Influence of the Soil Water Content and Distribution on Both the Hydraulic and Transpiration Performance of 'Manzanilla' Olive Trees

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Abstract
        This work was made with mature 'Manzanilla' olive trees in an orchard of a semi-arid area in southern Spain. Three water treatments were considered: Rainfed, in which the trees had rainfall as the only source of water supply; FAO, in which the trees were under localized irrigation to replace the crop water demand, with some roots left in drying soil; Pond, in which the whole rootzones of the trees were maintained under non-limiting soil water conditions for the whole dry season. Our aim was to obtain information on the mechanisms behind the reduction of transpiration (E_p) in the FAO trees, as compared to the Pond trees. Our results show a near-isohydric behaviour of the FAO trees, i.e. those trees under localized irrigation in which some roots are left in drying showed lower stomatal conductance than the Pond trees in which all roots were in wetted soil. This helped the FAO trees to maintain similar leaf water potentials than the Pond trees. In addition, the FAO trees maintained a constant difference between the water potential of the canopy and that in the soil. This has been described as an isohydrodynamic behaviour, and it is thought to be an improvement over a typically anisohydric behaviour. These mechanisms were behind the similar values of tree hydraulic conductance (K_p) found in the FAO and Pond treatments. The Rainfed trees showed lower K_p values because of the low E_p values of those trees, due to the low soil water availability in that treatment. Our results show, however, that the Rainfed trees were able to maintain similar values of K_p all throughout the dry season, which shows that the hydraulic efficiency of the xylem of those trees was little affected by embolism, despite of the high demanding conditions in the area.

INTRODUCTION
        Evidence shows that both the tree transpiration (E_p) and the production of mature fruit trees under field conditions are influenced not only by the amount of water supplied by irrigation, but also by the distribution of that water in the soil. Fernández et al. (2003) estimated E_p values from sap flow measurements in mature 'Manzanilla' olive trees under different irrigation regimes, and reported an E_p increase of 37% when trees under localized irrigation were suddenly irrigated with a pond irrigation that wetted the whole rootzone. This was despite of the trees under localized irrigation being irrigated daily with enough water to replace the crop evapotranspiration (ET_c). Pastor and Vega (2005) reported increases in the yield of mature 'Picual' olive trees irrigated with an increasing number of drippers, although with the same water amounts. It seems, therefore, that both water consumption and yield performance are reduced in olive trees in which part of their

root system is left under soil drying conditions during the irrigation season. Several mechanisms could be involved in that reduction, including changes on the soil-to-root hydraulic conductance (Tuzet et al., 2003), on the hydraulic efficiency of the xylem (Lo Gullo et al., 2003) and on root-to-shoot signalling mechanisms influencing stomatal closure (Davies et al., 2000). The existing literature for olive on that matter was reported by Fernández et al. (2009a). They outlined the lack of information on these aspects for olive trees growing under field conditions in semi-arid and arid areas.

The aim of this work was to evaluate the influence of different soil water regimes on the seasonal trends of stomatal conductance (g_s), leaf water status, E_p and hydraulic conductance (K_p) of mature 'Manzanilla' olive trees of an orchard located in a semi-arid area of south Spain. The experiments were design to obtain information on the mechanisms controlling the reduction of transpiration found in olive trees under localized irrigation.

MATERIALS AND METHODS

Orchard Characteristics and Water Treatments

The experiments were made during the irrigation season of 2007, in a 0.5 ha olive orchard (37°17' N, 6°3' W, 30 m a.s.l.) with 39-year-old 'Manzanilla de Sevilla' olive trees at 7×5 m spacing. 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. The total precipitation (P) collected in 2007 was 411.1 mm and the potential evapotranspiration (ET$_o$, FAO56 Penman-Monteith equation) was 1235.0 mm.

The orchard was divided into three plots, each with a different water treatment: 1) Rainfed, with rainfall as the only source of water supply; 2) FAO, in which trees were irrigated daily from May 14 to October 2, with enough water to replace ET$_c$. The irrigation system consisted of a lateral per tree row, with five 3 L h^{-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 h^{-1} dripper every 0.4×0.4 m. The grid covered a surface of 8×6 m, with the tree in the middle, enough to keep non-limiting soil water conditions in the whole rootzone, all throughout the irrigation season.

Hydraulic Conductance of the Trees

The K_p values were determined as $K_p = E_p \Delta \Psi^{-1}$, being E_p measured at the central hours of the day, when transpiration rates were relatively constant; $\Delta \Psi = \Psi_s - \Psi_l$, where Ψ_s (MPa) is the 'effective' soil water potential at the root surface and Ψ_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 sampled from 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.

Measurements

Diurnal time courses of Ψ_o and Ψ_l were recorded on June 26 (day of year (DOY) = 177), July 24 (DOY = 205) and August 28 (DOY = 240). Each sampling day we measured both variables from predawn to sunset, every 2.5 hours (Scholander chamber). Every sampling hour we sampled four sunlit and four shade leaves per treatment (two leaves of each type per instrumented tree). 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 each of the two instrumented trees per treatment).

The volumetric soil water contents (θ) in the soil around the instrumented trees was 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 (Granier, 1987).

The leaf area (LA, m^2 one side) of the instrumented trees was estimated as described by Fernández et al. (2006a), on June 20, July 31 and September 3. Half-hour values of main meteorological variables, recorded by an automatic weather station next to the olive orchard, where used to calculate the FAO56 Penman-Monteith ET_o.

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

RESULTS AND DISCUSSION

Clear differences on REW between the irrigated and rainfed treatments were observed all throughout the experimental period (Fig. 1a). For the FAO treatment, REW values measured within the irrigation bulbs show that the soil was kept around field capacity. Results on root distribution reported by Fernández et al. (1991) and on the size of the irrigation bulbs reported by Fernández et al. (2003), allow us to assume that some roots of the FAO trees were under soil drying conditions during that period. For the Pond trees the REW values show non-limiting soil water conditions in the whole rootzone.

The seasonal time course of LA for the instrument trees is shown in Figure 1b. Both in the FAO and Pond trees, LA increased during the irrigation season. This was not observed in the Rainfed trees, in which growth stopped at the end of June, likely because the lack of water in the soil (Fig. 1a). The decrease in LA observed in the Rainfed trees at the end of the experimental period (Fig. 1b) was due to the loss of old leaves.

Figure 2a shows the maximum g_s values ($g_{s\ max}$) measured on the sampling dates in the two instrumented trees of each treatment. The minimum values of Ψ_o recorded on the same days and in the same trees are shown in Figure 2b. These results show a near-isohydric behaviour of the instrumented trees. Thus, the stomatal closure was greater in the FAO trees than in the Pond trees (Fig. 2a), especially ate the end of August (DOY 240). At the end of July (DOY205), differences in $g_{s\ max}$ between the FAO and the Pond trees were not significant, but the daily evolution of g_s reported by Fernandez et al. (2009b) shows significantly lower g_s values in the FAO trees than in the Pond trees from ca 11.00 and 16 GMT. The lower g_s values generally found in the FAO trees helped them to keep similar values of Ψ_o than those recorded in the Pond trees (Fig. 2b). The mechanisms controlling this behaviour are not clear. Fernández et al. (2009b) suggested the possibility of a root-to-shoot signalling mechanism having being triggered in the FAO trees, because of part of their roots being in drying soil. They also mentioned a possible hydraulic limitation in the rootzone of the FAO trees. Whatever the mechanisms involved, Figure 2 shows a greater stomatal control in the olive trees under localized

irrigation than in those with the whole rootzone under non-limiting soil water conditions, which may explain the findings by Fernández et al. (2003) and by Pastor and Vega (2005) reported in the Introduction.

The E_p values per unit of LA, estimated from the sap flow measurements made in the two instrumented trees per treatment, are shown in Figure 3, together with the ET_o values estimated from the weather measurements carried out in the experimental farm. The seasonal dynamics of E_p echoed that of ET_o, for all treatments. Error bars show that the tree-to-tree variability of E_p was quite high, likely because the probe location effect (Fernández et al., 2006b) and also because of differences on LA among trees. Findings in other species suggest that the E_p values per unit of leaf area could have been greater in the trees of the same treatment with lower LA (Pataki et al., 1998; Walcroft et al., 2002). Fernández et al. (2009a) compared the seasonal trends of the daily whole-tree E_p values determined from the sap flow measurements with those determined with the crop coefficient approach (after deducing the losses by soil water evaporation) and with a transpiration model validated for the olive trees in the orchard by Diaz-Espejo et al. (2006). They concluded that the agreement between the E_p values estimated by the three methods was reasonably good. This give us confidence to assume that the E_p values determined from the sap flow measurements made in the instrumented trees were reliable enough to be used in the calculation of K_p. For the FAO trees, the high E_p values estimated at the beginning of the experimental period, until ca DOY 195, could have been due to both the high soil water availability and to the low total LA values of the trees on that period. Later in the season, the soil water outside the irrigation bulbs decreased significantly, which had two effects: lower soil water availability for the trees and greater stomatal closure (Fig. 2a). This, together with the increase on the total LA of the FAO trees during the experimental period (Fig. 1b), made that the E_p values per unit of LA of the FAO trees were, at the end of the season, similar than those of the Pond trees (Fig. 3).

The values of K_p and its components, for the instrumented trees of each treatment and at the three sampling dates, are shown in Figure 4. The $\Delta\Psi$ data (Fig. 4a) show that the trees were able to maintain constant values of Ψ_s-Ψ_l throughout the dry season. This behaviour of $\Delta\Psi$, described as isohydrodynamic, is thought to be an improvement over a typically anisohydric behaviour, in which greater differences between midday Ψ_l and Ψ_s values are recorded (Franks et al., 2007). Differences between treatments on the E_p values recorded at the central hours of the day (Fig. 4b) were small. The lowest values were recorded in the Rainfed trees, as expected, because of the lower soil water availability (Fig. 1a). For the irrigated trees, the low E_p values per unit of LA recorded on DOY 240 could have been due to both the decrease on the atmospheric demand (Fig. 3) and to the increase on LA recorded in the FAO and in the Pond trees (Fig. 1b). The values of K_p calculated from the mentioned $\Delta\Psi$ and E_p values are shown in Figure 4c. The hydraulic efficiency of the Rainfed trees was maintained all throughout the dry season, which suggests that the incidence of embolism in the xylem vessels was negligible. In a previous work, we used the vulnerability curves derived for olive by Ennajeh et al. (2008) to estimate the effect of the minimum Ψ_o values recorded in these trees on the percentage loss of conductivity (PLC), resulting ca 20% (Fernández et al., 2009a). Data in Fig 4c confirms the little incidence of embolism in the hydraulic efficiency of the Rainfed trees throughout the dry season, but shows that K_p values were generally lower in the Rainfed trees than in the irrigated ones, due to the lower E_p values of the Rainfed trees (Fig. 4b). This could have been due to the lowest soil water available in the Rainfed treatment, as compared to those of the FAO and Pond treatments (Fig. 1a). Also, a greater stomata closure was observed in the Rainfed trees than in the irrigated trees, likely induced by the lack of water in the soil, which surely contributed to the smaller values of E_p recorded in the Rainfed trees (Fig. 2a).

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Literature Cited

Davies, W.J., Bacon, M.A., Thompson, D.S., Sobeih, W. and Rodríguez, L. 2000. Regulation of leaf and fruit growth in plants growing in drying soil: exploitation of the plants' chemical signalling system and hydraulic architecture to increase the efficiency of water use in agriculture. J. Exp. Botany 350:1617-1626.

Diaz-Espejo, A., Hafidi, B., Fernández, J.E., Palomo, M.J. and Sinoquet, H. 2002. Transpiration and photosynthesis of the olive tree: a model approach. Acta Hort. 586:457-460.

Diaz-Espejo, A., Walcroft, A., Fernández, J.E., Hafidi, B., Palomo, M.J. and Girón I.F. 2006. Modelling photosynthesis in olive leaves under drought conditions. Tree Physiol. 26:1445-1456.

Ennajeh, M., Tounekti, T., Vadel, A., Khemira, H. and Cochard, H. 2008. Water relations and drought-induced embolism in olive (*Olea europaea*) varieties 'Meski' and 'Chemlali' during severe drought. Tree Physiol. 28:971-976.

Fernández, J.E., de la Torre, A., Morales-Sillero, A., Torres-Ruiz, J.M., Jimenez-Bocanegra, J.A. and de Cires, A. 2009b. Stomatal control by drying roots in olive trees under localized irrigation. Acta Hort. (in press).

Fernández, J.E., Díaz-Espejo, A., Infante, J.M., Durán, P., Palomo, M.J., Chamorro, V., Girón, I.F. and Villagarcía, L. 2006a. Water relations and gas exchange in olive trees under regulated deficit irrigation and partial rootzone drying. Plant Soil 284:273-291.

Fernández, J.E., Durán, P.J., Palomo, M.J., Diaz-Espejo, A. and Chamorro, V. 2006b. Calibration of sap flow estimated by the compensation heat pulse method in olive, plum and range trees: relationships with xylem anatomy. Tree Phyisol. 26:719-728.

Fernández, J.E., Morales, A., Martín-Palomo, M.J., Muriel, J.L., Romero, R. and Diaz-Espejo, A. 2009a. Seasonal changes on hydraulic conductance of mature olive trees under different water regimes. Acta Hort. 846:263-270.

Fernández, J.E., Moreno, F., Cabrera, F., Arrúe, J.L. and Martín-Aranda, J. 1991. Drip irrigation, soil characteristics and the root distribution and root activity of olive trees. Plant Soil 133:239-251.

Fernández, J.E., Palomo, M.J., Díaz-Espejo, A. and Girón, I.F. 2003. Influence of partial soil wetting on water relation parameters of the olive tree. Agronomie 23:545-552.

Franks, P.J., Drake, P.L. and Froend, R.H. 2007. Anisohydric but isohydrodynamic: seasonally constant plant water potential gradient explained by a stomatal control mechanism incorporating variable plant hydraulic conductance. Plant, Cell & Environment 30:19-30.

Granier, A. 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. Tree Physiol. 3:309-320.

Green, S.R., Clothier, B.E. and Jardine, B. 2003. Theory and practical application of heat-pulse to measure sap flow. Agron. J. 95:1371-1379.

Jones, H.G. 1983. Estimation of an effective soil water potential at the root surface of transpiring plants. Plant Cell Environ. 6:671-674.

Lo Gullo, M.A., Salleo, S., Rosso, R. and Trifilò, P. 2003. Drought resistance of 2-year-old saplings of Mediterranean forest trees in the field: relations between water relations, hydraulics and productivity. Plant Soil 250:259-272.

Moreshet, S., Cohen, Y., Green, G.C. and Fuchs, M. 1990. The partitioning of hydraulic conductances within mature orange trees. J. Exp. Bot. 41:833-839.

Pastor, M. and Vega, V. 2005. Diseño agronómico e hidráulico de una instalación de riego localizado. p.301-346. In: M. Pastor (ed.), Cultivo del olivo con riego localizado, Junta de Andalucía & Ediciones Mundi-Prensa.

Pataki, D.E., Oren, R. and Phillips, N. 1998. Responses of sap flux and stomatal conductance on *Pinus taeda* L. trees to stepwise reductions in leaf area. J Exp Bot. 322:871-878.

Tuzet, A., Perrier, A. and Leuning, R. 2003. A coupled model of stomatal conductance,

photosynthesis and transpiration. Plant, Cell and Environment 26:1097-1116.
Walcroft, A.S., Whitehead, D., Kelliher, F.M., Arneth, A. and Silvester, W.B. 2002. The effects of long-term, partial shading on growth and photosynthesis in *Pinus radiata* D. Don trees. Forest Ecology and Management 163:151-163.
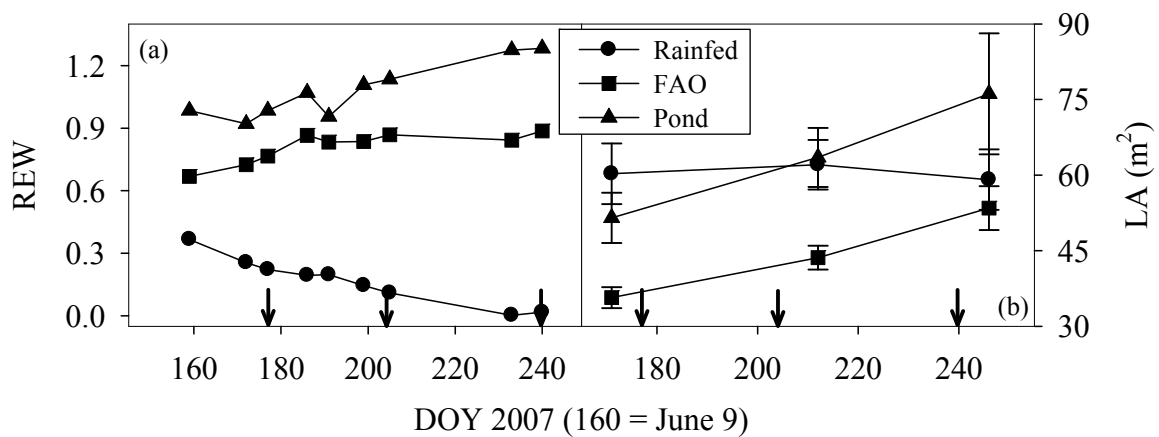
Figures

Fig. 1. Values of (a) the relative extractable water (REW) in the soil of each treatment, calculated from the volumetric soil water measurements in the orchard, and (b) of the leaf area (LA) of the instrumented trees (n=2±SE). The arrows indicate the dates at which the trees' hydraulic conductance was calculated. DOY = day of year.
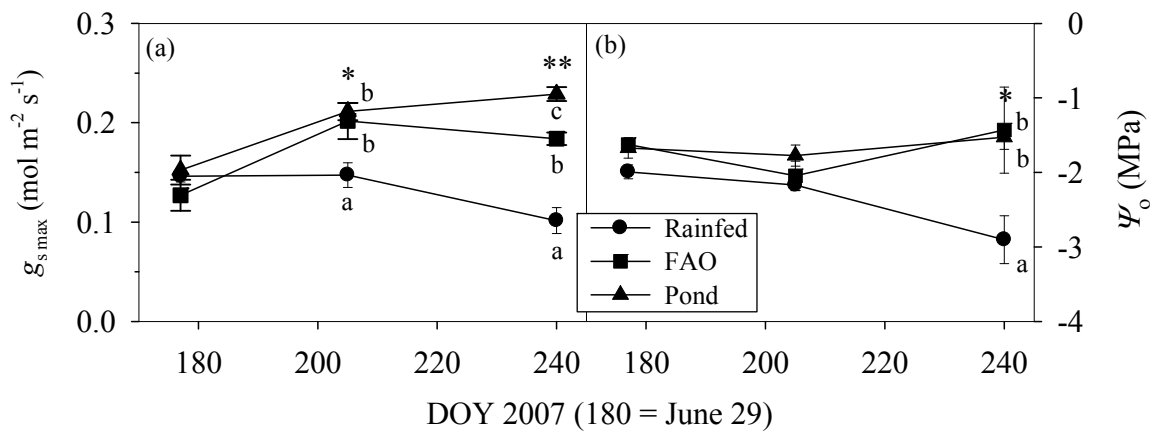
Fig. 2. Values of (a) maximum stomatal conductance ($g_{s\,max}$, $n=4\pm SE$) and (b) minimum water potential in sunlit leaves (Ψ_o, $n=4\pm SE$) measured in the instrumented trees of each treatment on the three sampling days. For all cases, $n=4\pm SE$. Mean values with different letters are significantly different; *$P\leq0.05$, **$P\leq0.01$: no asterisk means no significant differences. DOY = day of year.
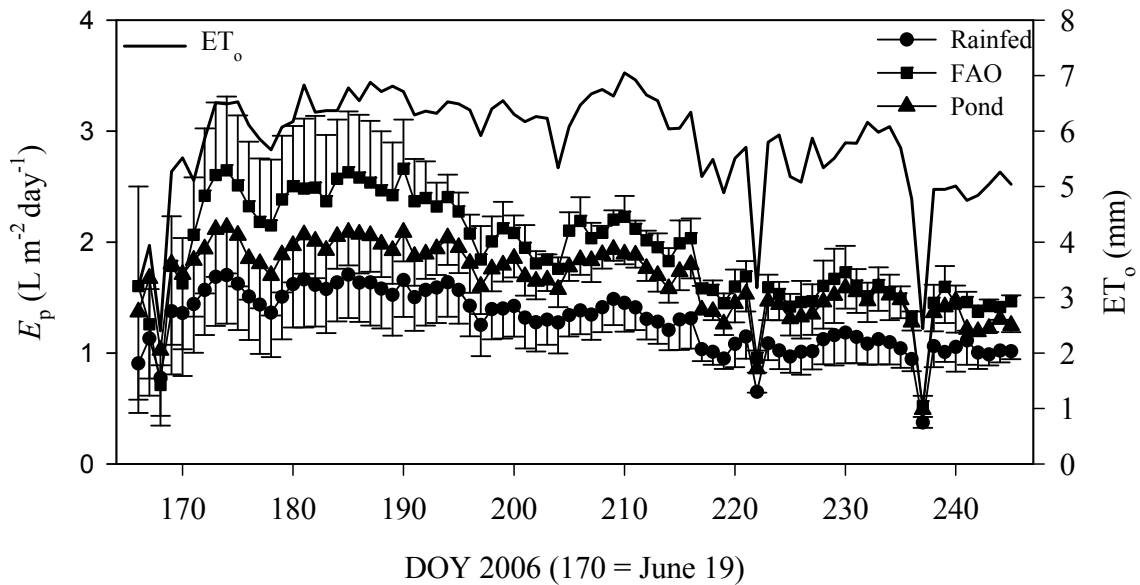

Fig. 3. Time course of the transpiration (E_p) of the trees instrumented with sap flow sensors ($n=2\pm SE$), and that of the FAO56 Penman-Monteith potential evapotranspiration (ET_o). DOY = day of year.
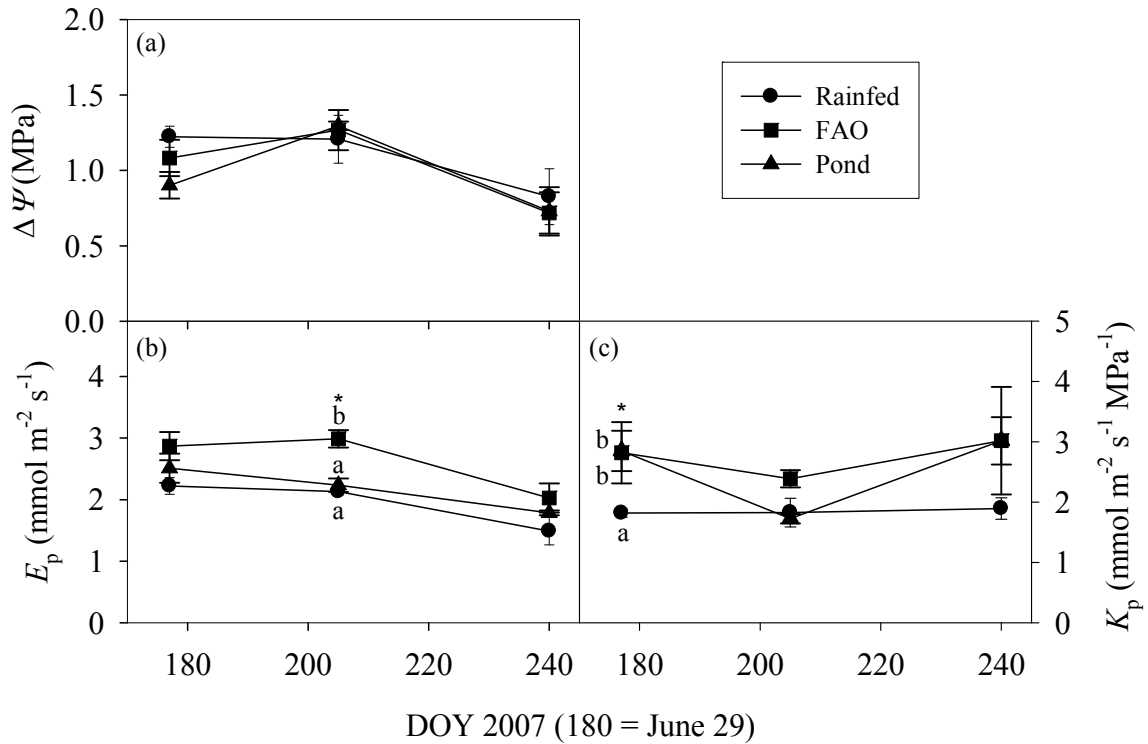
Fig. 4. Values of (a) the differences between the water potential of the soil and that of the canopy ($\Delta\Psi$) of representative trees of each treatment, (b) of the tree transpiration (E_p) derived from sap flow measurements in the same trees and at the same sampling hours, and (c) of the trees' hydraulic conductance (K_p) calculated as explained in the text. For all cases, n=4±SE. Mean values with different letters are significantly different; *$P{\leq}0.05$, **$P{\leq}0.01$: no asterisk means no significant differences. DOY = day of year.