

Transpiration and root water uptake by olive trees

Félix Moreno¹, J. Enrique Fernández¹, Brent E. Clothier^{2,3} and Steven R. Green²

¹Instituto de Recursos Naturales y Agrobiología de Sevilla, Consejo Superior de Investigaciones Científicas. Apartado 1052, Sevilla 41080, Spain and ²Environment Group HortResearch Institute P.B. 11–030 Palmerston North New Zealand. ³Corresponding author *

Received 16 August 1995. Accepted in revised form 26 April 1996

Key words: heat pulse sap flow measurement, irrigation, *Olea europaea* L., var. manzanillo, Penman-Monteith equation, transpiration

Abstract

While the cultivated olive tree (*Olea europaea* L.) is known to be sclerophyllous and effective at tolerating drought, little is known of its short-term water-use dynamics for most studies have been based on longer-term, water-balance information. We present here, for the first time, heat-pulse measurements of the sap flux measured not only within the semi-trunk of an olive tree, but also within a root excavated close to the stump. One tree in the olive grove near Seville in Spain had regularly received basin irrigation during the summer, whereas the other, growing on this deep silt loam, had been without water for over 3 months. Following a flood irrigation of 730 L to a dyked area around the tree, the regularly-irrigated olive maintained a transpiration rate of $1.65 \text{ mm}^3 \text{ mm}^{-2} \text{ d}^{-1}$, on a leaf area basis, for only 3 days following the irrigation. This rate was maintained for a total consumption of 110 L. It then began again to limit its rate of water use with transpiration falling below that predicted for well-watered conditions by the Penman-Monteith equation. The flow of sap in the near-surface root dropped concomitantly. Meanwhile the unirrigated tree was using water at just 0.78 mm d^{-1} . Yet following an irrigation of 870 L it only lifted its consumption to 1.12 mm d^{-1} , on a leaf area basis. Neither did it recover its leaf water potential following this wetting because of an inability to refill cavitated vessels. These data again show olive to be a parsimonious and cautious consumer of soil water.

Introduction

In the Mediterranean region, olive trees have traditionally been grown under rainfed conditions. Over the last two or three decades, however, many olive orchards have begun to adopt irrigation practices (Eris and Barut, 1995). In southern Spain, as in many other countries where olive has traditionally been a rainfed crop, irrigation is now being applied via microirrigation techniques, using drippers, minisprinklers, or localised flooding in small basins. The increasing use of irrigation has prompted research to determine exactly what are the water requirements of the sclerophyllous olive tree.

Certainly the cultivated olive tree (*Olea europaea* L.) is well known for its drought tolerance. Yet there is

a dearth of information and understanding of its short-term water-use dynamics, on the time scale appropriate for microirrigation - from hours to days. Most studies have been on the longer term, and the amount of water transpired by the olive tree has been determined from the water balance of the soil (Goldhamer et al., 1993; Michelakis and Vougioucalou, 1988; Moreno et al., 1988). Furthermore, little is known of the specific detail of the uptake strategy employed by the roots of olive trees. Nonetheless, longer-term studies of root activity of olive trees under irrigation have been carried out to identify the zones of activity where root water uptake is preferred, and to assess the root growth response of variously-irrigated olive trees (Fernández et al., 1991). Other physiological work has been carried out on the water relations of olive trees to infer the controls on the transpiration rate through measure-

* FAX No: + 6463546731. E-mail: clothierb@hort.cri.nz

ments of leaf conductance and water conduction in stems (Larsen et al., 1989; Lo Gullo and Salleo, 1988; Natali et al., 1985; Salleo et al., 1985; Thompson et al., 1983). Many of these studies used young olive trees, and in many cases the trees were grown in pots. From such studies it is clear that the olive tree is a parsimonious user of water, and that it has a prodigious ability to tolerate substantial soil water deficits throughout a large portion of its root zone. These experiments have contributed substantially to our knowledge of the soil-water-plant relationships of olive trees under different soil water regimes. However less well known are these relationships for mature trees growing in the field under conditions of commercial production. In fact there have been no direct measurements made of olive tree transpiration in the field, nor have direct observations been made of water uptake by their roots. In this study we intensely focus on the hydraulic functioning of just two olive trees, to obtain insight into the mechanisms controlling transpiration and root uptake.

Heat-tracer techniques to monitor sap flow can provide accurate measurements of tree water use on the time scale ranging from minutes through to months. This is allowing understanding to be garnered of how tree transpiration is controlled by the ambient microclimate and the prevailing levels of soil water in the root zone. Measurements of sap flow have been carried out in the trunks of many species (Cohen et al., 1983; Granier, 1985; Hinckley et al., 1994; Sakutarani, 1981; Steinberg et al., 1990). More recently heat-tracer techniques have now been employed to determine the short-term dynamics of water uptake by roots (Cabibel and Do, 1991; Green and Clothier, 1991). One of these techniques, the heat-pulse method as used by Green and Clothier (1988), has been used to provide detailed information concerning the flow of sap in the roots of kiwifruit, a profligate user of water (Green and Clothier, 1995). Kiwifruit vines have large xylem vessels such that their hydraulic resistance is known to be low (McAneney and Judd, 1983). The roots of these spendthrift vines could respond rapidly to localised wetting near the surface (Green and Clothier, 1995), such that microirrigation techniques would appear to be efficient (Clothier and Green, 1994). We present here tree water-use data derived from heat-pulse measurement of sap flow within the trunk of the sclerophyllous olive tree, a thrifty user of water which is known to have small xylem vessels that provide a huge resistance to flow (Salleo et al., 1985). Results are presented for both a regularly irrigated and an unirrigated olive tree in the dry environment of SW Spain. The observed

response to watering of both trees is discussed in terms of the hydraulic functioning of the tree, as are measurements of the sap flow made within a root of the well-watered tree.

Materials and methods

Site

This experiment was carried out at the experimental farm of the Institute for Natural Resources and Agrobiology of Seville (IRNAS, CSIC), which is located at Coria del Río close to the city of Seville in SW Spain (37° 17' N, 6° 3' W). The experiment began 30 August 1994 and ended on 30 November 1994.

The two trees used in this experiment were located within a 1 ha plot containing many 25-year-old olive trees (*Olea europaea* L., var. manzanillo) that are planted at a spacing of 7 × 7 m (Fig. 1). The soil there is a sandy loam with clay, silt, fine sand and coarse sand percentages of 22.6, 13.4, 36.5 and 27.5 respectively. The soil is over 2 m deep. Additional details on the soil's physical properties can be gleaned from Moreno et al. (1983, 1988). Here we present only the soil water retention data (Table 1). Down to -25 kPa these potential data were obtained from contemporaneous measurements of the tensiometer pressure potential and water content in the top 1.5 m of the soil, while a pressure-plate apparatus was used for the lower potentials. Early on, the trees were pruned to create two distinct branches, here termed semi-trunks, with the bifurcation being at a height of between 1–1.5 m. Since 1983, all the olive trees had been micro-irrigated by four 4 L h⁻¹ drippers per tree during the summer period from May to October. However, in April 1994, two trees were selected from within in the plot. One of them received about 650 L of irrigation, each week from May to September, by flooding a basin of 3 m radius around the trunk (Fig. 1). This tree we shall call the irrigated tree. Sapflow measurements began in this tree on day-of-year (DOY) 243, the 30th August, some 4 days after the previous irrigation of DOY 239. Another irrigation of 730 L was carried out on DOY 252. Meanwhile the other tree received just one basin irrigation in May, and subsequently received no water over the next 3 months, until after the experiment began. This tree is referred to as the unirrigated olive. Sapflow measurement within the semi-trunk of this tree also began on DOY 243. On DOY 255, this

Table 1. The soil water retention curve measured for the sandy loam at Coria del Río. Measurements for Ψ down -25 kPa derive from the smoothed curve fitted through paired readings obtained in the field from tensiometers and neutron probing down to 1.5 m. Lower values come from a pressure plate using undisturbed samples

Soil water potential Ψ (kPa)	Soil water content θ ($\text{m}^3 \text{m}^{-3}$)
0	0.331
-2.5	0.233
-5.0	0.202
-7.5	0.179
-10	0.169
-15	0.162
-25	0.153
-100	0.146
-500	0.110
-1000	0.105
-1500	0.101

previously unirrigated tree finally received a basin irrigation of some 870 L.

Sap flow measurement and transpiration prediction

Sap flow was monitored within the trunk of both the irrigated and unirrigated trees using the compensation heat-pulse technique (Green and Clothier, 1988; Swanson and Whitfield, 1981). Two sets of heat-pulse probes, each consisting of a heater of diameter 1.8 mm and two temperature probes, also of diameter 1.8 mm, were installed into parallel holes drilled radially into the semi-trunk at heights of between 1.2 and 1.4 m. The arrangement of the sensors is identical to that shown in Figure 2 of Green and Clothier (1995), except that the downstream probe was only 15 mm away from the heater. Sap velocity was calculated using the theoretical calibration of Swanson and Whitfield (1981) to account for the probe-induced effects of wounding. In their scheme this corresponds to wound radius of 2.0 mm. The temperature probes in the semi-trunk each had four microbed-thermistors at the four radial depths of 7, 14, 25 and 40 mm below the cambium. Volume flow rates were calculated by integrating the measured radial profile of sap velocity over the sapwood cross-section. The semi-trunk of the irrigated tree was of radius 64.8 mm, whereas the radius of the unirrigated semi-trunk was 58.7 mm.

Prior to the experiment, we carefully excavated a small pit near to the trunk of the irrigated olive tree to expose partially a single, large, woody root at a depth of 0.3–0.4 m and a distance of about 0.5 m from the stump. The root was virtually cylindrical and of radius 34.4 mm. Similarly-designed, but shorter heat-pulse probes were installed to monitor sap flow in this root, with the depths of measurement now being 5, 10, 15 and 20 mm below the cambium. The separation between the probes and the heater was reduced to accommodate the lower sap velocities anticipated in the root. The downstream probe was just 10 mm from the heater, with the upstream probe still positioned 5 mm away. After the probes were installed the soil was then gently repacked around the probes and the root. A Campbell CR10 data logger was used to control the firing of all the heat-pulses and the recording of all the temperatures, plus calculation of the subsequent heat-pulse velocities. Pulses of heat were initiated every 30 minutes and the velocity results stored to allow subsequent calculation every half an hour of the volumetric sap flow rate.

An automatic weather station was located some 50 m away from the experimental trees, and this recorded thirty-minute averages of global solar radiation and photosynthetically-active radiation, plus wind speed, air temperature, relative humidity and rainfall. These data were used, along with requisite plant measurements, to compute the Penman-Monteith transpiration for each instrumented semi-trunk.

The calculation procedure used here for Penman-Monteith transpiration follows that described in detail by Green et al. (1995), so only salient features are repeated here. The total leaf area of the semi-trunk (A , m^2) was considered to comprise an area of sunlit leaves A_1 , and a complementary area of shaded leaves, A_s (Sinclair et al., 1976). The Penman-Monteith equation summed over a canopy of either shaded, or lit, hypostomatous leaves gives the transpiration rate per unit leaf plan area E_p ($\text{g s}^{-1} \text{m}^{-2}$ leaf plan area) as the sum of three terms (Green, 1993),

$$\begin{aligned} \lambda E_p &= f_q \cdot \frac{sR_{n,1}}{s + \gamma(2 + g_{b,1}/g_{c,1})} \\ &+ f_p \cdot \frac{\rho c_p D_a g_{b,1}}{s + \gamma(2 + g_{b,1}/g_{c,1})} \\ &+ f_s \cdot \frac{\rho c_p D_a g_{b,s}}{s + \gamma(2 + g_{b,s}/g_{c,s})} \\ &= \text{I} + \text{II} + \text{III} \end{aligned}$$

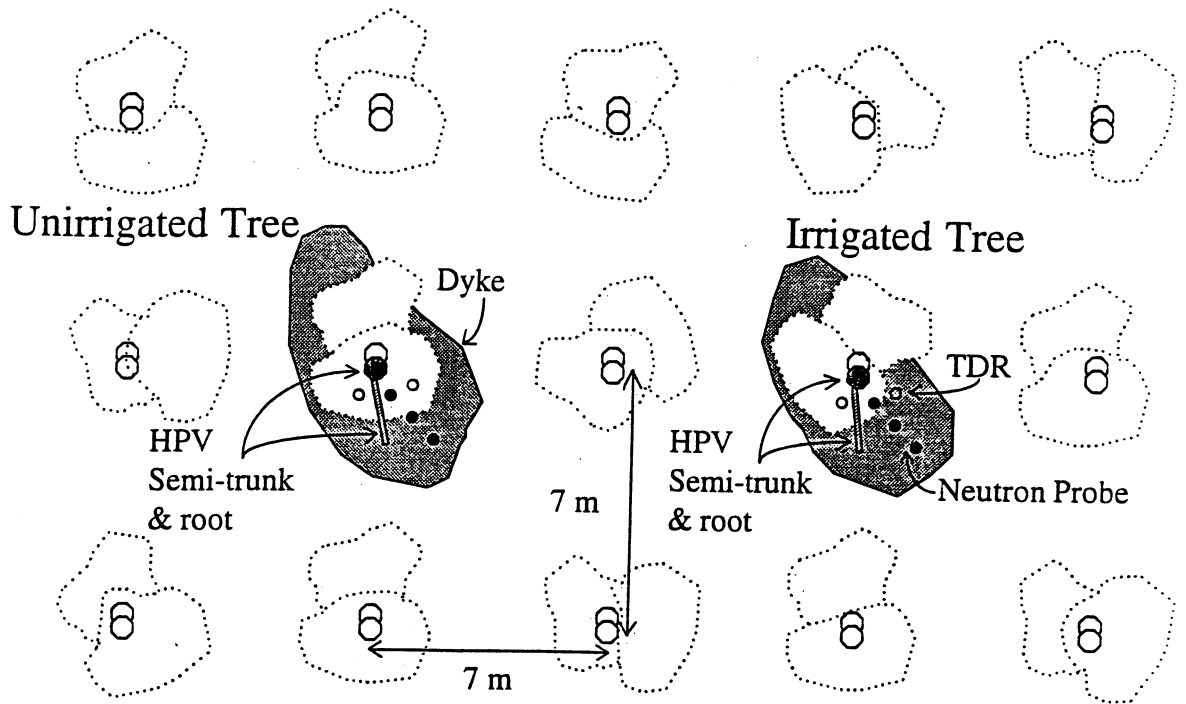


Figure 1. The layout of part of the olive grove at Coria del Río in which the experiments on two olive trees were carried out in September–November, 1994. Heat-pulse velocity (HPV) sensors were placed in a semi-trunk and root of two trees around which TDR (○) and neutron probe (●) measurements of soil water content were made.

where the subscript *l* or *s* refers either to lit or shaded leaves which occur in complementary fractions of $f_l (= A_l/A)$ and $f_s (= A_s/A)$. The net, all-wave radiation of the lit leaves is $R_{n,l}$ (W m^{-2} of leaf plan area), whereas it is assumed to be zero for the shaded leaves. Here D_a is the ambient vapour pressure deficit of the air (Pa), which we need to assume to be the same throughout the canopy. The term g_c is the leaf stomatal conductance (m s^{-1}) and g_b is the leaf-canopy boundary-layer conductance (m s^{-1}), λ is the latent heat of vapourisation (2.454 J kg^{-1}), s the slope of the saturation vapour pressure curve ($\text{Pa } ^\circ\text{C}^{-1}$), γ the psychrometric constant (66.1 kPa), ρ is the density of air (kg m^{-3}) and c_p is the specific heat capacity of the air at constant pressure (J kg^{-1}).

Unlike Green et al. (1995) we were not able to measure the net radiation $R_{n,l}$ so it was estimated from the measure incoming shortwave global radiation assuming an albedo of 0.2, and a longwave loss of -40 W m^{-2} . From measurements of the shadow area on the ground A_G , along with the assumption of a spherical leaf-angle distribution we estimate the area of sunlit leaves to be $A_l = 2A_G$ (Green, 1993). Thus the fractions f_l , and f_s could be obtained using measurements of A . The leaf boundary-layer conductances were set equal

for both the lit and shaded leaves, and were calculated from the measured wind speed via the empirical relationship of Landsberg and Powell (1973)

$$g_b = 0.0172p^{-0.56} \sqrt{\frac{u}{d}} \quad (1)$$

where u is the windspeed at mid-canopy height that was inferred from our nearby measurements. The characteristic leaf dimension d taken to be 0.04 m, and p the ratio of the foliage density 'seen' by the wind was considered to be 5. This latter parameter is the total leaf area to the area of foliage projected in the vertical plane. The stomatal conductance function g_c of the lit leaves we assume to be of the form proposed by Thorpe et al. (1980) for apples, viz.

$$g_c = g^* \left(\frac{1 - \alpha D_a}{1 + \beta/R_p} \right) \quad (2)$$

where g^* is the reference stomatal conductance (m s^{-1}), and R_p is the incident photosynthetically-active radiation on the leaf, which was taken to be half the globally-incident value by assuming a spherical leaf-angle distribution. By fitting to measurements of stomatal conductance made on the well-watered olive. α was found to be 0.2 kPa^{-1} , with $\beta = 75 \mu\text{mol m}^{-2} \text{ s}^{-1}$.

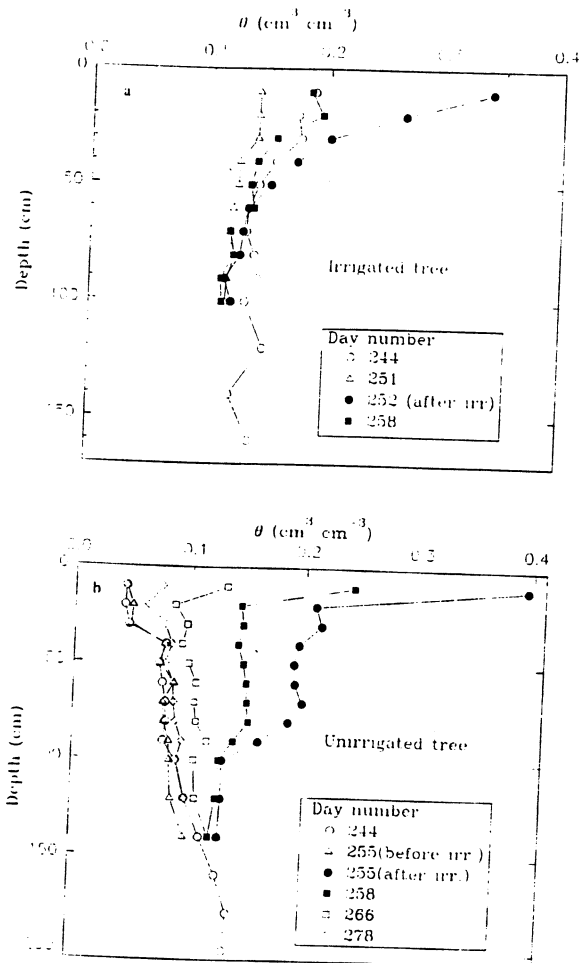


Figure 2. The depthwise profiles of soil water content θ ($\text{m}^3 \text{m}^{-3}$) measured at various times before and after irrigation a) for the irrigated olive tree at a radial distance of 0.5 m from the trunk, and (b) at 1.5 m from the trunk for the unirrigated tree. In (a) the tree was irrigated on the morning of DOY 252, and for (b) on DOY 255.

and $g^* = 10 \text{ mm s}^{-1}$. On the basis of no detectable difference in the measured values of g_c between shaded and lit leaves, Equation 3 was also taken to apply to the shaded leaves, so that the partitioning of the last two terms is simply on the basis of the respective leaf areas. Typically, under the late summer conditions in Andalusia, Equation 3 appropriately gives mid-morning conductances up to a maximum of around $6\text{--}7 \text{ mm s}^{-1}$ (Fernández et al., 1993).

Soil water and plant measurements

The soil volumetric water content (θ) of the top 150 mm of the soil profile was measured using a time-domain-reflectometry (TDR) with a Tektronix Model 1502C. The TDR waveguides comprised three paral-

lel stainless steel rods, 2 mm in diameter, and 0.15 m long. A portable computer was used to record and analyse the TDR wave-forms using an analysis similar to that of Baker and Allmaras (1990). Measurements were made at two different locations away from each trunk (Figure 1). The volumetric water content of the soil from 0.2 down to a maximum depth of 2 m was measured every 0.1 m using a neutron probe (Troloxer Model 3300) in access tubes installed at the three distances of 0.5, 1.5, and 1.5 m away from each tree (Figure 1). Measurements were taken frequently, both prior to, and following each of the irrigations.

The total leaf area on the instrumented semi-trunk of the irrigated tree was estimated at $A = 21 \text{ m}^2$, whereas the whole tree was considered to have a leaf area of 63 m^2 . This area was determined by counting the number of leaves on a typical branch (1330), and then adding up the number of such typical branches per semi-trunk. The irrigated tree had 55 branches on the instrumented semi-trunk, and 112 on the other semi-trunk. The mean area of an individual leaf was found to be 290 mm^2 on the area basis of direct tracings made on 10 randomly-chosen leaves. This value was smaller at 260 mm^2 for the unirrigated tree, but as there were more branches on the instrumented semi-trunk (86) its leaf area was estimated at $A = 29 \text{ m}^2$. However the whole tree was estimated to possess a lower leaf area of just 42 m^2 . For the instrumented semi-trunk of the irrigated tree, a shadow area of $A_G = 3 \text{ m}^2$ was mapped out on the ground. So the area of lit leaves was estimated as $A_l = 6 \text{ m}^2$ (Green, 1993), giving f_l , here as 0.29. For the instrumented semi-trunk of the unirrigated tree $A_G = 4.5 \text{ m}^2$, so that $f_l = 0.31$. The leaf area results also allow the total semi-trunk water use (L hr^{-1}) to be predicted from the Penman-Monteith expression of Equation 1 by multiplying λE_p and A .

Leaf water potential was measured frequently using a pressure chamber (Soil Moisture Co., Santa Barbara, CA, USA). At each sampling, during mid-afternoon, the leaf water potential was measured on 6 sunny leaves of each tree. To parameterise Equation 3, the diurnal pattern of leaf conductance was measured every 2 hours on 6 sunny and shaded leaves with a transient porometer (Delta-T Devices MK3, Cambridge, UK).

Results and discussion

Soil water and leaf water potential

The soil water content profiles were measured on DOY 244, some 5 days after the flooding of the dyked area around the irrigated tree on DOY 239. For simplicity only the profile measured 0.5 m from the tree is shown in Figure 2a. From these measured water contents (Figure 2), the potential below a depth of about 0.5 m would now be inferred to have been drier than -100 kPa (Table 1). By comparing this with the θ profile measured a week later on DOY 251, it can be seen that the roots of this tree were extracting water quite uniformly over the measured profile. Prior to the next irrigation the potential at 1 m would have reached about -0.5 MPa. The irrigation of DOY 252 thoroughly wetted the top 0.15 m, with the wet front reaching down to about 0.8 m. Over the next 6 days, root extraction of water was limited to the top 0.7 m. This is the active zone of root uptake found for an irrigated olive tree by Fernández et al. (1991) using a ^{32}P tracer technique.

Meanwhile, on DOY 244, the profile of θ around the unirrigated tree was quite different. Here only the profile measured 1.5 m from the trunk is shown in Figure 2b. Above about 1.25 m, $\theta \leq 0.1$ (Figure 2) so that the potential would have been less than -1.5 MPa. The surface soil was exceptionally dry, $\theta \leq 0.05$, and over the next eleven days there was little or no change in θ in the top 1 m. However, there was evidence that up until the morning of DOY 255, root water extraction was occurring at depths below 1 m. The midday irrigation on DOY 255 can be seen to have wetted the soil to a depth of about 1.4 m. Over the next 3 weeks the roots consumed virtually all of this water, for it is unlikely that drainage would have occurred beyond 1.5 m, as the hydraulic conductivity at $\theta \approx 0.1$ would be low. Thus the uptake strategy adopted by this unirrigated tree quickly switched from one of extraction by deep roots beyond the dry surface soil, to one of near-surface consumption following irrigation.

The leaf water potentials measured during early to mid-afternoon are shown in Figure 3. While some scatter can be associated with varying weather conditions at the time of sampling, a distinct seasonal rise can be seen as winter approaches, and the autumnal rains arrive. Early on, during mid to late summer, the minimum potentials were around -2 MPa for the irrigated tree. These minima are similar to values found by others (Fernández et al., 1993; Larsen et al., 1989; Natali et al., 1985). A midday minimum of -3 to -3.5

mPa, as measured on the unirrigated tree prior to DOY 250, indicates drier conditions than those encountered here by Fernández et al. (1993), whilst our conditions are still somewhat wetter than the -4 MPa observed in stressed olive trees grown in pots by Natali et al. (1985).

Following irrigation of the previously-unirrigated tree on DOY 255, the difference in the leaf water potentials between the two trees which had been up to 1.5 MPa, fell straightaway to just 0.3 MPa. But unlike the fully-rewetted potted olives of Natali et al. (1985), this difference did not collapse to zero following irrigation. Fernández et al., (1993) found for their field-grown, but less-stressed olives, complete recovery following rewetting took three days. However in our case for this single tree, there was no full recovery. By DOY 262 when root-zone soil-water potentials were back to around -1 MPa (Figure 2; Table 1), the difference in leaf water potentials had again widened to about 1 MPa. It was not until the onset of the cooler weather, and the arrival of the autumnal rains on DOY 293 that the difference in leaf water potential disappeared. This failure to recover fully following a substantial irrigation differs from the results of Natali et al. (1985), and Fernández et al. (1993). In the former case, all of the roots of the 3-year old trees grown in pots would have been fully wetted by the irrigation. In the case of Fernández et al. (1993), the degree of stress was less, yet even so the recovery did take 3 days. In an earlier study, Fernández et al. (1991) found tree roots out beyond 3.5 m from the trunk, yet the dykes for our irrigation extended on average out to just 3 m. Also our basin wetting only reached a depth of about 1.4 m, and the extraction data between DOY's 244 and 255 showed uptake activity below that depth. So inevitably our wetting had left some roots dry even though water was freely available throughout a substantial part of the root zone. Some chemical signalling by these dry roots might have assisted the recovery in potential (Tardieu and Davies, 1993), but here there was a failure to recover fully. Hydraulically, olives have been found to have narrow xylem vessels (Salleo et al., 1985), such that the resistance to sap flow in the roots and trunk is high (Larsen et al., 1989). Also it is known that olive leaves have relatively elastic cell walls such that leaf water potential changes relatively slowly for a given change in symplastic water (Lo Gullo and Salleo, 1988). These hydraulic features both suggest any recovery following rewetting will be slow, as we have observed. Before exploring this in more detail we first turn our attention to sapflow observations made in the irrigated olive tree

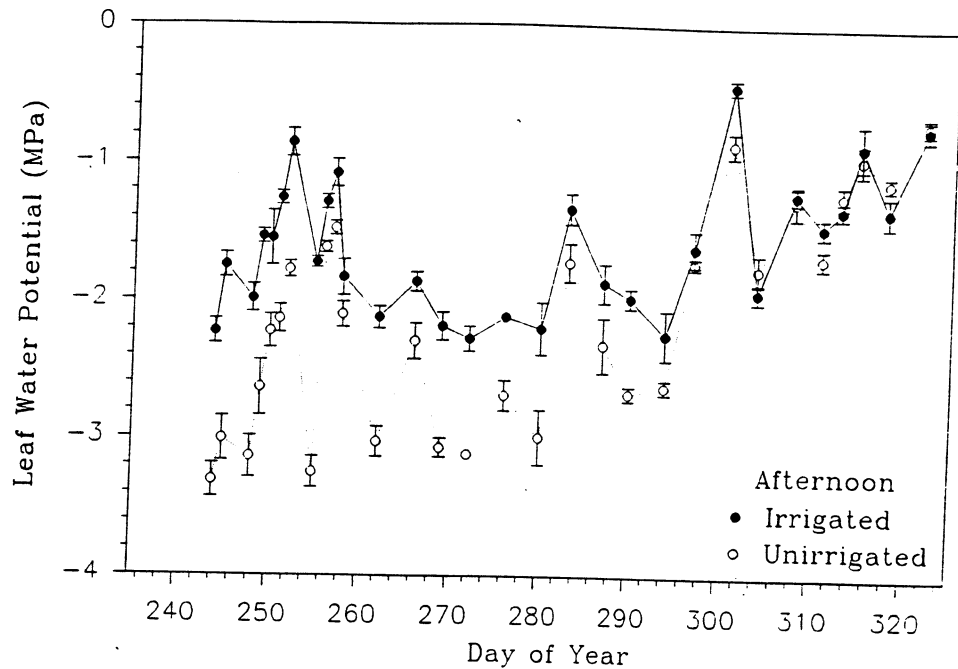


Figure 3. The mean and standard deviation of the leaf water potential measured mid-afternoon on 6 sunny leaves from both the irrigated (●) and unirrigated (○) olive trees. The irrigation of the irrigated tree on DOY 252 is discussed in the text, as is the isolated wetting of the unirrigated tree on DOY 255. The autumnal rains began on DOY 293.

when it was well watered for the three days following the irrigation on DOY 252.

Transpiration by the irrigated tree

Half-hourly measurements of the sap flow in the semi-trunk of the irrigated olive tree is shown in Figure 4 along with predictions from the Penman-Monteith model (Eq. 1). The agreement between that predicted and that measured is good. Daily water use by this semi-trunk of leaf area 20.9 m^2 was between 35 and 39 L. When expressed on a leaf area basis this equates to a rate of about $1.65 \text{ mm}^3 \text{ mm}^{-2} \text{ d}^{-1}$. This rate is quite high on a total leaf area basis and reflects the high global radiation input which peaked at 850 W m^{-2} , the high daytime temperatures of $35 \text{ }^\circ\text{C}$, and the large vapour pressure deficits, D_a , of around 3 kPa. Also shown in Figure 4 is the partitioning of the three terms from Equation 1, namely the transpiration due to direct radiation on the lit leaves (I), the D_a -driven evaporation from lit leaves (II), and that associated with the D_a surrounding the shaded leaves (III). Because, f_1 is estimated at just 0.3, the dominant term is the D_a -driven loss of water from the shaded leaves. Furthermore the late afternoon maintenance of λE_p due to the persistence of an elevated D_a can be seen by comparison of the radiation and D_a terms (I vs. II, III).

The extended record of sap flow in both the semi-trunk and root of the irrigated tree is shown in Figure 5, along with the predictions of A times λE_p from Equation 1. Over the entire period DOY 249 to 257, the ratio of flow in the root to that in the semi-trunk remained constant at 38%, despite the irrigation on DOY 252. On this basis we would expect to find about 6–8 roots of this size emanating from the stump of the tree. We did not detect this many lateral roots as we excavated around the stump; hence we must assume that the 'missing' roots headed deeper into the soil at a steeper angle. That prior to rewetting, the unirrigated tree was extracting water at depth would also indicate the deep presence of potentially active roots (Figure 2). Nonetheless this one large, near-surface root is itself supplying the bulk of the semi-trunk's entire water use. This reliance on near-surface water we also observed from the changing profile of θ (Figure 2). The peak sap flux densities observed in the root were around 0.09 mm s^{-1} , and 0.07 mm s^{-1} in the semi-trunk. These flux densities here are of the same order found in apples by Cabibel and Do (1991), but much lower than the 1 mm s^{-1} found in the large-xylemed stem of kiwifruit by Green and Clothier (1995).

Although the ratio of stem to root flow remained constant, there is a significant and systematic change in both, due mainly to the changing distribution of

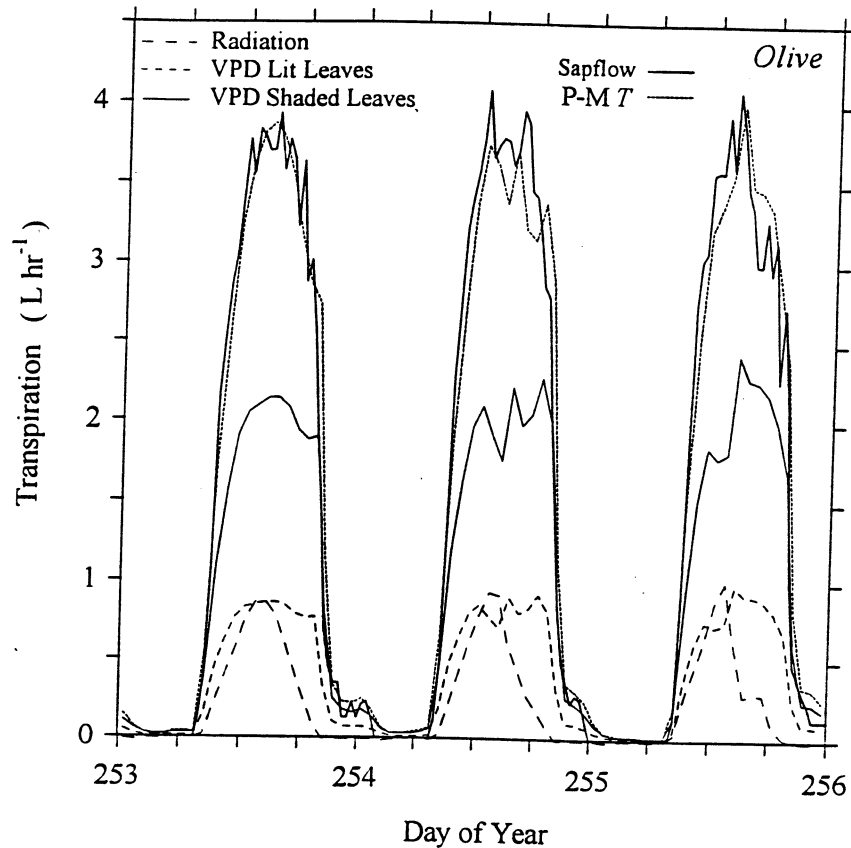


Figure 4. The measured (—) and predicted (---) transpiration from the semi-trunk of the irrigated olive tree over the three days following irrigation on DOY 252. Shown here are the three terms of the Penman-Monteith expression (Eq. 1); namely the radiation term (I) (---), the vapour pressure deficit (D_a) driven term associated with the lit leaves (II) (---), and this term for the shaded leaves (III) (—).

water in the rootzone. Despite the previous irrigation on DOY 239, some 4 days later the flow in the root was already dropping as water becomes less available. Over the next 9 days the peak flow in the root fell by 40% as the near surface soil water potential dropped to around -0.5 MPa (Figure 2; Table 1). Measurements in the semi-trunk, which began on DOY 249, showed semi-trunk sap flow declining relative to that predicted for well-watered conditions by the Penman-Monteith model (Eq. 1). During the early morning, the measured sap flow tracked the Penman-Monteith predictions, however the rates began to diverge by about 0900–1000 hrs. On DOY 251, well-watered transpiration should have peaked at 1600 hrs according to Equation 1 in Figure 5. The peak sap flow measured in the root occurred earlier at about 1500 hrs, while sap flow in the semi-trunk had already begun its rapid decline by 1400 hrs, some two hours earlier than it should have. As we noted in Figure 2, by DOY 251 this irrigated tree was already beginning to seek water from deeper in the profile. In seeking deeper water it

appears that this olive tree is sufficiently prescient to begin limiting its consumption. The irrigation on the morning of DOY 252 resulted in an immediate jump in the sap-flux density in both the root and semi-trunk (Figure 5), even though by late afternoon the tree could still not match atmospheric demand. However over the next 3 days the measured rate matched that predicted (Figure 4). Such a rapid recovery is akin to that found with potted trees by Natali et al. (1985), although it is more rapid than that found for a stressed tree by Fernández et al. (1993).

Just 2 days after wetting, as before, sap flow again began to drop off. By the fourth day after irrigation, flow in the semi-trunk no longer matched atmospheric demand. Again water use began to be curtailed, despite there being, it would appear, still a substantial amount of water available in some parts of the root zone. Nonetheless there would still have been some dry roots in other places. This presence of dry roots somewhere in the rootzone may have provided a sufficiently strong signal for the tree to begin adopting

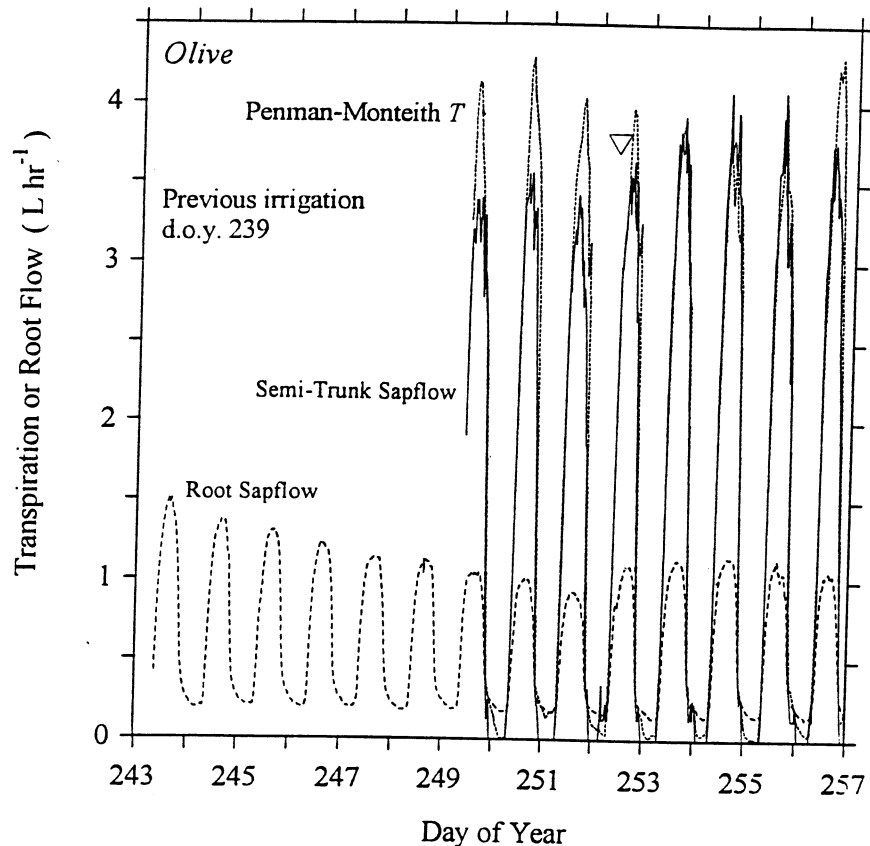


Figure 5. The sapflux measured in a 34.4 mm radius root of the irrigated olive tree (---), along with that measured in the 64.8 mm radius semi-trunk (—) that possessed an estimated leaf area of 20.9 m². Also shown is the transpiration predicted using the Penman-Monteith expression of Equation 1 (- - -). An irrigation of 730 L occurred on the morning of DOY 252

this prudent strategy of cautiously beginning to limit its water use (Tardieu and Davies, 1993).

Transpiration by the unirrigated tree

As expected, prior to DOY 255 the measurements of sapflow in the unirrigated tree were not well-predicted by the Penman-Monteith expression using the same parameters found to be successful for the irrigated tree following wetting. Despite the larger leaf area on the semi-trunk of the unirrigated tree (29 cf. 21 m²); the peak sap flow rates are substantially less (2 cf. 3.5 L hr⁻¹). Not surprisingly, having been without additional water for 3 months, this tree is under water stress. The rate of water use, on a leaf area basis, is here just 0.78 mm d⁻¹, whereas the irrigated tree, when just irrigated, was transpiring at twice that rate. The source of this water must have been deep in the profile, for our observations of sapflow in the surface root only revealed a residual flow there of some 0.03 L hr⁻¹, less than 2% of the semi-trunk's usage. Further, there was

no sap flow observed in the outer annuli of this root, normally the region of highest velocities. Only weak flow was noted in the core of the root. The outer xylem vessels must have cavitated, having been resident in dry soil for over three months. If the Penman-Monteith model were now used with a stomatal conductivity function adjusted so that g^* was just one third that of the well-watered value, namely a maximum of 3.3 mm s⁻¹, then a good prediction results for DOY's 253 and 254 (Figure 6). Measurements of stomatal conductance to provide an integrally-correct measure of the tree's total behaviour are difficult to obtain. Rather, we have adopted an inverse approach.

This previously dry tree was then irrigated between 1000–1200 hrs on DOY 255. However unlike the irrigation of the regularly watered tree, there was here no immediate surge in sap flow (Figure 6). Rather it was not until the next day that transpiration increased above that predicted with $g^* = 3.3$ mm s⁻¹, and even then the tree did not return to the well-watered rate that would have been predicted with a g^* of 10 mm s⁻¹.

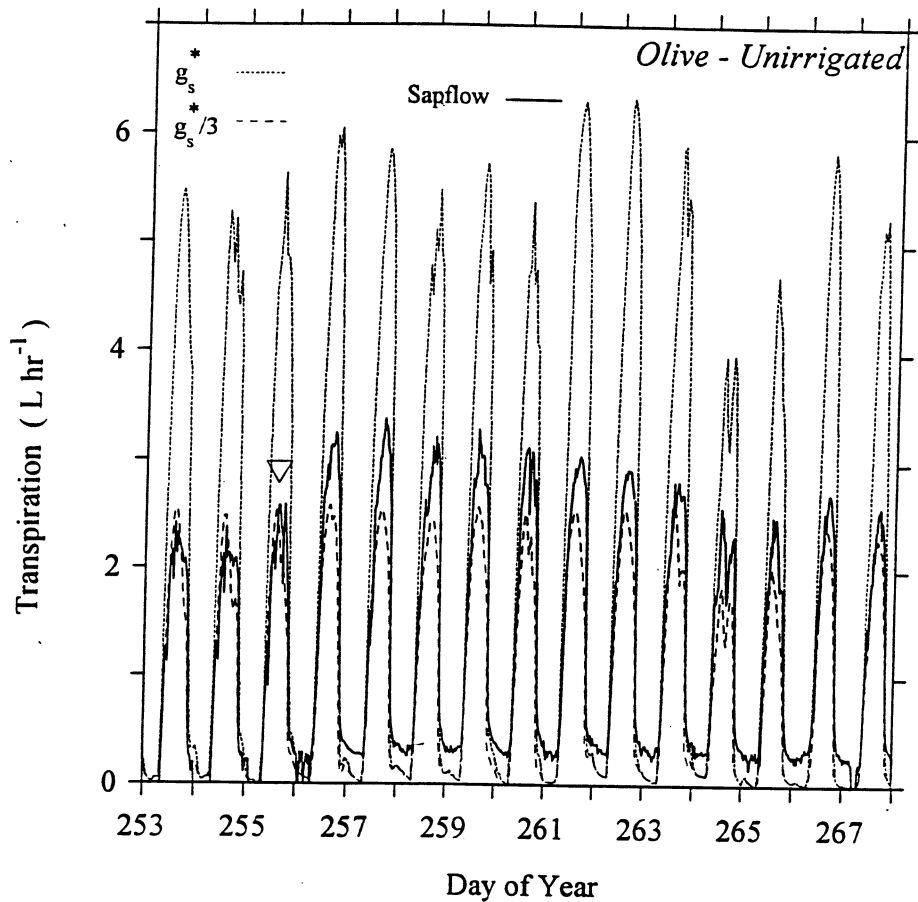


Figure 6. The sapflux measured in the 58.7 mm radius semi-trunk of the unirrigated olive tree (—) which had an estimated 29 m² of leaf. Also shown is the transpiration predicted using the Penman-Monteith expression of Equation 1 (· · ·). The prediction (---) using a reference conductance (g^*) one third the irrigated value is also shown. An irrigation of 870 L occurred on the morning of DOY 255 (∇).

The lag in responding to rewatering, akin to the tardy recovery found by Fernández et al. (1993), contrasts with the rapid recuperation within one day for the other tree. As already noted, the large hydraulic resistance to flow within the vascular system of olive trees, plus the elasticity of the leaf cell walls, assists in explaining the slow recovery. An inability to refill cavitated xylem vessels in the semi-trunk might also be involved. Certainly our sapflow observations in the surface root indicated this. The flow in the root now rose to supply just 3% of the semi-trunk's water, still well less than the relative ratio of cross-sectional areas. No reestablishment of sapflow in the root's outer annuli was noted, as the cavitated vessels still remained empty.

Despite the rewatering with some 870 L, the tree never did fully recover. Its rate of transpiration climbed only to 1.12 mm d⁻¹, on a leaf area basis. This ties in with the observation that the leaf water potentials remained different between the two trees. That the

previously stressed tree did not fully recover following this single basin flooding appears related to the inability to refill cavitated xylem vessels, as we observed in the surface root, and to a lesser extent in the semi-trunk. In fact after about 12 days, the transpiration rate dropped back to that predicted using $g^* = 3.3 \text{ mm s}^{-1}$, despite there being water held in the soil at potentials greater than -0.5 MPa beyond a depth of 0.5 m (Figure 2: Table 1). Olive is again found to be a miserly user of water.

One final and interesting feature of the sapflow data in Figure 6 is the onset of nocturnal sap ascent in the semi-trunk following the rewatering on DOY 255. Rather than nighttime transpiration, as observed in kiwifruit by Green et al. (1989), this is more likely to be recharge of the woody and leaf tissue that had become dehydrated during the day (Caspari et al. 1993). No nocturnal sap ascent was observed in the irrigated semi-trunk (Figure 5), although it was noted

there in the root, indicating some capacitance recharge in the trunk.

Conclusions

Sap flow measurements in the trunk and root of olive trees have revealed details of the sclerophyllous nature of the hydraulic functioning of these trees. Soon after rewatering, the regularly watered olive rapidly increased its transpiration, however after just three days it again began to limit its water usage, possibly in response to signalling from other roots that had remained dry during the irrigation. The unirrigated olive which had remained without additional water for over 3 months, was found to be extracting water from depth, and transpiring at half the rate, on a leaf area basis, of the well-watered tree. When water was re-supplied to this severely stressed tree, it did not respond immediately. Neither did it return to the well-watered rate. The cavitated xylem vessels in the surface root, observed prior to the irrigation, we found not to refill after this single wetting. This tree only increased its transpiration by about 40% and this increase lasted for just 12 or so days before transpiration again dropped back to the stressed rate of usage. The leaf water potential observations corroborated this failure to recover fully following a single irrigation. These new data reinforce the view of olive as being a parsimonious and prudent user of soil water.

Acknowledgements

Thanks are due to the CSIC which provided the funds for this experiment, and to Mr A Hoyas and Mr O Blázquez for help with the field measurements.

References

- Baker J M and Allmaras R R 1990 System for automating and multiplexing soil moisture measurements by time-domain reflectometry. *Soil Sci. Soc. Am. J.* 54, 1–6.
- Cabibel B and Do F 1991 Mesures thermiques des flux de sève et comportement hydrique des arbres. II. Evolution dans le temps des flux de sève et comportement hydrique des arbres en présence ou non d'une irrigation localisée. *Agronomie* 11, 757–766.
- Caspari H W, Green S R and Edwards W R N 1993 Transpiration of well-watered and water-stressed Asian pear trees as determined by lysimetry, heat-pulse and estimated by a Penman-Monteith model. *Agric. For. Meteorol.* 67, 13–27.
- Clothier B E and Green S R 1994 Root zone processes and the efficient use of irrigation water. *Agric. Water Manage.* 25, 1–12.
- Cohen Y, Fuchs M and Cohen S 1983 Resistance to water uptake in a mature citrus tree. *J. Exp. Bot.* 34, 451–460.
- Eris A and Barut E 1995 Olive growing in Turkey. *Chron. Hortic.* 35, 14–16.
- Fernández J E, Moreno F, Cabrera F, Arrue J L and Martín-Aranda J 1991 Drip irrigation, soil characteristics and the root distribution and root activity of olive trees. *Plant and Soil* 133, 239–251.
- Fernández J E, Moreno F and Martín-Aranda J 1993 Water status of olive trees under dry farming and drip irrigation. *Acta Hortic.* 335, 157–164.
- Goldhamer D A, Dunai J and Ferguson L 1993 Water use requirements of manzanillo olives and responses to sustained deficit irrigation. *Acta Hortic.* 335, 365–371.
- Granier A 1985 Une nouvelle méthode pour la mesure des flux de sève dans le tronc des arbres. *Ann. Sci. For.* 42, 193–200.
- Green S R 1993 Radiation balance, transpiration and photosynthesis of an isolated tree. *Agric. For. Meteorol.* 64, 201–221.
- Green S R and Clothier B E 1988 Water use of kiwifruit vines and apple trees by the heat-pulse technique. *J. Exp. Bot.* 39, 115–123.
- Green S R and Clothier B E 1991 Heat pulse measurement of sap flow in trees and vines. *In Proc. Sym. Sap Flow Measure.. Am. Soc. Agron., Oct 27th 1991, Denver, USA.* pp 11–12. Am. Soc. Agron, Madison, WI, USA.
- Green S R, McNaughton K G and Clothier B E 1989 Observations of night-time water use in kiwifruit vines and apple trees. *Agric. For. Meteorol.* 48, 251–261.
- Green S R and Clothier B E 1995 Root water uptake by kiwifruit vines following partial wetting of the root zone. *Plant and Soil* 173, 317–328.
- Green S R, McNaughton K G, Greer D H and McLeod D J 1995 Measurement of the increased PAR and net all-wave radiation absorption by an apple tree caused by applying a reflective ground covering. *Agric. For. Meteorol.* 76, 163–183.
- Hinckley T M, Brooks J R, Čermák J, Ceulemans R, Kučera J, Meimzer F C and Roberts D A 1994 Water flux in a hybrid poplar stand. *Tree Physiol.* 14, 1005–1018.
- Landsberg J J and Powell D B B 1973 Surface exchange characteristics of leaves subject to mutual interference. *Agric. Meteorol.* 13, 169–184.
- Larsen F E, Higgins S S and Al Wir A 1989 Diurnal water relations of apple, apricot, grape, olive and peach in an arid environment (Jordan). *Sci. Hortic.* 39, 211–222.
- Lo Gullo M A and Salleo S 1988 Different strategies of drought resistance in three Mediterranean sclerophyllous trees growing in the same environmental conditions. *New Phytol.* 108, 267–276.
- McAneney K J and M J Judd 1983 Observations of kiwifruit (*Actinidia chinensis* Planch. root exploration, root pressure, hydraulic conductivity, and water uptake. *N.Z. J. Agric. Res.* 26, 507–510.
- Michelakis N and Vougioucalou E 1988 Water used, root and top growth of olive trees for different methods of irrigation and levels of soil water potential. *Olea* 19, 17–31.
- Moreno F, Vachaud G and Martín J 1983 Caracterización hidrodinámica de un suelo de olivar. *Fundamento teórico y métodos experimentales.* *Anal. Edaf. Agrobiol.* 42, 695–721.
- Moreno F, Vachaud G, Martín-Aranda J, Vauclin M and Fernández J E 1988 Balance hídrico de un olivar con riego gota a gota. *Resultados de cuatro años de experiencias.* *Agronomie* 8, 521–537.
- Natali S, Xiloyannis C and Angelini P 1985 Water consumptive use of olive trees (*Olea europaea*) and effect of water stress on leaf water potential and diffusive resistance. *Acta Hortic.* 171, 341–351.

- Sakuratani T 1981 A heat balance method for measuring water flux in the stem of intact plants. *J. Agric. Meteorol.* 37, 9–17.
- Salleo S, Lo Gullo M A and Oliveri F 1985 Hydraulic parameters measured in 1-year-old twigs of some Mediterranean species with diffuse-porous wood: Changes in hydraulic conductivity and their possible functional significance. *J. Exp. Bot.* 36, 1–11.
- Sinclair T R, Murphy C E and Knoerr K R 1976 Development and evaluation of simplified models for simulating canopy photosynthesis and transpiration. *J. Appl. Ecol.* 13, 813–829.
- Steinberg S L, McFarland M J and Worthington J W 1990 Comparison of trunk and branch sap flow with canopy transpiration in pecan. *J. Exp. Bot.* 41, 653–659.
- Swanson R H and Whitfield D W A 1981 A numeric analysis of heat-pulse velocity theory and practice. *J. Exp. Bot.* 32, 221–239.
- Tardieu F and Davies W J 1993 Integration of hydraulic and chemical signalling in the control of stomatal conductance and water status of droughted plants. *Plant Cell Environ.* 16, 341–349.
- Thompson R G, Tyree M T, Lo Gullo M A and Salleo S 1983 The water relations of young olive trees in a mediterranean winter: Measurements of evaporation from leaves and water conduction in wood. *Ann Bot.* 52, 399–406.
- Thorpe M R, Warrit B and Landsberg J J 1980 Responses of apple leaf stomata: A model for single leaves and a whole tree. *Plant Cell Environ.* 3, 23–27.

Section editor: H Lambers