 - 21.5	2.8 - 10.7	5.2 - 19.1	8.4 - 21.5
	shrinkage range (mm)	0.06 - 0.26	0.12 - 0.46						
	CDD (°C)			172.0	669.3	2011.8	48.7	620.1	1949.7
	SDI (mm)				8.12			6.26	

Table 2 – Statistical values of the cross timing procedure: "a", intra-cultivar comparison; letter "b", inter-cultivar comparison. The Glk (*Gleichläufigkeit*) is a measure of the day-to-day agreement between the interval trends of two chronologies based upon the sign of agreement, or the sum of the equal slope intervals as a percentage. Glk is significant, $P < 0.05$, at 62%, and highly significant, $P < 0.01$, at 67%. The GSL is the statistical significance of the Glk significance for the Glk-value: * = 95%; ** = 99%; *** = 99.9%. The TVBP is the Baillie– Pilcher *t*-value that is commonly used as a statistical tool for comparing and cross timing of time series. It determines the degree of correlation between curves. This method eliminates low-frequency variations in the time series, as each value is divided by the corresponding 5 days moving average.

			Glk (%)	GSL	TVBP
2004					
	a	Canino	85 - 94	***	100.0
		Cipressino	80 - 93	***	100.0
		Leccino	74 - 88	***	100.0
		Maurino	74 - 94	***	100.0
	b	Canino - Cipressino	96	***	100.0
		Canino - Leccino	92	***	100.0
		Canino - Maurino	86	***	100.0
		Cipressino - Leccino	94	***	100.0
		Cipressino - Maurino	86	***	100.0
		Maurino - Leccino	88	***	100.0
2005					
	a	Canino	77 - 89	***	100.0
		Cipressino	77 - 86	***	100.0
		Leccino	83 - 87	***	100.0
		Maurino	80 - 85	***	100.0
	b	Canino - Cipressino	87	***	100.0
		Canino - Leccino	90	***	100.0
		Canino - Maurino	83	***	100.0
		Cipressino - Leccino	86	***	92.4
		Cipressino - Maurino	83	***	100.0
		Maurino - Leccino	84	***	100.0
2006					
	a	Canino	81 - 88	***	100.0
		Cipressino	83 - 90	***	100.0
		Leccino	82 - 90	***	100.0
		Maurino	74 - 91	***	100.0
	b	Canino - Cipressino	85	***	100.0
		Canino - Leccino	92	***	100.0
		Canino - Maurino	85	***	100.0
		Cipressino - Leccino	84	***	100.0
		Cipressino - Maurino	89	***	100.0
		Maurino - Leccino	86	***	100.0