Seasonal changes on hydraulic conductance of mature olive trees under different water regimes

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Keywords: *Olea europaea*, sap flow, irrigation, transpiration, modelling

Abstract

The well know stomata control of olive trees under stressing conditions proved to be an efficient mechanism to prevent the loss of hydraulic efficiency during the dry season. Trees with a localized irrigation system that replaced 100% of the crop water demand (FAO trees), as well as Dryfarming trees, were able to keep similar differences between the water potential in the soil and that in the leaves, all throughout the dry season. The differences were of the same order than those in trees with non-limiting soil water conditions in the whole rootzone (Pond trees). As a consequence of stomatal closure, the tree transpiration late in the season was reduced in the FAO trees, but the hydraulic conductance remained unaffected. Results suggest that a root-to-shoot signalling mechanism could have been responsible for stomata control in the FAO trees. At the end of the dry season, values of hydraulic conductance were lower in Dryfarming than in the irrigated treatments, but, once again, the recorded leaf water potential values, when compared to vulnerability curves, suggest that the low hydraulic conductance in those trees was mainly due to a reduced tree transpiration caused by stomatal closure, rather than to a severe loss of the hydraulic efficiency.

INTRODUCTION

The olive tree shows an outstanding adaptation to drought (Fernández and Moreno, 1999). Among other mechanisms, the olive tree shows a reduction on the tree total transpiration (E_p) during the periods with high atmospheric demand (Tognetti et al., 2004), which helps to avoid values of water stress within the plant falling beyond the threshold for safe hydraulic functioning. Depending on the conditions, this reduction on E_p could be due just to a lack of water in the soil or to a marked stomatal control, which occurs in olive under conditions of high water stress (Fernández et al., 1997). The mentioned stomatal closure may be related to a root-to-shoot signalling mechanism occurring in trees with roots in drying soil. Fernández et al. (2003) used sap flow measurements to derive daily E_p values in mature 'Manzanilla' trees with a localized irrigation system that supplied enough water to replace the crop water demand (ET_c). They observed an increase of 37% on E_p when the trees were suddenly irrigated with a pond irrigation that wetted the whole rootzone. The reduction on E_p may be also related to a reduction on the whole-tree hydraulic conductance (K_p), due to accumulation of xylem embolism during the dry season. The possible feedback loops or feed-forward regulations

between the internal water status of the plant, E_p and K_p are not well known for the olive tree. Most the work concerning the hydraulic efficiency of the olive tree has been made with young trees growing in pots (Salleo and Lo Gullo, 1983; Nardini et al, 2006). To our knowledge, the only papers showing seasonal trends of K_p for mature olive trees growing in the field are those by Tognetti et al., (2004, 2005). The experimental trees were 11 and 12-year-old 'Kalamata' olive trees growing in an area of sub-humid climate, with greater annual precipitation (P) and lower atmospheric demand on the summer months than in most Mediterranean areas where the olive grows. Any new evidences on the mechanisms governing the seasonal trends both of E_p and K_p are of interest for improving deficit irrigation strategies, which are compulsory in most olive orchards (Fernández et al., 2003; Pastor, 2005).

The aim of this work was to investigate the seasonal trends of K_p in 39-year-old 'Manzanilla' olive trees growing under field conditions in a semi-arid area of south Spain. We wanted to know to what extent localized irrigation restricted E_p and K_p, and whether any observed reduction on K_p was due to the lack of water in the soil or to other mechanisms such as those mentioned above.

MATERIALS AND METHODS

Orchard characteristics and water treatments

The experiments were made in a 0.5 ha olive orchard with 39-year-old 'Manzanilla de Sevilla' olive trees at 7 m × 5 m spacing (37º 17' N, 6º 3' W, 30 m a.s.l.). The trees have a single trunk with two main branches from 0.7 to 1.5 m above ground. Average values of canopy volume and leaf area density at the end of the growing season were 42 m^3 and 1.6 m^2 m^{-3}, respectively. The soil is a sandy loam of about 1.6-2.0 m depth, depending on the location. The texture is quite homogeneous, with average values of 14.8% clay, 7.0% silt, 4.7% fine sand and 73.5% coarse sand. The climate is typically Mediterranean, with a mild, wet season from October to April; the rest of the year is hot and dry. In 2007, the experimental year, precipitation (P) and potential evapotranspiration (ET_o, FAO56 Penman-Monteith equation) were 411.1 mm and 1235.0 mm, respectively.

The orchard is divided into three plots, each with a different water treatment: 1) Dryfarming, with rainfall as the only source of water supply; 2) FAO, in which trees were irrigated daily from May 14 to October 2, to replace the crop evapotranspiration (ET_c, mm). The irrigation system consisted of a lateral per tree row, with five 3 L $hour^{-1}$ drippers per tree, 1 m apart. With this system some roots were left in drying soil. Irrigation doses were calculated with the crop coefficient approach, as described by Fernández et al. (2006a). Basically, ET_c was calculated as $ET_c = K_c K_r ET_o$, with crop coefficient (K_c) values of 0.76 in May, 0.70 in June, 0.63 in July and August, 0.72 in September and 0.77 in October. The coefficient related to the percentage of ground covered by the crop (K_r) was 0.71; 3) Pond, in which the trees were irrigated with a grid of pipes with a 2 L $hour^{-1}$ dripper every 0.4 m × 0.4 m. The grid covered a surface of 8 m × 6 m, with the tree in the middle, enough to keep non-limiting soil water conditions in the whole rootzone, all throughout the irrigation season.

Determining the tree hydraulic conductance

The K_p values were determined as $K_p = E_p (\varPsi_s - \varPsi_l)^{-1}$, being E_p measured at the central hours of the day, when transpiration rates were relatively constant; $\varPsi_s$ (MPa) is the 'effective' soil water potential at the root surface and $\varPsi_l$ (MPa) is the 'effective' leaf

water potential for the whole canopy (Jones, 1983). Both Ψ_s and Ψ_l were determined at the same hours than E_p. The values of Ψ_l were estimated as $\Psi_l = \alpha \, \Psi_o + (1- \alpha) \, \Psi_i$ (Moreshet et al., 1990), where Ψ_o (MPa) is the leaf water potential of sunlit leaves outside the canopy, Ψ_i (MPa) is the leaf water potential of shade leaves inside the canopy, and α is the fraction of sunlit and shade leaves (calculated as 0.43 for the orchard conditions by Diaz-Espejo et al., 2002). We assumed that $\Psi_s = \Psi_{l \, predawn}$, being $\Psi_{l \, predawn}$ the average value of water potential measured at predawn in leaves of the base of the trunk.

The values of E_p were determined from sap flow measurements made with the Tz compensation heat-pulse method (Green et al., 2003), calibrated for our orchard conditions by Fernández et al. (2006b). Three sets of probes were installed into the trunk of each two representative trees per treatment. Each probe had four thermocouples, at 5, 12, 22 and 35 mm below the cambium. Heat pulses (60 W over 1 s) were applied every 30 min. We were worried about not getting reliable estimations of E_p due to the high probe-to-probe variability caused by the irregular conductive tissue in such old trees. Therefore, we modelled the daily E_p values with the Penman-Monteith equation described by Moreno et al. (1996), improved with the f functions for the leaf stomatal conductance (g_s) validated by Diaz-Espejo et al. (2006) for our orchard conditions. In addition, we derived average monthly E_p values in the orchard from the ET_c values determined with the crop coefficient approach explained above, plus estimations of the water lost by evaporation from the soil surface, E_s (Fernández, 2006).

Measurements

Diurnal time courses of Ψ_o and Ψ_i were recorded on June 26 (day-of-year = DOY = 178), July 27 (DOY = 206) and August 28 (DOY = 241), i.e. from the time the treatments were well established to the end of the dry season. Each sampling day we measured both variables from predawn to sunset, every 2.5 hours (Scholander chamber). Every sampling hour we sampled 6 sunlit and 6 shade leaves per treatment (2 leaves per tree, 3 trees per treatment). The sampled leaves were the fourth or fifth from the apex of current year shoots at about 1.5-1.0 m above ground. Measurements of stomatal conductance (g_s) were made in the same type of leaves, at the same hours (Licor 6400, two leaves in three trees per treatment).

The volumetric soil water contents (θ) in the soil around three representative trees per treatment were measured every 7-10 days, at 0.1, 0.2, 0.3, 0.4, 0.6 and 1.0 m depth, and at 1, 2, and 3 m from the tree trunk (Profile probe). From the θ values we calculated the relative extractable water (REW) of the soil.

The leaf area (LA, m^2 one side) of the trees in which θ was measured was estimated as described by Fernández et al. (2006a). We used those LA values as an input to the E_p model. Half-hour values of the main meteorological variables were continuously recorded by an automatic weather station next to the olive orchard.

Analyses of variance were performed on the data to compare the effect of the treatments on Ψ_l, Ψ_s, E_p and K_p. Separation of means were obtained by the least significant differences (LSD) test.

RESULTS AND DISCUSSION

The imposed water conditions caused clear differences between treatments on the soil water status (Fig. 1a). The soil of the Pond trees was between saturation and field capacity most of the time, while that of the FAO trees remained close to field capacity. Under these conditions, similar values of Ψ_l and Ψ_s were recorded in the trees of both treatments.

The availability of soil water in the Dryfarming treatment was decreasing throughout the dry season, causing an increasing water stress both in the soil and in the trees (Fig. 1).

The dynamics of tree transpiration determined for each treatment from the sap flow records (E_{p-sf}) echoed that of ET_o (Fig. 2). The trends of E_{p-sf} were also consistent with the tree transpiration values estimated from the crop coefficient approach and estimations on soil water evaporation (E_{p-cc}): for the FAO treatment, values of E_{p-sf} and E_{p-cc} were quite similar, except on the periods of variable ET_o, because a single E_{p-cc} value was calculated per month. For the Dryfarming treatment the E_{p-sf} values were usually lower than the estimated E_{p-cc} value, as expected. For the pond treatment, the values of E_{p-sf} were above that of the E_{p-cc}, most of the time. This was also an expected result, because the E_{p-cc} values determined after Fernández et al (2006a) were validated for trees of the FAO treatment, which had lower soil water availability than the Pond trees (Fig. 1a). The agreement between the time courses of E_{p-sf} and those of the modeled tree transpiration (E_{p-m}) were reasonably good, except for the Pond treatment, suggesting that the soil water routine included in the model need to be adjusted for ponding conditions. Results in Fig. 2 shows that the E_{p-sf} values were reliable and that we could use them with confidence to calculate K_p.

Figure 3a shows that the olive trees were able to maintain the same value of Ψ_l-Ψ_s throughout the dry season. This was due, at least in part, to a reduction in g_s occurring in the less watered trees, observed in the sampling days of July and August. Thus, in the FAO trees the average maximum value of g_s recorded on August 28 was 0.177 mol m^{-2} s^{-1}, while 0.227 mol m^{-2} s^{-1} were recorded at the same time in the Pond trees. In the Dryfarming treatment, the maximum value of g_s recorded on that day was 0.092 mol m^{-2} s^{-1}. This reduction in g_s may explain the lowest E_p values recorded in the FAO trees as compared to those of the Pond trees (Fig. 3b), and illustrates one of the well known adaptation mechanisms to drought in olive: the tree closes stomata to reduce E_p and thus to minimize the risk of the water potential in the xylem falling below the threshold for cavitation. In the Dryfarming treatment the Ψ_l-Ψ_s difference was also maintained throughout the dry season, but E_p decreased more than in the irrigated treatments (Fig. 3a,b), probably because of the marked decrease in soil water availability (Fig. 1a).

Results on Ψ_o suggest that little reduction of the hydraulic efficiency could have been due to the appearance of embolism in the xylem vessels. In the FAO trees, the minimum Ψ_o value recorded during the experimental period was -2.05 MPa in July 24. The vulnerability curves obtained for olive by Ennajeh et al. (2008) shows that that water stress value may cause a percentage loss of conductivity (PLC) below 20%. Late in the season, the values of K_p in the FAO trees were, in fact, similar to those in Pond trees (Fig. 3c). The Lowest Ψ_o values recorded in the Dryfarming trees (minimum Ψ_o average of -2.9 MPa on August 28) suggest PLC values little over those of the FAO trees. The smaller K_p values observed in that treatment late in the season, as compared to those of the irrigated trees, could have been due not only to the appearance of embolism in the xylem, but also, and perhaps mainly, to both the lack of water in the soil and the reduction in g_s.

It seems, therefore, that the stomatal control of the olive trees was able to keep stress levels within the trees low enough to avoid a significant loss of hydraulic conductance within the plant. Now, the cause of such an efficient stomatal control remains unknown. The FAO trees surely had their roots under a wide range of soil water content, because of the heterogeneity of water distribution in the rootzone caused by the localized irrigation. Under those conditions, a root-to-shoot signalling mechanism could have been triggered. This agrees with observations by Fernández et al. (2003) in the same orchard. They

observed a clear increase in $E_{p\text{-}sf}$ in very few days after applying pond irrigation to dryfarming trees (7 days) and to trees previously under localized irrigation (2 days). This quick recover of $E_{p\text{-}sf}$ suggests an increase on g_s as a response to the new soil water status, rather than a recovery of any possible damage to the conductive xylem caused by the appearance of embolism.
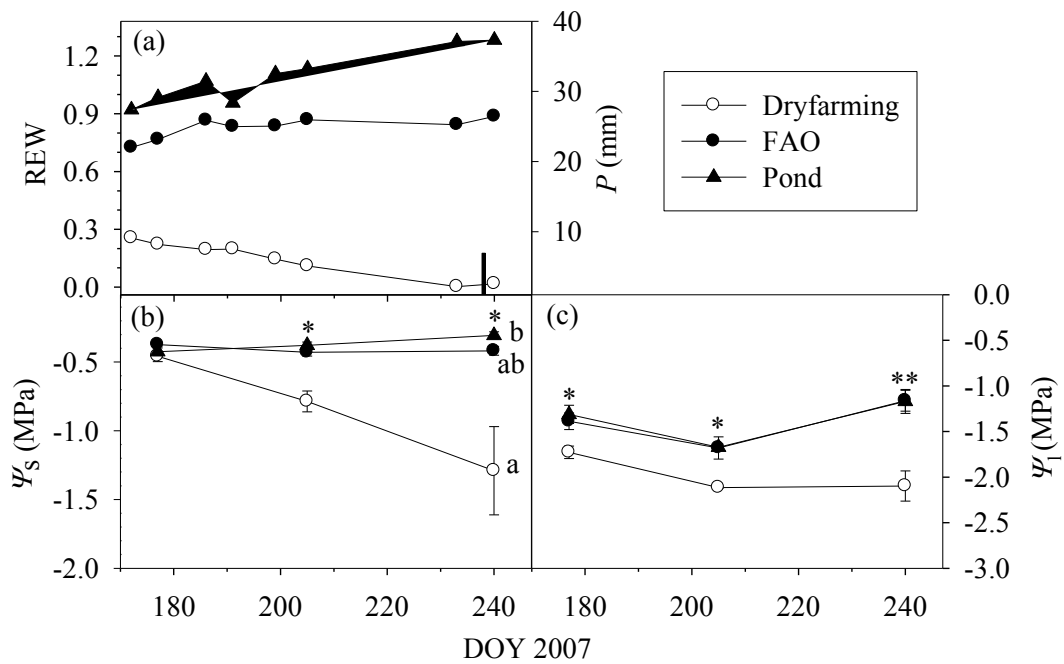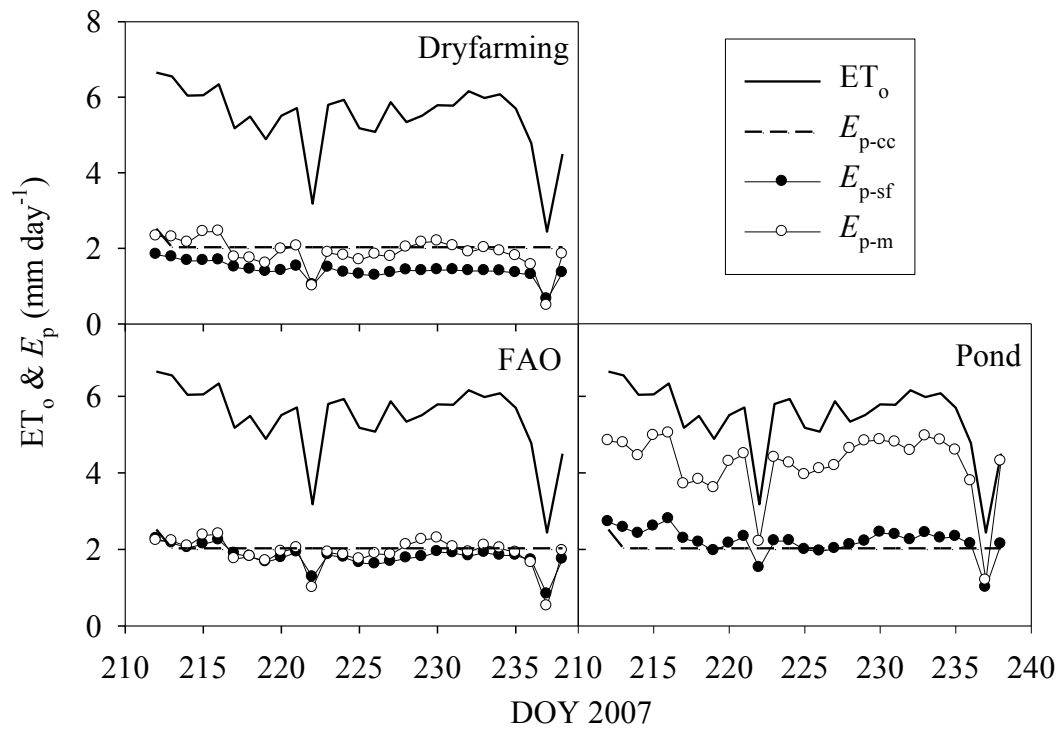
ACKNOWLEDGEMENTS

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Figures

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