



Heat-pulse measurements of sap flow in olives for automating irrigation: tests, root flow and diagnostics of water stress

J.E. Fernández^a, M.J. Palomo^a, A. Díaz-Espejo^a, B.E. Clothier^b,
S.R. Green^b, I.F. Girón^a, F. Moreno^a

^a*Instituto de Recursos Naturales y Agrobiología, CSIC, Apartado 1052, 41080 Sevilla, Spain*

^b*Environment Group, HortResearch, PB 11-030, Palmerston North 5301, New Zealand*

Abstract

The compensation heat-pulse method for measuring sap flow is tested here in olive trees (*Olea europaea* L.). We describe a rigorous three-way examination of the robustness of the technique for this species, and examine the potential of the technique for an automatic control of the irrigation system. Two tests were carried out using heat-pulse gear inserted into the stem of 12-year-old ‘Manzanilla’ olive trees. One test used forced-flow through a stem section, and the other involved measured water uptake by an excised tree. The measured sap flow in these two tests was in agreement with calculations from heat-pulse velocities when using a standard ‘wound correction’ to account for the presence of the probes and the disruption to the sap flow. Thus, this technique for monitoring transpiration can, we feel, be used with confidence in olives.

The third experiment was carried out in the field, where we analysed sap flow data from two 29-year-old olive trees — one tree was under regular drip irrigation and the other was from dry-farming conditions. We use measurements of sap flow in the trunk to examine the hydraulic functioning of the tree, and to explore some diagnostics of water stress. Our heat-pulse measurements in the irrigated olive tree exhibited a profile of sap flow that was weighted towards the outer xylem of the tree trunk while the water-stressed trees in the field showed a profile of sap flow weighted towards the centre of the trunk. The loss of hydraulic functioning in the outermost section of the vascular system, as a result of water stress, we consider to be due both to stomatal control and to embolisms in the xylem vessels.

The fourth experiment was also carried out in the field, in which sap flow measurements were made at three locations in the trunk as well as in two roots of another 29-year-old olive tree. The soil explored by each root, on opposite sides of the trunk, was differentially wetted by separate irrigation of each side. Our data showed that the surface roots were able to absorb water

immediately after wetting, despite a reasonably prolonged period of moderate drought. Root activity quickly shifted to the regions where the soil had been wetted. A root in dry soil exhibited no flow at night, whereas sap flows of about 0.02 l h^{-1} were measured around midnight in the root drawing water from the wetter soil. Our observations suggest that the hydraulic behaviour of the trunk and surface roots might be used as a diagnostic of the onset, or severity, of water stress. Here there is not the imperative to replicate, for the prime goal is not transpiration estimation. Rather interpretation of the diurnal dynamics is used to infer the onset, or severity of water stress.

The compensation heat-pulse seems a suitable technique for automatically controlling the irrigation system of olives, and probably other trees, based either on the estimation of the short-time dynamics of transpiration, or on changes in the hydraulic behaviour of the trees.

1. Introduction

Irrigation is seen as important for the future development of olives in the water-short Mediterranean region (Fernández and Moreno, 1999). It is imperative for sustainable irrigation of olives in the Mediterranean and elsewhere, that water be used judiciously and without wastage. To achieve this, the water use of the olive tree needs to be known, in real time if possible. Further advantage will accrue if a technique can be developed to diagnose the onset and severity of water stress in the olive tree, for such a technique could be used to schedule the timing of irrigation based on the plants' actual need for water.

A variety of methods are available to measure, or estimate, plant water use in the field. Heat-pulse (Huber, 1932; Cohen et al., 1981) and heat-balance measurements (Vieweg and Ziegler, 1960; Sakuratani, 1981) of sap flow can be used to monitor tree transpiration, and explore the short-term water-use dynamics of trees (Green et al., 1989; Moreno et al., 1996). The relative merits of these techniques have been the subject of recent reviews (Swanson, 1994; Braun, 1997; Smith and Allen, 1996). Research on the development of an automatic control unit for irrigation systems, based on the heat balance system for stem segments, has already been conducted by Nadezhdina and Cermak (1997). As we move beyond of the use of these techniques in research, towards routine monitoring and smart irrigation controllers, we now consider it prudent to test rigorously the applicability of the compensation heat-pulse technique in the xerophytic olive.

In the case of heat-pulse, which is necessarily an invasive procedure, there is a disruption of xylem tissue associated with the placement of the sensors. Consequently, the measured heat-pulse velocity must be corrected for the effects of probe placement and so-called wounding. Swanson and Whitfield (1981) were the first to publish a set of correction factors derived from a numerical solution to the equation for heat and water flow in a porous medium (Marshall, 1958). Green and Clothier (1988) subsequently investigated these correction factors for two different tree species. Apple trees behaved as expected, while kiwifruit did not. Green and Clothier (1988) concluded that the large xylem vessels and interstitial woody matrix affects the thermal homogeneity of kiwifruit. They also derived new correction factors specific to their Teflon probes and the wider probe spacing used in kiwifruit, and they concluded that it would be prudent to carry out a

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Keywords: Olive; Water stress; Roots; Heat pulse; Hydraulic behaviour; Xylem; Embolisms

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test of the heat-pulse technique when embarking on a detailed study in trees with a greatly different xylem structure.

Thus, the first objective of this study was to evaluate the heat-pulse technique for its applicability with the xerophytic olive tree whose xylem vessels are extremely narrow, with a diameter rarely greater than 50 μm (Fernández and Moreno, 1999). For this species we expected the standard wound corrections of Swanson and Whitfield (1981) would be appropriate, but an assessment was carried out using mature olive trees in order to check the accuracy of the heat-pulse technique. Two tests were performed, using a stem section through which water was forced at a known rate, and using an excised olive tree placed in a bucket of water.

As the heat-pulse technique moves beyond a research tool (Moreno et al., 1996; Dichio et al., 1998), towards being an instrument that might have potential in a smart irrigation-control system (Fernández et al., 1998), it is necessary to understand the limitations of the technique, and to explore its full potential. The second objective of this study, therefore, was to assess the natural spatial-variability of sap flow in the tree trunk since this will largely determine the appropriate number of probes needed for a reliable measure of tree transpiration. We will then introduce a gradient in soil water availability, by partially irrigating the tree's root zone, to see if such an irrigation changes the pattern of sap flow within the tree trunk. We anticipate that changes in sap flow in the xylem of the outer annulus will be related to changes in soil-water availability in the root zone. Next, we examine flow in surface roots that draw their water from zones of differing water content. The impact of irrigation on sap flow in these roots, and the ability of the plant to selectively remove water from the drip zone is discussed. Finally, we scrutinise the diurnal traces of flow in these roots to see whether any diagnostics of the onset, or severity, of water stress can be derived. Earlier, Moreno et al. (1996) and Fernández et al. (1996) used the heat-pulse method to monitor the attempt by a severely droughted olive tree to recover from water stress. In that case, the tree was unable to rehydrate the embolised vascular system of its surface roots with a single wetting. Rather it maintained its reliance on the restricted supply of water it could obtain from its deep roots. Here we are interested in understanding hydraulic behaviour under the less-severe stress conditions that might prevail during normal irrigation, or even regulated deficit irrigation. Furthermore, we seek plant-based measures that might be used to schedule irrigation so that a certain level, or absence, of water stress can be maintained.

2. Materials and methods

2.1. Experimental site and instrumentation

Experiments were carried out on La Hampa, the experimental farm of the Instituto de Recursos Naturales y Agrobiología, at Coria del Río near Seville in Spain (latitude $37^{\circ}17'N$, longitude $6^{\circ}3'W$, altitude 30 m). The soil at the La Hampa station is a sandy loam of about 2 m depth, and has a saturated volumetric water content of $0.33 \text{ m}^3 \text{ m}^{-3}$, and a water content of $0.10 \text{ m}^3 \text{ m}^{-3}$ at a soil matrix potential of -1.5 MPa . Weather variables were continuously measured using an automatic weather station located some

40 m from the experimental trees. Average values for global solar radiation, net radiation, photosynthetically active radiation, wind speed, rainfall, and the temperature and relative humidity of the air, were recorded at 30 min intervals.

In May 1997, both an excision experiment and a forced-flow perfusion experiment were carried out using stem sections from an olive tree (*Olea europaea* L., 'Manzanilla'). These experiments were similar to those of Green and Clothier (1988), except that for our perfusion experiment, we had to use much higher pressures to force water through the olive stems because of the extremely low hydraulic conductivity of the olive wood. Throughout the dry season of 1997, we also measured sap flow in both an irrigated and a dryland tree in the field, as well as in a tree with irrigation applied to just half of the root zone. Sap flow measurements were also carried out in the trunk of both trees during the dry season of 1998.

The heat-pulse instrumentation consisted of two temperature probes inserted 15 mm downstream and 5 mm upstream from a linear heater probe. The temperature probes had a diameter of 1.8 mm, and comprised four copper–constantan thermocouples to measure the sap velocity at four radial depths. For the perfusion and the excision experiments the thermocouple sensors were at depths of 10, 20, 30 and 40 mm below the cambium and for the field measurements these depths were 5, 12, 22 and 35 mm. For the experiments we used a pulse length of 2 s. The probes, and the associated electronics and software to run the system and calculate sap flows were made by the Environment and Risk Management Group of the HortResearch in Palmerston North, New Zealand. The whole system was controlled by a Campbell CR10X data logger (Campbell Scientific Inc., USA), and powered by a 12 V battery.

2.2. Perfusion experiment

A special high-pressure device was built to force water through stem sections from the olive tree (Fig. 1). For this perfusion experiment we used a 0.3 m long stem section obtained from a tree of similar age and character to the tree used in the excision experiment. After removing the bark, the stem section was sealed into a thick-walled aluminium box using epoxy resin for strength, and silicon rubber to ensure an airtight seal (Fig. 1). This process took about 2 days for the glue and sealant to dry. Two sets of heat-pulse probes were then installed in the stem section some 150 mm away from where the stem exited the pressurised box.

A 0.05 mol l⁻¹ KCl solution, made with distilled water containing the red-dye safranin that had been filtered through a 0.45 µm membrane, was used as the injection fluid. The chamber was pressurised up to 0.4 MPa, and the solution forced through the stem at rates of between 0.5 and 14 l h⁻¹. Flow through the stem section was collected at the distal end that was vented to the atmosphere. Once a steady flow rate was achieved, the heat-pulse velocity was monitored using two sets of probes on opposite sides of the stem. The diameter of the stem section where the probes were located was about 80 mm, excluding the bark. After the device was dismantled, the stem section was cut transversally and the cross sectional area of flow, \bar{A} (mm²), was inferred by planimetry of the safranin-stained area. For the test described here, $\bar{A} = 5530$ mm², so that all of the sapwood was conducting the injection fluid.

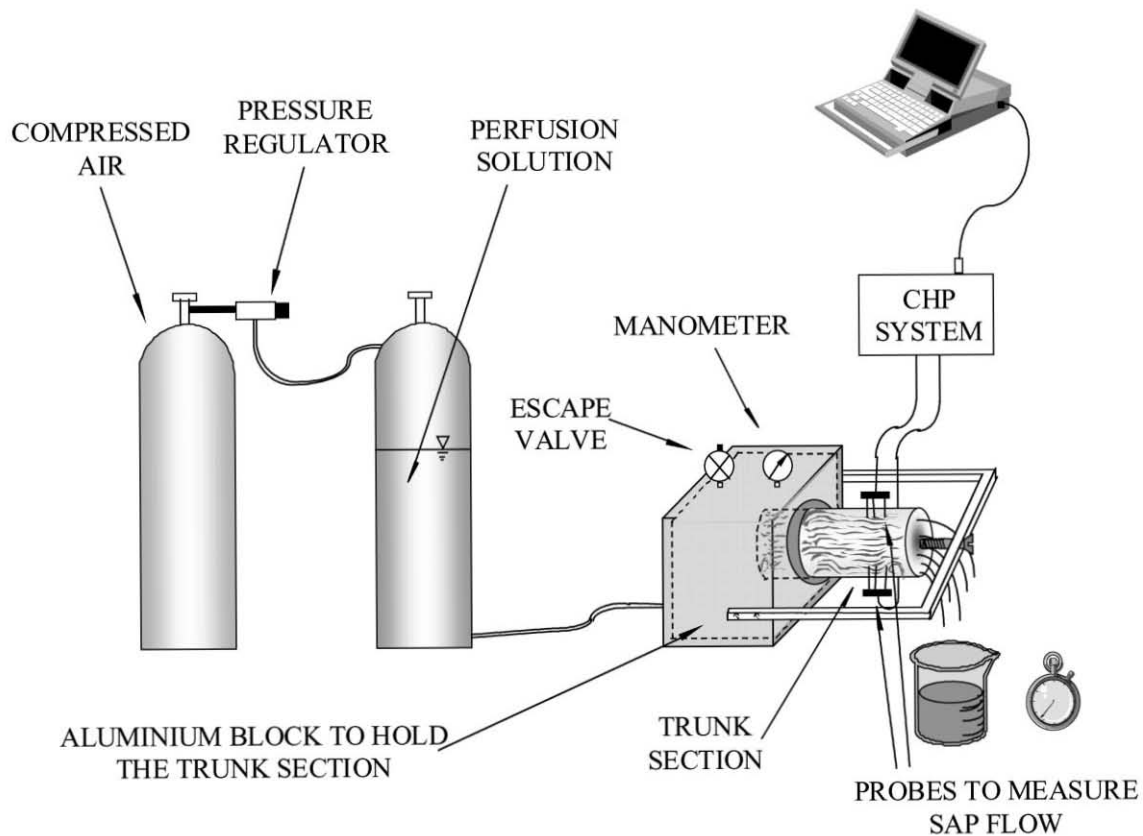


Fig. 1. Components of the high-pressure device used to force a known flux of solution through a trunk section of olive. Also shown are heat-pulse probes for measuring the sap flow. The flow rate can be adjusted by varying the pressure of air with the pressure regulator attached to the bottle of compressed air.

Table 1

Physical and physiological characteristics of the two trees whose sap flow profiles are shown in Fig. 5^a

	Irrigated tree (treatment I)	Dryland tree (treatment D)
Trunk radius at height of 0.6 m (mm)	94	92
Days since soil last wetted	1	68
Average water content near tree (0–1 m), θ ($\text{m}^3 \text{m}^{-3}$)	0.27	0.14
Tree height (m)	4.6	4.4
Tree leaf area (m^2)	61.2	64.4
Midday leaf water potential (MPa)		
22 July	–1.73	–2.18
16 September	–1.41	–2.16
Daily evaporation calculated using FAO–Penman (mm)	6.1	7.7
Daily transpiration from sap flow measurements (l)	74.0	38.8

^a The information for the irrigated tree relate to 6 August, whereas for the dryland tree they are for 15 August.

2.3. Excision experiment

A 12-year-old tree of height about 4 m was selected for the excision experiment. This tree, was slightly smaller, and had somewhat fewer leaves ($\approx 2/3$) than the orchard trees used in later experiments (Table 1). The excision experiment commenced before dawn, when the stem was cut at ground level. Immediately, the butt was placed in a container of clean water, while the tree was kept in an upright position by a metal support specially built for that purpose. The trunk was then recut under water some 150 mm from the butt to remove any air emboli that might have been created during the first cutting. While still submerged, the butt was then placed in another container that was filled with distilled water containing the red-dye safranin. Shortly after dawn, sets of heat-pulse probes were installed into the north and south side of the tree trunk. Sap flow was subsequently monitored every 30 min. The trunk diameter where the probes were located was estimated to be 108 mm, excluding bark. Water consumption by the tree was measured by regularly refilling the container back to a constant water level. The water surface in the container was covered with vegetable oil to minimise evaporative water loss. The entire system was maintained operational for 3 days.

2.4. Data analysis

Signals from the heat-pulse equipment were analysed using the standard compensation technique (Swanson and Whitfield, 1981; Green and Clothier, 1988) so only the salient details are repeated here. The temperature rise following the release of a pulse of heat is measured at distances X_d (15 mm) downstream and X_u (–5 mm) upstream from the heater needle. The heat-pulse velocity, V (mm s^{-1}), is then calculated as

$$V = \frac{X_d + X_u}{2t_z} \quad (1)$$

where t_z (s) is the time delay for the temperatures to become equal at the points X_d and X_u . The heat-pulse velocity V must be corrected to account for the probe-induced effects of wounding and the thermal heterogeneity introduced by finite probes of different thermal properties. We follow Swanson and Whitfield (1981), wherein a corrected heat-pulse velocity V_c (mm s^{-1}) is derived from the measured heat-pulse velocity V using

$$V_c = a + bV + cV^2 + dV^3 \quad (2)$$

where a , b , c , and d are the correction factors that depend on the probe size, spacing and material composition (Swanson and Whitfield, 1981). Given our intent to use heat-pulse more extensively in olives, we deemed it prudent to check that the standard coefficients are indeed appropriate. From the corrected heat pulse velocity, V_c , it is possible to infer the sap flux density, J (mm s^{-1}), using

$$J = (0.505F_M + F_L)V_c \quad (3)$$

where F_M and F_L are the volume fractions of wood and water, respectively (Edwards and Warrick, 1984). We determined the values of F_M and F_L for each experimental tree. In the experiments described in the next sections, F_M and F_L were determined every 2 weeks. Finally, the volumetric sap flux, Q (l h^{-1}), can be determined by integrating the measured sap velocity profile, $J(r)$, over the area of conducting sapwood

$$Q = \int_H^R 2\pi r J(r) dr \quad (4)$$

where R is the stem radius (m), H the radius of the heartwood (m), and r the radial distance from the centre (m). In practice, this integral must be approximated using a least-squares regression fit to the measured velocity profile. The software allows for three different integration routines as described below.

Method (1): the volumetric flux Q is calculated by integrating the fitted profile of $\langle J(r) \rangle$

$$Q = 2\pi \int_H^R r \langle J(r) \rangle dr \quad (5)$$

where the operator $\langle \rangle$ is used to represent the regression fit.

Method (2): Q is calculated by integrating the fitted profile of sap flux density, $\langle rJ(r) \rangle$

$$Q = 2\pi \int_H^R \langle rJ(r) \rangle dr \quad (6)$$

Method (3): Q is calculated as the weighted sum of the product of sap velocity, V_i , and the associated sapwood area, A_i across the n sensors as follows:

$$Q = \sum_{i=1}^n A_i V_i \quad (7)$$

This third integration scheme was considered by Hatton et al. (1990) to be the best method for analysing velocity profiles exhibiting strong curvature due to more rapid flow in the outer annuli. Because of water stress, some of our profiles exhibited unusual shapes, and so, in addition to testing the validity of the correction coefficients that turn V

into V_c (Eq. (2)), we also assessed the need to consider the influence of the integration scheme on the estimates of Q via Eqs. (5)–(7).

2.5. Impact of Irrigation amount on tree water use

Two separate field experiments were set up at the La Hampa site. In the first field experiment, sap flow measurements were carried out in a 0.5 ha grove of 29-year-old ‘Manzanilla’ olive trees planted at a spacing of 7 m \times 5 m. Two 4.5 m tall trees were selected from the middle of the olive grove. Each tree had a single trunk with two main branches bifurcating at about 1–1.5 m from ground level. On 16 July 1997, we inserted three sets of heat-pulse probes into the trunks of both trees, and subsequently we monitored sap flow every 30 min. The entire system was kept running until the beginning of October.

Different irrigation regimes were applied to the two trees. One tree was growing under dry-farming conditions with rainfall as the only source of water. We will refer to this tree as being from treatment D. The other tree received a daily irrigation to replace the crop-water demand as calculated using the FAO–Penman equation (Doorenbos and Pruitt, 1977). Mantovani et al. (1991) have shown this calculation to be the most appropriate for this area of Spain. Irrigation to this tree was supplied by a single drip line along the row, using five (3 l h⁻¹) emitters per tree placed on the soil surface at a spacing of about 1 m apart. We will refer to this irrigated tree as being from treatment I.

Routine measurements of soil water content (θ , m³ m⁻³), were made around each of the instrumented trees, at intervals of 10–15 days apart. The depthwise profile of the soil’s volumetric water content from 0.2 down to 1.5 m was measured every 0.1 m using a neutron probe (Troxler 3300, NC, USA) in access tubes installed at a distance of 0.5, 1.5 and 2.5 m away from the trunk. For the top 0.2 m layer of the soil, θ was measured gravimetrically.

Prior to the sap flow measurements, there had been just 101 mm of rainfall between the end of March until 6 June, and negligible rainfall was recorded during the rest of the experiment. Some additional details are given in Table 1. As a result, the soil around Tree D was just 0.04 m³ m⁻³ off the permanent wilting point (–1.5 MPa) whereas the soil around Tree I remained quite close to its saturated value (Table 1). Although measurements of leaf water potential, ψ_L , were not made on the 3 days for which we present heat-pulse data (6 and 15 August), intensive measurements of ψ_L were made on other days which bracketed these (22 July and 16 September; Table 1).

Sap flow measurements were also carried out in the same D and I trees during the irrigation season of 1998. The water supply treatments were the same as in 1997. New sets of heat-pulse probes were inserted in the trunk of both trees on 14 and 15 July. The probes recorded sap velocities every 30 min, until the end of August.

2.6. Partial irrigation and root-sap flow

In the second field experiment, a single representative tree was selected at the beginning of May 1997, from another part of the orchard where the trees were of a similar size but planted at a 7 m \times 7 m spacing. Until the middle of summer this tree had been

irrigated once per week by supplying water inside a small earthen-dyke of 2.5 m radius around the tree. Then, on 2 June the pond was divided by a small transverse earthen-dyke along the northwest–southeast diagonal. This permitted separate semi-irrigations to the ‘north’ and ‘south’ side of the tree. On 14 October, day-of-year (DOY) 287, the northern pond was irrigated with 70 mm of water. The irrigation began at 10.25 GMT, and lasted for 1 h. Three days later (DOY 290), the southern pond was irrigated with 155 mm of water. Irrigation began at 10.22 GMT and lasted for 31 min.

Two small soil pits were excavated on the north and south side of the tree trunk, to a depth of about 0.3 m, and a significant lateral root was partially exposed in each pit. A single set of heat pulse probes was installed in each root, and a distance of about 0.4 m from the trunk, so we could monitor root-sap flow. The root diameters at the implantation sites were 30.4 mm for the southern root and 29.6 mm for the northern root. The excavated soil was gently repacked into the pit after probe installation.

Heat-pulse probes were also installed at three equal spacings around the azimuth of the tree trunk, some 1.25 m above the ground where the trunk diameter, excluding the bark, was about 180 mm. One probe set was installed in the north side of the trunk, the so-called N probe, another at west–southwest, our W probe, and the third was at east–southeast side which we termed our E probe. Thus, the N and E probes should tend to be influenced by water uptake derived from the northern dyke, whereas the W probe set would be expected to be more influenced by water uptake from the southern dyke (Fig. 2). Between DOY 284 and DOY 297, sap flow was monitored in the trunk and in the two roots, once every half-hour. Our intention here was to examine spatial variability in sap flow around the trunk, as induced by azimuthal variation in soil water availability. We also wanted to assess the consequence of this variability on the determination of the transpiration of the whole tree as calculated from the sap flow measurements.

The volumetric water content of the soil from 0.3 to 1.6 m depth was measured every 0.1 m using the neutron probe. An access tube was installed on 2 June in each of the dyked areas about 1.7 m from the trunk. At the surface, θ was measured by time-domain-reflectometry (TDR) using a Tektronix cable tester (Model 1502C, Beaverton, OR, USA). Two TDR waveguides of length 150 and 300 mm were installed close to each access tube. We measured θ on the days before and after the irrigation of DOY 287, and thereafter θ was measured at 3–4-day intervals.

2.7. Penman–Monteith model of tree transpiration

The weather data, together with certain plant physiological measurements, were used in 1997 to calculate transpiration rates of the tree of the second field experiment using the Penman–Monteith equation (Green, 1993; Moreno et al., 1996). However, as we had no direct measures of the canopy leaf area, the Penman–Monteith calculations are expressed solely on a per unit leaf area basis ($l\ h^{-1}\ m^{-2}$). We will refer to these calculations as the normalised Penman–Monteith transpiration (E_p^*). The calculation procedure directly followed that carried out by Moreno et al. (1996) and represents the three-way sum of transpiration due to net radiation falling directly on lit leaves, plus water loss due to a vapour pressure deficit in the air surrounding both the sunlit and shaded leaves. The normalised values of E_p^* provided us with a datum against which our observations of sap

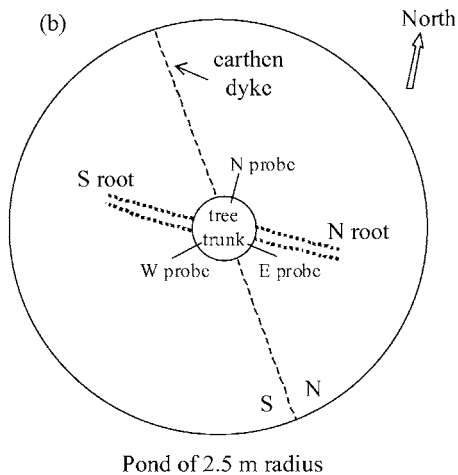
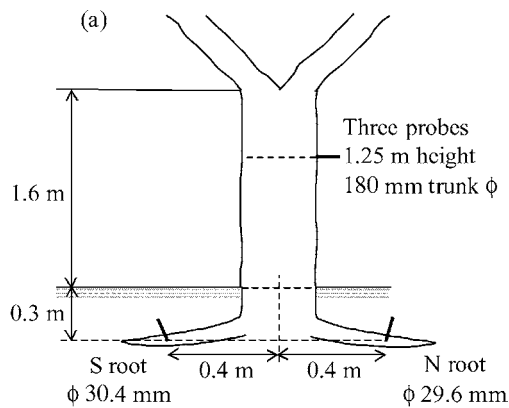


Fig. 2. Probe location in the tree of the field experiment 2 (a) and orientation of both the probes in the trunk and the instrumented roots, as well as of the dyke used for differential irrigation of each side of the tree (b).

flow can be referenced. This datum also allows us to interpret changes either in relation to a plant-induced change in behaviour, or a response due to change in the environment of the soil.

3. Results

3.1. Forced flow through a stem section

By altering the pressure in the chamber of the aluminium box (Fig. 1), we were able to mimic the range of sap flows found in the field. Heat-pulse and flow-rate measurements

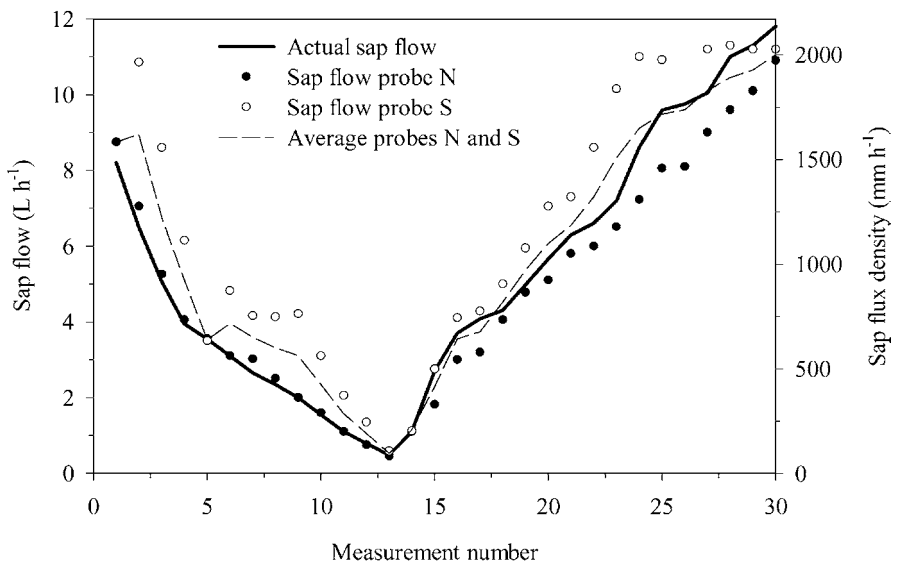


Fig. 3. A comparison of actual sap flow to that measured by heat-pulse during the perfusion experiment. The average of both probes is shown, as well as the flow rate through the trunk as recorded by the measured efflux. The measurements were 10–15 min apart, using a pressure gradient which first varied from 0.22 down to 0.02 MPa, and then returned back to 0.31 MPa. The sap flows were calculated from the measured heat-pulse velocities using the analysis procedure of Green and Clothier (1988) and a wound width of 2.0 mm.

were made at the same time, at approximately 15–20 min intervals. Fig. 3 shows first a sequence of flow decreasing from about 9 down to 0.5 l h^{-1} . This drop in sap flow was achieved by reducing the chamber pressure from 0.22 down to 0.02 MPa. When the pressure was incrementally raised back up 0.31 MPa, the corresponding flow rate climbed back to around 11 l h^{-1} . On the right-hand side of Fig. 3, we present for comparative purposes the average sap flux density (mm h^{-1}) simply calculated from the left-hand axis values of Q (l h^{-1}) divided by the stem cross-sectional area, \bar{A} (m^2). The values of sap flow, Q , for the two probes in Fig. 3, were calculated using a wound width of 2.0 mm in the analysis procedure of Green and Clothier (1988), following Swanson's model (1983). In calculating Q , the first integration method (Eq. (5)) gave the best results, although there was little difference between the three methods. These test results obtained from a single stem-section under forced flow provide our first evidence that standard heat-pulse procedures will work in the xerophytic olive tree.

3.2. Water uptake by an excised tree

We now examine the results obtained from the excised tree. During the first day of the excision test, the tree consumed water from the reservoir at rates that peaked at around $3\text{--}4 \text{ l h}^{-1}$ (Fig. 4). Such rates are expected for a tree of this size, under these ambient weather conditions. Unfortunately, measured transpiration decreased markedly on the second day, and there was only a negligible amount of water consumption on the third

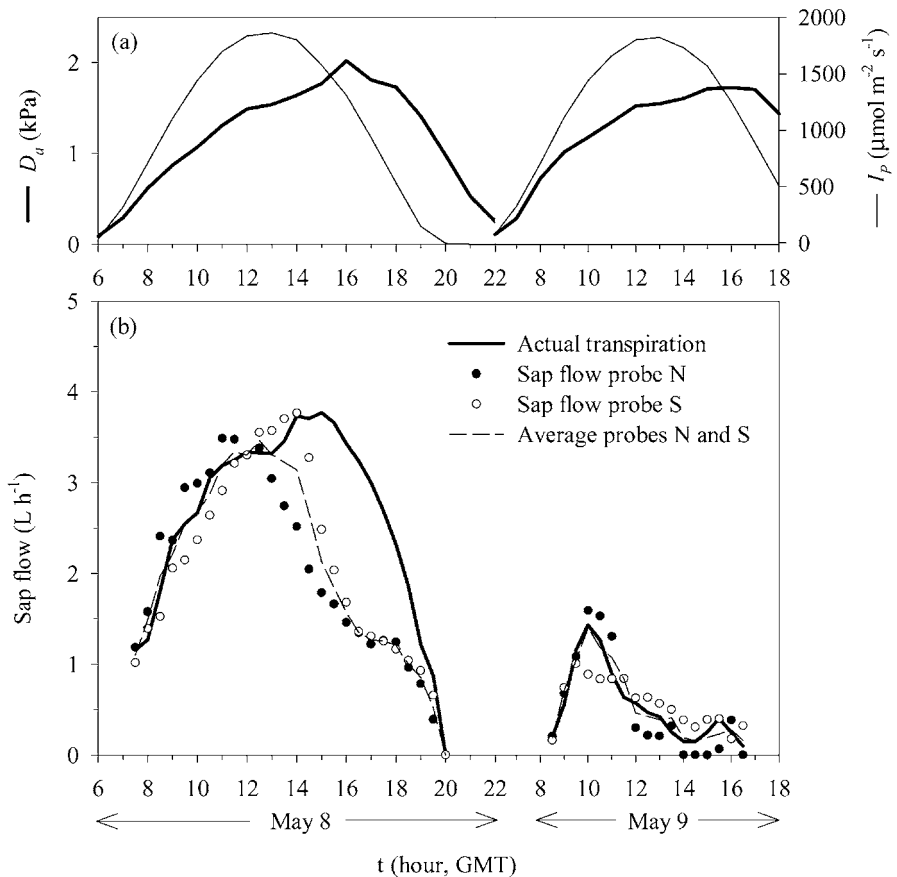


Fig. 4. Weather conditions (a) and the diurnal trace of water uptake by the olive tree over the first 2 days of the excision experiment (b). Also shown are the measured sap flows recorded by two probe sets installed in the trunk, as well as the average from both probe sets. The reasons for the divergence from the measurements are discussed in the text. D_a is the vapour pressure deficit of the air; I_p is the photon flux density.

day, despite similar weather conditions across the 3 days (Fig. 4). This progressive loss of hydraulic functioning of the vascular system was probably due to clogging, by phloem exudates, of the proximal entrance to the xylem vessels at the cut face. A similar loss in hydraulic function after 3–4 days was also observed in the excision experiments of Green and Clothier (1988).

Initially, throughout the morning of the first day, there was good agreement between measured water consumption and the sap flow calculated using the results from the perfusion experiment. Our faith in the heat-pulse system is maintained. But there was a serious and widening mismatch beginning early in the afternoon of 8 May. To explain this divergence we analysed the sap flux density (Eq. (3)) profiles recorded on that day (Fig. 5). In the morning we observed the sap velocity to be greatest in the outer annuli. As the atmospheric demand rose towards midday (Fig. 4(a)), the velocity profile steepened

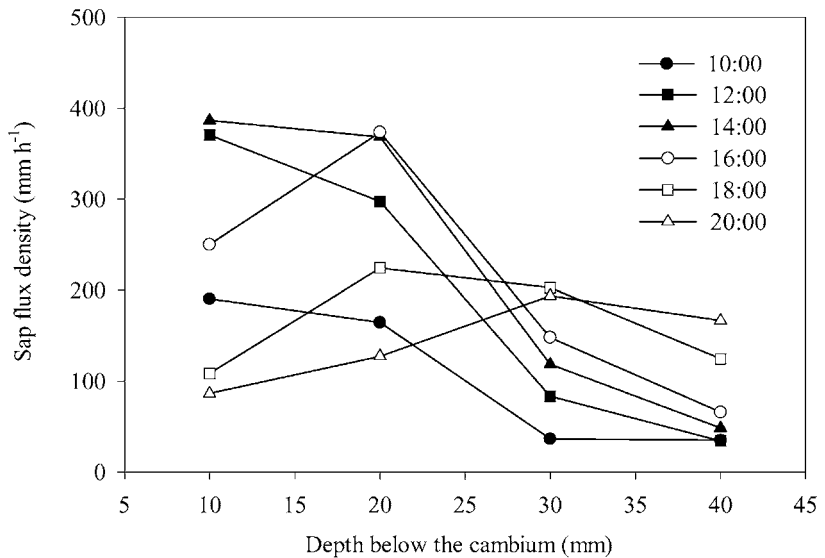


Fig. 5. The within-trunk profile of sap density for the north probe set in the excised tree on 8 May (see Fig. 4). The sapwood had a radius of 59 mm, so that the inner sensor was a distance of 19 mm from the stem centre.

so that the bulk of the flow was in the outermost 20 mm. However by 14.00 h, the profile near the cambium first flattened, then developed a reverse slope with some loss of flow in the outer vessels. The weather conditions and water consumption would suggest that the level of sap flow should have been maintained. An internal change in hydraulic behaviour must have occurred, and this is also borne out by the divergence of the measured consumption from the calculated sap flow (Fig. 4(b)). This downward trend of flow in the outer annulus continued through 18.00 h, until at 20.00 h the greatest velocities were then being recorded in the interior depths. When analysing the cross-section of the trunk at the location of the heat-pulse probes, the area stained by the safranin revealed that in some areas the sapwood reached a maximum depth of 49 mm below the cambium.

We suggest that this loss of sap flow is a result of emboli forming in those vessels of the outer annuli, due to the water stress probably caused by blockages to water supply at the entrance to the xylem vessels in the butt. The changed velocity profiles indicate a greater reliance on flow towards the centre of the trunk, beyond a depth of 30 mm, in a zone where the sensors in our probes have not, it would seem, adequately sampled the flow. Hence the late-afternoon divergence of our sap flow estimates from the measurements of consumption is considered to be due to sampling inadequacies in our current set up. Our probes are designed to detect the flows nearer the cambium, which normally dominate the integral for Q . In addition, any changes in the azimuthal distribution of sap flow around the stem circumference could contribute to the mismatch of results. Despite this loss of water supply to the tree, there was some small amount of transpiration the next day (9 May), that is in reasonable agreement with our sap flow calculations.

The change in the radial pattern of sap flow during the excision experiment may be attributed to water stress brought about by xylem blockages as a result of excision. We now show that a changing radial pattern of flow can also occur naturally when olive trees experience water stress. Indeed we have frequently observed in the field changes in the radial pattern of sap flow following the onset of water stress.

3.3. Field experiment 1

Here we present some typical examples of sap velocity profiles to highlight the critical role of the xylem in the outermost annuli. Fig. 6(a) shows a set of velocity profiles measured on 6 August from a representative tree in the irrigated plot (treatment I). This tree had received regular daily irrigation, and the midday leaf water potential, ψ_L , would have been in the normal range of -1.4 to -1.7 MPa (Table 1). Integration of the velocity profiles on this day, suggests the tree would have transpired about 74.0 l of water. Fig. 6(b) shows similar measurements from a tree in the dryland plot (treatment D) which had not received any water for over two months (Table 1). These results were obtained on 15 August, when the midday ψ_L was lower than -2.1 MPa and the tree was likely to be under a mild water stress. The total transpiration from this tree, on this day, was just 38.8 l, which was much lower than that of the irrigated tree, even though the weather was both warmer and drier than the 6 August (Table 1).

Despite the unusual shape of the sap velocity profile in this water-stressed tree, there was very little change in the calculated sap flow as determined by the three radial integration schemes of Eqs. (5)–(7). Therefore we used Eq. (5) as in the experiments described in the previous sections. For the dryland tree (Fig. 6(b)), the temporal pattern in the sap velocity profile remained similar to that of the well-watered tree for the innermost three sensors only (Fig. 6(a)). Flow in the outer annulus always remained low. This loss of flow in the most recent and largest xylem vessels is, we feel, due to a breakdown in the hydraulic functioning of the vascular system brought about by prolonged water-stress as a result of a shortage in available soil–water. It would seem that the major conducting vessels have embolised to the extent that there is neither continuity, nor flow, through the outer annulus of sapwood.

On the other hand, stomatal control in the younger leaves (Fernández et al., 1997a,b) linked to the outer xylem vessels may also have played a role in reducing the sap flow in that area of the xylem. Since this annulus comprises a significant part of the tree's conducting area ($\approx 20\%$), the olive's water use is curtailed, and as a consequence the midday ψ_L has dropped to more than 0.5 MPa below that of its well-watered neighbour (Table 1). The sap velocity profile here is reminiscent of that which became evident in the excised tree after 14.00 h (Fig. 5). Furthermore, we have observed elsewhere this same phenomenon in a single probe set due to the onset of water stress. Variability aside, it would almost seem by comparison of Fig. 6(a) and (b), there has been some compensation by the innermost xylem vessels to partly offset the lack of flow in the outermost vessels.

Fig. 7 shows the relationships between the daily transpiration values (E_p), of both the D and I trees, and the potential evapotranspiration (ET_o) calculated using the FAO–Penman equation and the meteorological data recorded by the weather station of the farm.

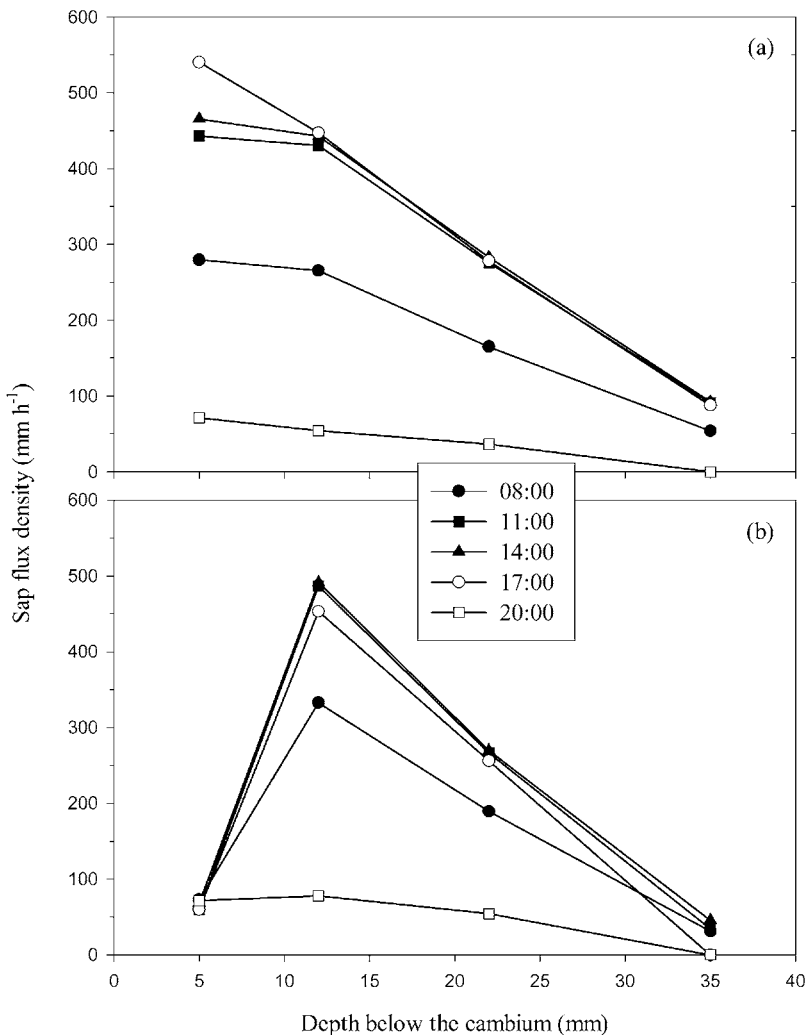


Fig. 6. The diurnal change in the radial pattern of sap flow from probes in (a) a well-watered olive tree (treatment I; see text for details) at La Hampa on 6 August 1997; and (b) a water-stressed olive tree (treatment D; see text for details) at La Hampa on 15 August 1997. Both figures shows the sap flows measured with one of the three sets of probes installed in the trunk of each tree. The others sets of probes gave similar results.

A similar agreement ($r^2 = 0.73$) was obtained for the I and the D trees. As expected, lower values of E_p were recorded in the D tree than in the I tree, for the same ET_o value. In fact, the maximum value of E_p recorded in the D tree was 55 l per day, whereas in the I tree it amounted to more than 70 l per day. The atmospheric demand was greater in 1998 than in 1997, and so was E_p . In the D tree, greater values of E_p were recorded in 1998 than in 1997, for ET_o values of about 4–8 mm per day. This could be due to a greater leaf area in the second experimental year.

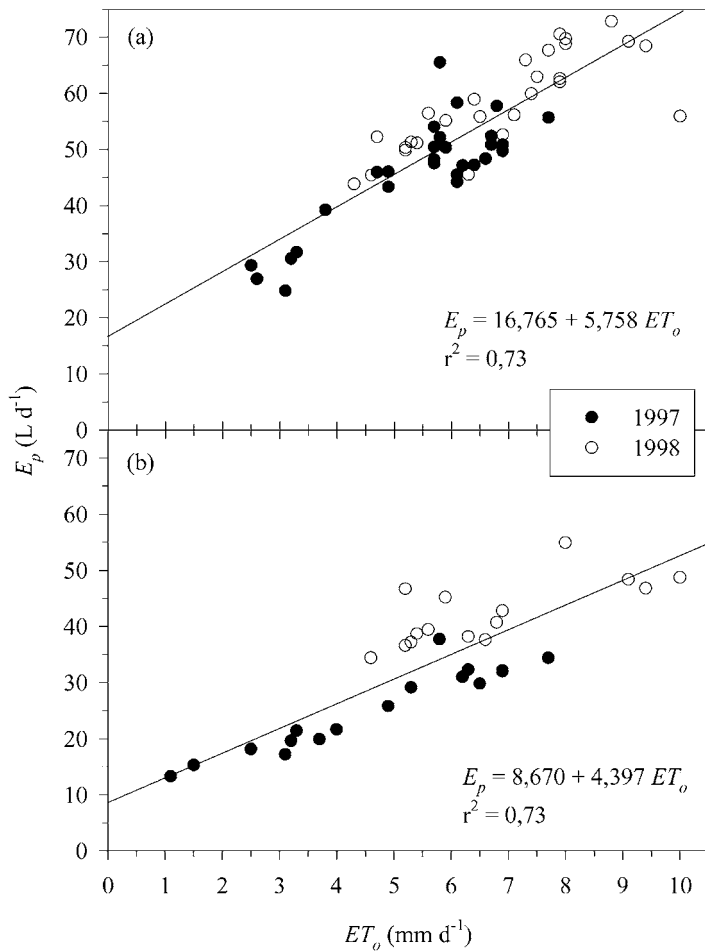


Fig. 7. Relationships between the daily transpiration of (a) the I and (b) the D trees estimated from sap flow measurements (E_p), and the potential evapotranspiration (ET_o) calculated using the FAO–Penman equation and the meteorological data recorded by the nearby weather station. The measurements were carried out during the dry seasons of 1997 and 1998.

3.4. Field experiment 2: root-sap flow

Heat-pulse measurements of sap flow in the tree roots are shown in Fig. 8. Before the irrigation on DOY 287, sap flow rates were considerably greater in the S root than in the N root (Fig. 8(a)) despite the roots having a similar size and despite the measured θ apparently being quite similar on both sides of the tree. This enhanced flow may be due to the S root actually exploring some wetter soil that was not detected by the single neutron-probe measurement. Therefore it would seem that the supply of water to the N root was limited by the dryness of the soil on the north side. Prior to irrigation, an elevated level of

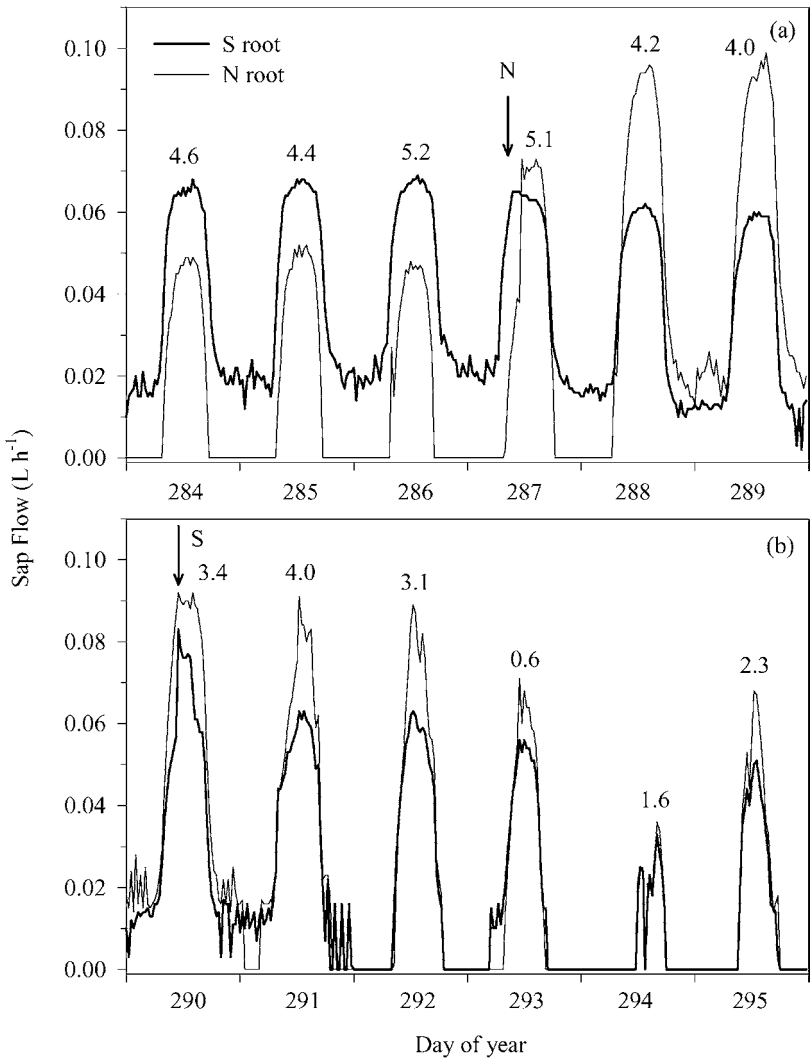


Fig. 8. Sap flows monitored in a root of the north side (N root) and south side (S root) of the olive tree used in the field experiment 2. In (a), the arrow represents an irrigation of 70 mm of water applied to the northern sector of the tree on DOY 287 at 10.25 GMT; (b) the arrow represents an irrigation of 155 mm of water applied to the southern sector of the tree on DOY 290 at 10.22 GMT. The number at the top of each daily curve is the ET_o of that day.

nocturnal sap flow was recorded in the S root, which no doubt supplied water to recharge the tree's water status during the night. However, at the same time in the N root, negligible sap flow was recorded at night, presumably due again to a limitation of readily available water in the soil root zone.

Following irrigation, we observed a rapid rise in the sap flow in the wetted, N root just about 1 h after irrigation on the N side. The roots obviously took up water soon after the surrounding soil became wet. At the same time that the sap flow dramatically increased in

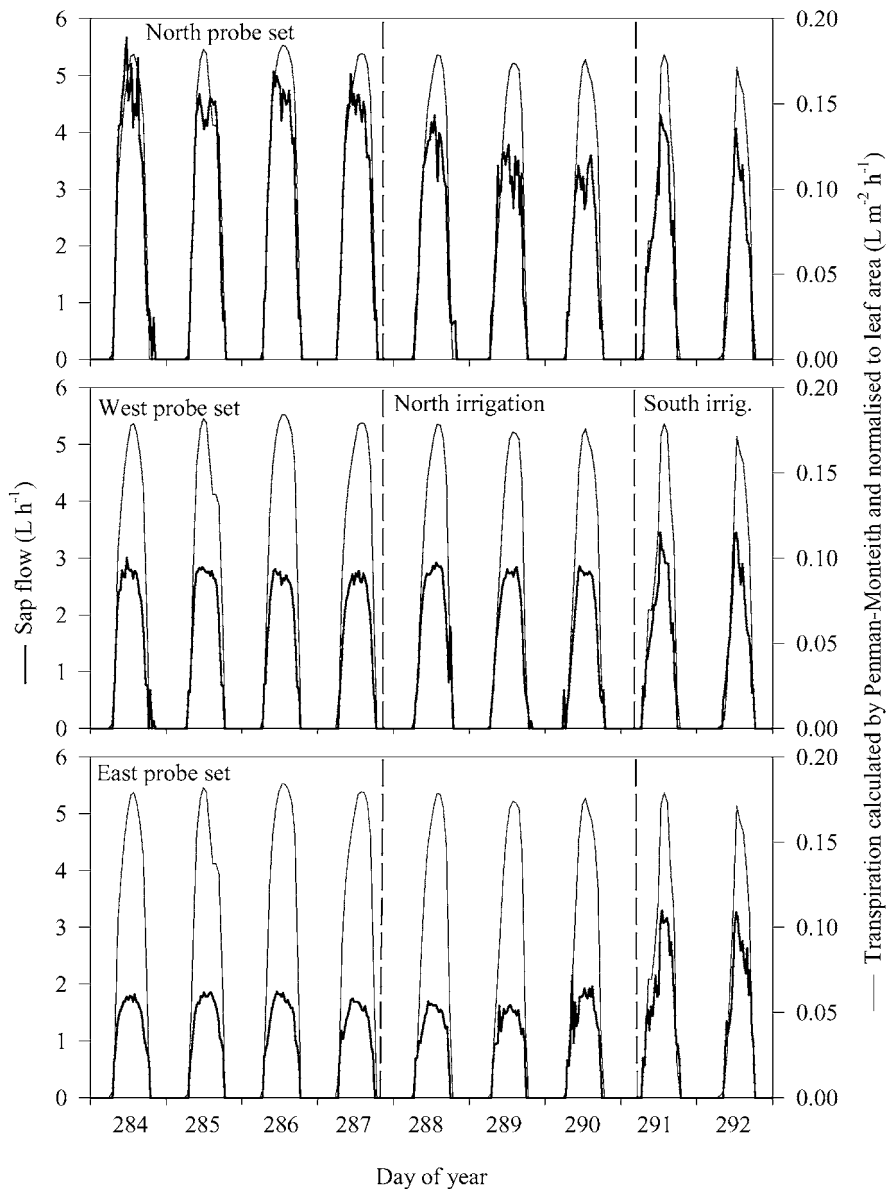


Fig. 9. The sap flow measured by the three probe sets in the trunk of the experimental olive tree from day 284 until 291 (thick lines). The time for the irrigation events in the northern and southern sectors sides around the tree are marked. Also shown is the normalised Penman–Monteith calculation of transpiration for the whole tree (thin lines).

the N root, there was a small but general decrease in the flow in the S root. The tree preferentially extracts water from where it is most easily available.

Another more subtle feature of the hydraulic behaviour of these roots is that before the irrigation of the N side on DOY 287, sap flow in the S root began about half to 1 h earlier

than in the N root. Likewise flow in the evening ceased about 1 h earlier in the N root. However, after irrigation, the two diurnal traces of sap flow were more-or-less in concert. After irrigating the S side on DOY 290 (Fig. 8(b)), the root water uptake of the S root increased, although the N root continued to be the one with the greatest water uptake.

3.5. Penman–Monteith model of tree transpiration

The predicted values of E_p^* several days either side of the irrigation events are shown in Fig. 9. The sap flows determined from the three probe sets are also shown in that figure. Marked differences in measured sap flow can be seen between the three probe sets. This is likely due to the naturally irregular nature of the sapwood of mature olive trees (Fernández and Moreno, 1999). In cultivated olives this variability is enhanced by pruning which leaves many gnarled scars and knots around the circumference of the trunk. Differences in the local transpiration derived from different parts of the canopy might also contribute to variability in measured sap flow around the trunk.

The daily values of E_p^* were similar throughout this 2 week period (Fig. 9), reflecting the relatively stable weather conditions. Integrated over the day, the three measured sap flow rates were initially quite different (Fig. 10), which highlights the need for replication of probes if the desire is for an accurate measure of tree transpiration. The mean sap flow measured in the trunk using all three probes follows the general pattern of E_p^* as determined by the Penman–Monteith calculations, and suggests a small rise in tree water

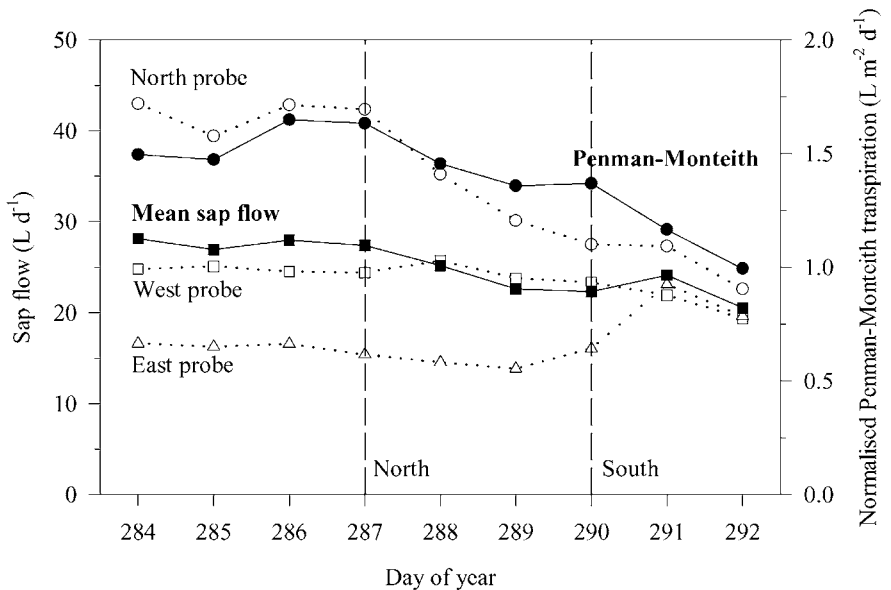


Fig. 10. Daily mean values of the sap flow measured in the trunk of the experimental tree (■) from day 284 until 291 and daily values measured by each one of the three probe sets (open symbols). Also shown is the Penman–Monteith estimated transpiration for the whole tree normalised to leaf area (●). The days for the irrigation events on the northern and southern sides of the tree are marked.

use following the second irrigation on DOY 290. The values of E_p^* are between 1.0 and 1.6 l m⁻² per day (Fig. 10). Three years earlier, Moreno et al. (1996) reported values of E_p^* around 1.65 l m⁻² per day for a well-irrigated tree in the same experimental orchard, but closer to 0.78 l m⁻² per day for an unirrigated tree. These latter measurements were made at about the same time of the year and on trees having a similar size to the present study.

4. Discussion

For both the excision and the perfusion experiments, the best agreement between the actual sap flow and the rates calculated from heat-pulse measurements was obtained using the correction factors for a wound width of 2.0 mm (Green and Clothier, 1988), and with the integration method of Eq. (5). Our confidence on these results is strengthened by the fact that, despite no replications of either the perfusion or the excision experiments, both experiments showed similar results. In addition, the data analysis of the sap flow velocities measured in the field, under very different conditions of atmospheric demand and soil water content, led to consistent results across the whole range (Fig. 7).

Anatomical studies by Barret et al. (1995) in rainforest and eucalypt forest species showed the effective diameter of the wound extends about 0.3 mm either side of the drill hole. On the other hand, when the distance between xylem vessels is lower than 400 μ m a wound width of 2.0 mm was reported as adequate by Swanson (1983). Our own anatomical measurements of the xylem vessels in olive showed the averaged distance between a group of vessels is about $193.5 \pm 71.5 \mu$ m ($n = 20$), with an average distance of $19.8 \pm 5.3 \mu$ m ($n = 20$) between the vessels within a group. Thus, a wound width of 2.0 mm is justified for olive. While Hatton et al. (1990) recommended Eq. (7) as the most adequate when the sap velocity profiles has a strong curvature close to the cambium, our own results for the olive show there to be little difference between the three integration methods described above.

In this study, we observed a large variability in sap velocities within the tree trunk (Figs. 9 and 10). Fernández et al. (1998) has already commented on the variability in the cross-sectional area in the trunk of a mature olive tree. This variation is exacerbated by the gnarled scars and knots left by pruning in the early years. We also observed that the degree of sap flow variability can change in response to a change in the spatial pattern of readily-available soil–water within the tree’s root-zone. For example, prior to irrigation, the three stem probes gave peak sap flows of 1.9, 2.8 and 4.5 l h⁻¹ (Fig. 8), yet after the first irrigation to just the northern part of the root zone the corresponding flow rates peaked at 1.9, 3.0, 3.5 l h⁻¹, respectively. Here it would seem that an increase in azimuthal variation of θ in the root zone, has resulted in a drop in the variability between our three probes sets. By DOY 292, following the second semi-irrigation on DOY 290, whereas the mean mid-afternoon flow rate is little changed at 2.6 l h⁻¹, the variation, given as the range over the mean of the three probes, is much reduced at 19%. For this day, the range in the daily total of the three measures of sap flow is just 3.2 l out of a daily flow of some 20.5 l. So it would now seem that just one to two probes would only be required to provide a robust measure of the tree’s transpiration. Thus, somewhat paradoxically, an increase (DOY 287–290), then a decrease (>DOY 290) in the azimuthal variation in water content around the tree, has led to a reduction in the results from the different probe sets.

If a good measure of the olive tree's transpiration is sought, then somewhere between two to four probe sets will be needed. But it is likely that through judicious selection of implantation sites, albeit with difficulty around the trunk of cultivated olive, the number required will be at the lower end of this bracketing. However, if it is only sought to observe variations in the dynamics and relative changes in the hydraulic functioning of the tree, then the requirement for replication lessens.

In looking at the flows of sap in the two roots over DOY 284–286 (Fig. 8), the N root is seen not to be conducting as much water as its diametrically opposite companion. It would seem initially that the N root is drawing water from drier soil, for although the S root is just 5% bigger in cross-sectional area, the flow there is 1.4 times that of the N root. The response to irrigation is sudden when this N root is wetted. Here the root has responded more dramatically than the well-irrigated root of Moreno et al. (1996) because the 'catchment' soil here is drier. Also the root here was still hydraulic functioning prior to wetting, whereas the lack of response in the unirrigated root of Moreno et al. (1996) was presumably because emboli there had resulted in a cessation of significant sap flow.

The rapid response here is similar to other non-root observations of the quick recovery of the olive tree following periods of drought (Natali et al., 1985; Jorba et al., 1985; Fernández et al., 1997a,b). After the first semi-irrigation, the ratio of flow in these similar-sized roots now favours the N root in the ratio of 1.65. Prior to irrigation, the N root was supplying about 1.7% of the tree's water, whereas afterwards this had doubled to 3.4%. Thus, the tree has preferentially shifted its root activity to favour uptake from that region of soil which had recently been wetted. The same behaviour has also been observed in kiwifruit vines by Green and Clothier (1995), although they noted a sustained rise in the dependence of uptake from the wetted soil, over a period of days after wetting. This they attributed to new root growth in the wetted soil. Our data do not extend sufficiently long after the irrigation to see if the same response might have occurred here.

Nocturnal flow, presumably to supply recharge of the tree's storage, also occurs now in the N root once the northern-sector soil has been wetted. The complete absence of measured root flow at night prior to the irrigation in the N root, and the sluggishness in the measured diurnal trace of this root prior to wetting, might be due to one of two causes, or a combination of both. We stopped searching for a cross-over time in the temperature traces of the up and downstream sensors after 500 s, and so we may have missed recording some really low flows at night in the N root. Alternatively, it may have been that reverse flow at night (Sakuratani et al., 1999), the so-called hydraulic lift, may have been acting in the counter direction to result in the unusual shape of the trace of sap flow in the N root prior to DOY 287. Such a flow would result in nocturnal measurement of zero values, and the onset of reverse flow in the late afternoon, and its maintenance in the morning, would lead to a shortened period of measured positive flow. Resolution of this will need to await a detailed study.

In this study, we did not measure in detail the leaf area of the entire tree, so in referencing our sap flow measurements to the ambient weather using the Penman–Monteith formula, we have had to limit our comparison to a matching with that normalised to the leaf area. This stresses the need to measure the total leaf area of the tree, and highlights the need for better and easier techniques to measure leaf area in the field. Prior to the irrigation on DOY 287, our tree had been without water for a period of some 38

days. As a measure of the impact of the two semi-irrigations, we examine changes in the ratio of the measured sap flow to the normalised Penman–Monteith transpiration. Over the days 284–286, prior to the first wetting, the ratio of the measured sap flow to the normalised E_p^* was 18.0 m^2 , whereas over the 2 days 291–292 following both wettings, this was 20.7 m^2 . A rough estimation of the leaf area showed that this latter value is more likely to be closer to the actual leaf area. The 15% change in this ratio, following wetting, is probably due to a rise in the canopy conductance as a result of some release of the water stress. So it would seem that over the period of 35 days without irrigation or rain, this tree had, by DOY 284, developed some degree of water stress. Comparison of the transpiration determined from sap flow measurement over 8 days, with the calculated E_p^* values in Figs. 8 and 9, reveals a coherency that confirms that the heat-pulse technique is a useful tool for monitoring both the short and medium-term dynamics of water use in olives.

We have found the compensation heat-pulse technique to be suitable for the design of an automatic system for the irrigation of an olive orchard. It appears possible to irrigate with the adequate doses and frequency to keep the plants within a certain prescribed level of water stress. Our results show that three different strategies, at least, could be adopted in the development of such a system.

Estimation of the total water consumed by representative trees in the orchard. This approach requires of a high number of sensors for an accurate estimation of E_p . In addition, the soil evaporation (E_s , mm) must be estimated to obtain the value of ET_o in the orchard, needed for the calculation of the irrigation dose. This can be done either from empirical measurements or from models especially adapted for the orchard conditions. Good examples of these two ways of estimating E_s in olive tree orchards are given by Palomo et al. (1998) and Bonachela et al. (1999).

Monitoring the changes in the hydraulic behaviour of the tree induced by water stress. The shape of the sap velocity profile measured in the trunk, or the features of the hydraulic behaviour of the roots mentioned in Section 3.4 could be used as signals for the automatic controller. This approach requires significant data processing.

Monitoring the SP_2/SP_1 rate (SP_1 = sap flow in a representative tree of the orchard, irrigated with enough water to cover the tree demand; SP_2 = sap flow in a representative tree of the orchard, irrigated with the water dose applied in the orchard). A decrease in the SP_2/SP_1 rate indicates that the trees in the orchard are consuming water below the maximum potential E_p . This is a simple and clear signal for an automatic controller able to supply water as a function of the transpiration dynamics. This approach does not require an estimate of E_s , and it needs a reduced number of sensors and little data processing. Besides, the errors due to both the probe location and to the tissue reaction will be minimised, since the system will only use relative values of sap flow.

5. Conclusions

From the results presented here, we have shown that the heat-pulse technique for measuring sap flow is a tool of two-fold benefit in olives. With appropriate replication, it can be used as a research tool to provide a robust measure of the tree's water use and hydraulic functioning. Furthermore, it has potential to be used as a device to provide a

signal from which decisions can be made concerning the need for, and timing of, irrigation.

Our two tests have confirmed that a robust measure of transpiration can be obtained using the compensation heat pulse technique in olives. The technique can be used with a wound width of 2.0 mm, and using the standard set of correction coefficients of Green and Clothier (1988). Little impact was observed in the choice of the integration procedure that is used to transform the velocity profile into a volume flux. Some differences in flow were found between the two different probe sets in the stem section, or excised tree. This illustrates some need to replicate in order to account for spatial variability.

In the water-stressed olive tree of field experiment 1, and in many other instances of drought-affected trees in the field, we have noted a loss of flow in the xylem vessels of the outer annuli. This presumably occurs as a result of stomatal control in young leaves and of cavitation within the vessels. Under such circumstances, the unusual nature of the velocity profiles means that our standard probes, which are weighted to measure near the cambium, might not adequately sample the flow. Furthermore, in such cases, the scheme we normally use for radially integrating $J(r)$ (i.e. Eq. (5)) might not be accurate (cf. Hatton et al., 1990). This then highlights the need for some care when radially integrating profiles of sap velocity to infer the volumetric rate of transpiration by trees.

In field experiment 2, we have extended our measurements of sap flow to observe flow in an olive tree under some degree of water stress. First, we have examined the spatial variability of measured sap flow in the trunk, and we have noted variation due to the natural variation in the flow paths in the sapwood. The range in the values from three sensors was almost equal to the mean value computed from the trio. Furthermore, we examined how variation might also be dependent on azimuthal variation in the availability of soil water around the tree. In our case, increasing the latter, actually decreased the variability in the inter-probe range down to under 20% of the mean. Some two to four sensors would seem sufficient for olive to permit robust measurement of the tree's water use, although this might be further reduced by judicious placement of the probes in 'smooth and straight' sections of the trunk. We consider that monitoring the flow in the outer annuli of the trunk or main roots may provide an early and sensitive indicator of either the onset, or severity of water stress. So if heat pulse gear were to be used as a device for controlling the irrigation system, the need to record accurately the tree's water use is diminished. Rather a control device would be seeking to detect changed hydraulic behaviour consequent upon the onset of water stress. Fewer sensors will be required, but more analysis of the diurnal traces will be needed to deduce the appropriate information. It would seem that a focus on flow in the outer xylem vessels may offer the best hope. Another option, probably the most advantageous one, is simply to use the slope of the SP_2/SP_1 ratio for operating the irrigation controller. With this approach, soil evaporation does not have to be estimated, the required number of sensors is low and the data processing is reduced to a minimum.

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