Stomatal Control and Hydraulic Conductivity in 'Manzanilla' Olive Trees under Different Water Regimes

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Abstract

We studied the response of leaf water potential (Ψ_l), stomatal conductance (g_s), leaf specific hydraulic conductivity (K_l) and percentage loss of hydraulic conductivity (PLC) in current-year shoots of 40-year-old 'Manzanilla' olive trees under three water treatments: Rainfed, in which rainfall was the only source of water; FAO, in which the trees were under localized irrigation to replace crop water demand; Pond, in which the whole root zone of the trees was maintained under non-limiting soil water conditions throughout the irrigation season. In the FAO trees, some roots were left in drying soil during the irrigation season. Results suggest near-isohydric behavior of olive trees. FAO trees maintained Ψ_l values similar to those of Pond trees by increasing stomatal closure. In Rainfed trees, g_s values were smaller than in the irrigated trees, but stomatal closure did not prevent Ψ_l values from falling below those of the irrigated trees, likely because of the dramatic decrease in soil water content observed in the Rainfed treatment. Values of K_l and PLC showed no differences between treatments throughout the irrigation season. During that period, the PLC values ranged from 38% to 50%, which shows that even the well-irrigated Pond trees were unable to maintain their hydraulic efficiency, likely because of the high atmospheric demand in the area.

INTRODUCTION

In trees with localized irrigation, some of the roots may be left in drying soil during the irrigation season. This can reduce stomatal conductance (g_s) in those trees as compared to others in which irrigation wets the entire root zone. This may occur even though the trees under localized irrigation are irrigated daily with enough water to replace crop evapotranspiration (ET_c) (Fernández et al., 2003, 2009). The reduction in g_s may be due, at least in part, to changes in the hydraulic efficiency of the xylem caused by cavitation (Milburn, 1991). This was observed for *Olea oleaster*, among other species, by Lo Gullo et al. (2003), who worked with 2-year-old wild olive plants in pots. Raimondo et al. (2009) and Ennajeh et al. (2008) studied the hydraulic efficiency in current-year shoots of young olive trees in pots. As described by the cohesion-tension theory, water ascends in plants in a metastable state of tension, i.e., at negative pressure (Steudle, 2001). The relationship between that tension and the degree of embolism in the xylem conduits illustrates the hydraulic efficiency of the xylem (Cruiziat et al., 2002). The degree of embolism is characterized by the percentage loss of hydraulic conductivity (PLC). One of the most useful indices to describe the resistance of a

species to xylem cavitation is the threshold xylem pressure at which loss of conductivity begins to increase rapidly, often referred to as the air entry pressure (P_e) (Meinzer et al., 2009).

The aim of this work was to evaluate the effect of different water treatments on leaf water potential ($\varPsi_l$), g_s, leaf specific hydraulic conductivity (K_l) and PLC in current-year shoots of 40-year-old 'Manzanilla' olive trees growing in a semi-arid area of southern Spain. Results from this study were compared with previously obtained vulnerability curves to clarify aspects related to the hydraulic efficiency of the olive tree as influenced by water treatment.

MATERIALS AND METHODS

Orchard Characteristics and Water Treatments

The experiments were carried out in an experimental orchard with 40-year-old 'Manzanilla' olive trees at 7 m × 5 m spacing (37º 17' N, 6º 3' W, 30 m a.s.l.). The climate is typical Mediterranean, with a mild, wet season from October to April; the rest of the year is hot and dry. Crop management and crop and soil characteristics are described elsewhere (Fernández et al., 2006).

In 2009, the orchard was divided into three different plots, each with a different irrigation treatment: 1) Rainfed, with rainfall as the only source of water supply; 2) FAO, in which the trees were irrigated daily from 6 May to 2 Oct at 100% ET_c. Water was supplied with a lateral per tree row, five 3 L/h drippers per tree, 1 m apart. This system left part of the roots in drying soil. The ET_c values (Fig. 1) were calculated using the crop coefficient approach, as described by Fernández et al. (2006); 3) Pond, in which the trees were irrigated by a grid of pipes with a 2 L/h 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 maintain non-limiting soil water conditions for the entire root zone, throughout the irrigation season.

Measurements

On 23 Jun [day of year (DOY) = 174], 28 Jul (DOY = 209) and 25 Aug (DOY = 237), g_s was measured with a Li-6400 (Li-Cor, Lincoln, NE) in sunlit, well-developed leaves close to the apex of current-year shoots. Six leaves per treatment (two per tree from three representative trees) were sampled from 0830 h to 09.30 h GMT, when maximum values of g_s ($g_{s\ max}$) were recorded. Minimum daily values of $\varPsi_l$ were recorded from 1300 h to 1400 h GMT, in the same number of leaves of the same type, with a Scholander chamber (Soilmoisture Equipment Corp., Santa Barbara, CA).

Hydraulic conductivity (K, m^4/MPa s) in segments of current-year shoots was determined as described by Sperry et al. (1988), with a XYL´EM apparatus (Bronkhorst, Montigny les Cormeilles, France). Leaf areas distal to the shoot segments (LA, m^2) were measured with a Li-3000C equipped with a Li-3050C (Li-Cor), to calculate the K_l (m^2/MPa s):

$$K_l = K/LA \tag{1}$$

The maximum vessel length in olive was estimated at 0.22 m by Lo Gullo and Salleo (1990). From each treatment, ca. 0.5-m long branches were sampled by cutting them under water to prevent air entry into the vessels. The branches were immediately sealed in double layers of black plastic bags with wet paper inside, to minimize dehydration and artificial embolism while transporting to the lab. The branches were

sampled on the same days as the aforementioned $g_{s\,max}$ recordings. Five 3-cm segments of current-year shoots per treatment were cut under water with a razor blade, debarked and connected to the XYL´EM apparatus. Filtered (0.22 μm) and degassed 50 mM KCl solution was perfused with a pressure gradient of 3 kPa to measure the initial K_l ($K_{l\,ini}$ m^2/MPa s). Later, and to evaluate the degree of embolism in the samples, these were perfused with the same solution for 20 min at 0.15 MPa, which has been shown in previous measurements to suffice to remove any embolism. Then, K_l was measured again at 3 kPa, to obtain the maximum K_l ($K_{l\,max}$, m^2/MPa s). The percentage loss of hydraulic conductivity (PLC) was determined as:

$$PLC = 100(K_{l\,max} - K_{l\,ini})/(K_{l\,max}) \qquad (2)$$

The volumetric soil water content (θ_v) in the soil of the three sampled trees per treatment was recorded every 7 to 10 days with a Profile probe (Delta-T Devices, Cambridge, UK) 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 trunk of each tree. These measurements were used to calculate the relative extractable water (REW) of the soil using the equation given by Granier (1987).

RESULTS AND DISCUSSION
Clear differences in REW were recorded between the Rainfed and irrigated treatments (Fig. 2). In both the FAO and Pond treatments, the soil was close to field capacity throughout the irrigation season. Decreasing values of REW were recorded in the Rainfed treatment, as expected.

Rainfed trees showed smaller $g_{s\,max}$ values than irrigated trees throughout the dry season (Fig. 3a). In July and August, smaller values of $g_{s\,max}$ were recorded in the FAO trees than in the Pond trees, but the differences were not significant. The trends of Ψ_l values recorded in the trees of each treatment (Fig. 3b) were similar to those of $g_{s\,max}$ (Fig. 3a). Differences in Ψ_l between the Pond and FAO trees were, however, smaller than those of $g_{s\,max}$. Measurements of $g_{s\,max}$ and Ψ_l performed in the orchard by Fernández et al. (2009) during the dry season of 2007 yielded similar results, except that the g_s values were significantly lower in the FAO trees than in the Pond trees, indicating marked stomatal control in the trees with localized irrigation. This suggests near-isohydric behavior of the FAO trees, since they were able to maintain Ψ_l values similar to those in the Pond trees by adjusting stomatal opening. This near-isohydric behavior has been described by Franks et al. (2007) for other species. In the Rainfed trees, stomatal control was not sufficient to prevent decreasing values of Ψ_l (Fig. 3), likely because of the dramatic decrease in REW recorded in this treatment (Fig. 2).

Despite the observed differences in Ψ_l and $g_{s\,max}$ between treatments, similar values both of K_l (Fig. 4a) and PLC (Fig. 4b) were found for all treatments throughout the experimental period. We determined a P_e value of -1.43 MPa using the vulnerability curves created for the trees in the orchard by Chamorro et al. (2007). Although we did not measure stem water potential (Ψ_{stem}), the episodes of high atmospheric demand occurring in the area before and during the experimental period (Fig. 1) could have caused an occasional drop in Ψ_{stem} values below P_e in the experimental trees of all treatments. This, in turn, might cause runaway embolism (Meinzer et al., 2009), which could then be responsible for the relatively high PLC values recorded in all trees (Fig. 4b). Cruiziat et al. (2002) reported that positive or close to positive Ψ_{stem} values may be required to dissolve embolisms in xylem vessels. Data in Fig. 4, however, show that this was not sufficient for recovery of hydraulic efficiency in our 'Manzanilla' trees. In both FAO and Pond trees, near-zero Ψ_{stem} values were recorded almost every day (data not

shown), but the PLC values in both treatments ranged from 38% to 50% throughout the experimental period. It appears that if there is recovery of hydraulic efficiency, it must occur later in the season.

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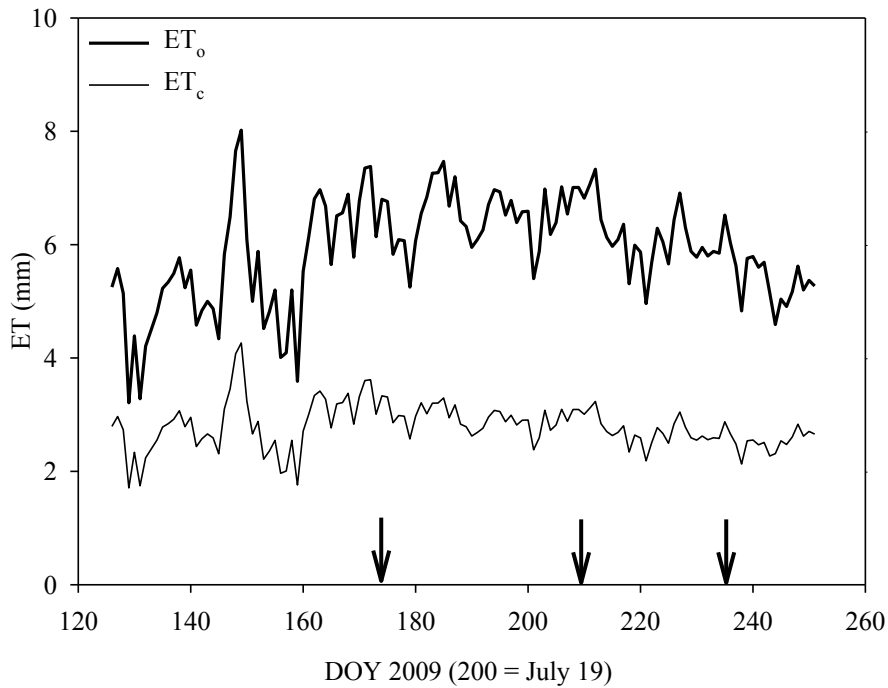
Figures

Fig. 1. Time course of potential (ET$_o$, mm) and crop (ET$_c$, mm) evapotranspiration in the olive orchard during the irrigation period. DOY = day of year. Arrows indicate sampling dates.
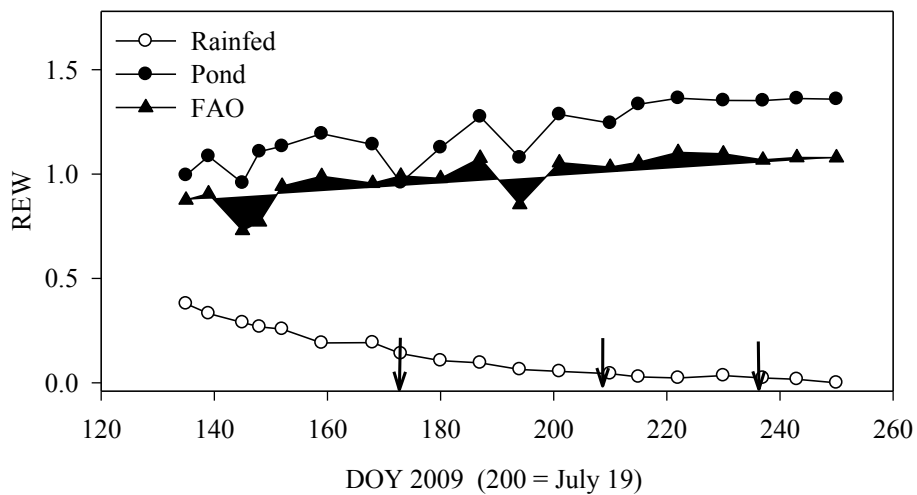

Fig. 2. Time course of relative extractable water (REW) in the soil of each treatment during the irrigation period. DOY = day of year. Arrows indicate sampling dates.
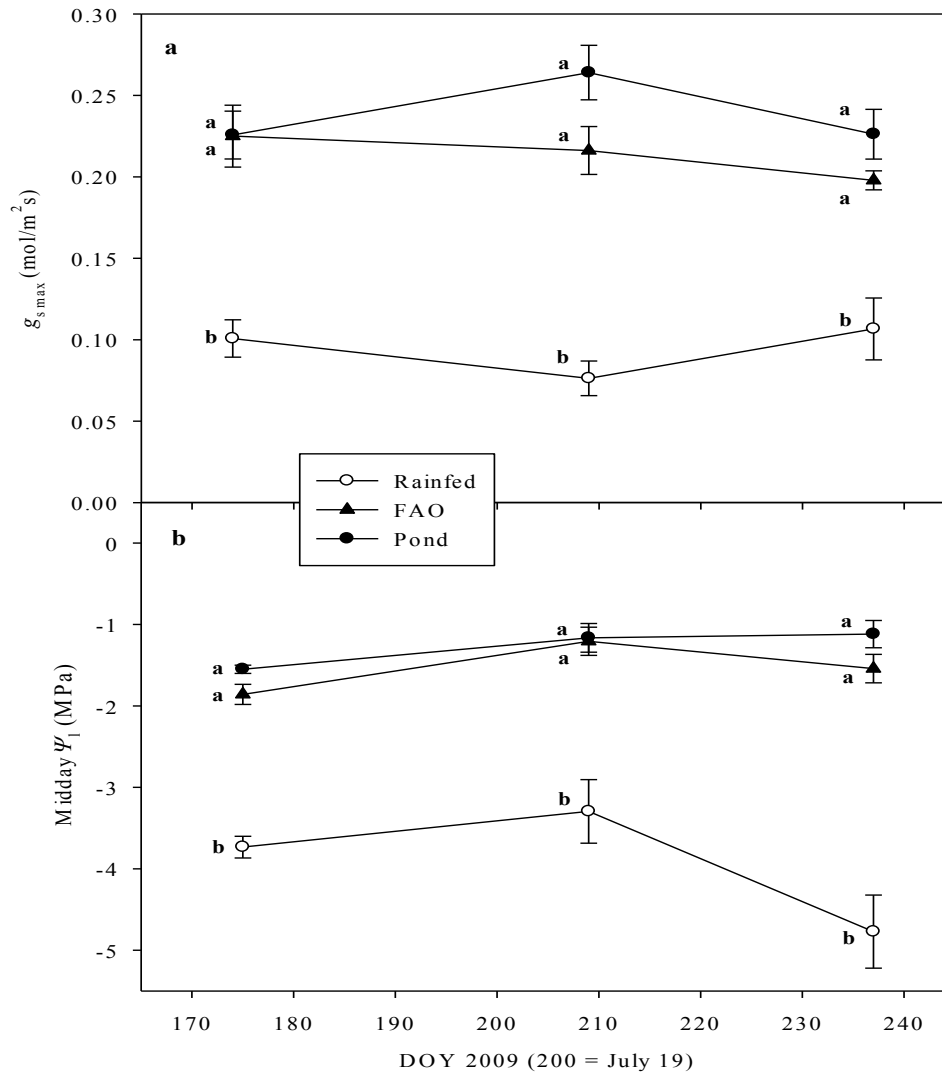
Fig. 3. Time course of maximum stomatal conductance ($g_{s\ max}$) (a) and midday leaf water potential (Ψ_l) (b). n = 3-5 ± SE. Mean values with different letters are significantly different at $P \leq 0.05$. DOY = day of year.
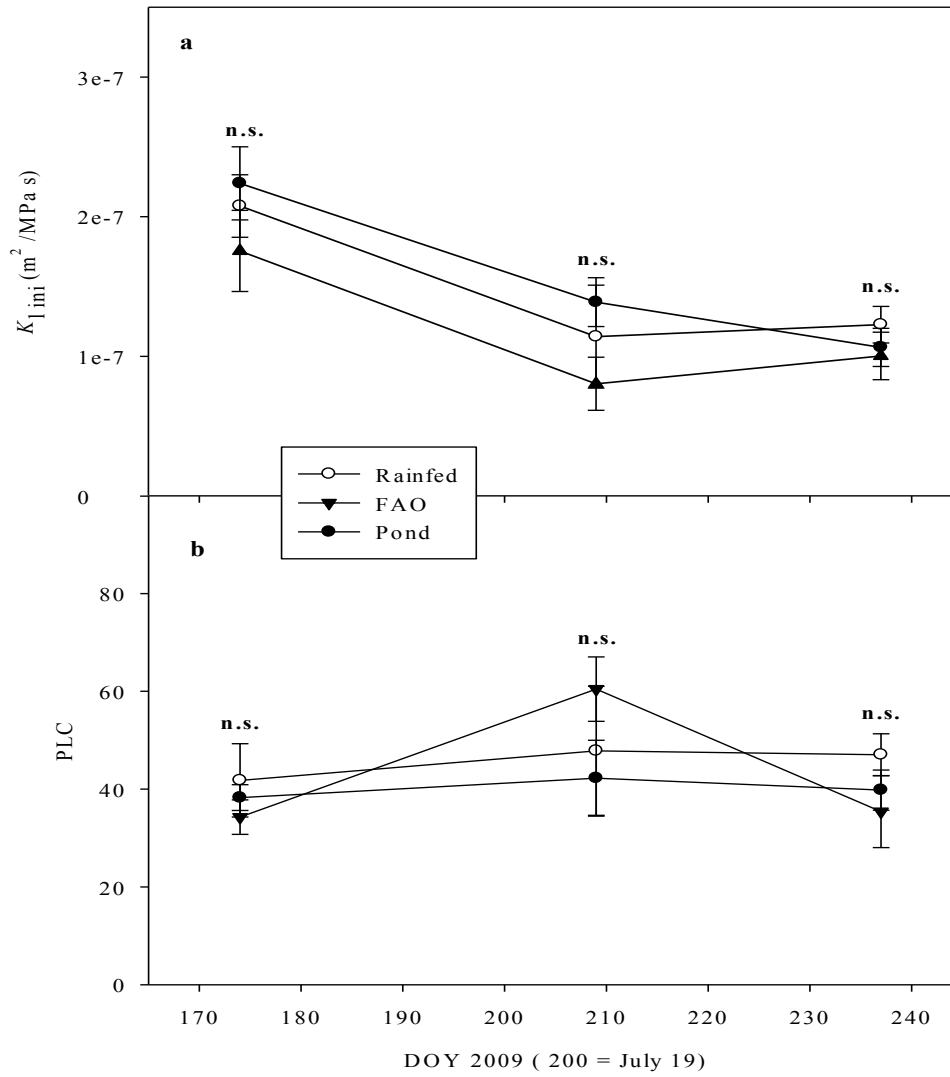
Fig. 4. Time course of initial leaf specific hydraulic conductivity ($K_{l\,ini}$) (a) and of percentage loss of hydraulic conductivity (PLC) (b). n = 3-5 ± SE. n.s. = no significant difference. DOY = day of year.