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ORIGINAL PAPER

Stem and whole-plant hydraulics in olive (*Olea europaea*) and kiwifruit (*Actinidia deliciosa*)

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Abstract A field study and an experiment under controlled conditions using pressure-flux relationships were conducted to compare the stem and whole-plant conductance in olive (*Olea europaea*) and kiwifruit (*Actinidia deliciosa*) species. Anatomical observations were also made on one-year-old stem to determine the conductive area of vessels (A_{ves}) and the total xylem area (A_{xyl}). Results show that A_{ves} of kiwifruit twigs was ~2.5-fold of that in olive twigs, and the hydraulically weighted mean diameter was up to threefold that of the olive ones. One-year-old olive twigs had lower hydraulic conductivity (k) than the kiwifruit, while values of leaf-specific conductivity (i.e. k normalised per unit leaf area) were higher than the kiwifruit (i.e. ~49 and 29 × 10^{-6} kg m^{-1} s^{-1} MPa^{-1}, respectively). In the field experiment, the flux of sap (heat balance method) and differences in water potential through the soil–plant system (ΔP) were used for both species to calculate the whole-plant conductance that was normalised per unit leaf area (leaf-specific whole-plant conductance, $K_{\mathrm{plant,LA}}$). Values of $K_{\mathrm{plant,LA}}$ are attributable to the combined effect of the ΔP and anatomical features of conduits. Olive species showed a larger ΔP (2.4 MPa at midday) than the kiwifruit (0.5 MPa) which contributed to lower $K_{\mathrm{plant,LA}}$ in *Olea* than the *Actinidia* plants. This information, combined with vessel density data, contributes to explain differences amidst olive and kiwifruit species, in terms of susceptibility to some drought-related hydraulic impairments induced by the Mediterranean environment.

Keywords Hydraulic conductivity · Kiwifruit · Olive · Plant conductance · Sap flow · Xylem vessels

Introduction

Mediterranean ecosystems are characterised by almost complete lack of precipitation during the summer period coupled with high temperatures and high light intensities. Under these environmental conditions, plants evolved a number of survival adaptations of functions and structures including hydraulic systems. For example, a Mediterranean native species such as *Olea europaea* (L.) evolved narrow (25–30 μm diameter) high vessel density (~440 per mm^{-2}) (Trifilò et al. 2007). Nowadays distribution at global scale of some cultivated crops may be affected also by economic pressure. This is the case with kiwifruit (*Actinidia deliciosa* var. *deliciosa*, C.F. Liang et A.R. Ferguson) which originates from habitats characterised by high humidity, abundant rainfall (1,200–1,800 mm year^{-1}) and by a moderate intensity of sunlight (Montanaro et al. 2009 and reference therein). Under these non-limiting conditions kiwifruit evolved more sparse vessels (~4 per mm^2) with a larger diameter (up to 500 μm) (Condon 1992). These species are currently cultivated in most of the Mediterranean countries and are of economic significance. They have different water relations under summer conditions (e.g. high irradiance and temperature, frequent water shortage). That is, kiwifruit vines despite a high seasonal irrigation volume (10–12,000 m^3 ha^{-1}, Holzapfel et al. 2000) can show some drought-related symptoms (leaf

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burning and roll, reduced photosynthetic capacity) (Montanaro et al. 2007, 2009) whilst olive trees with only 2–3,000 m^3 ha^{-1} maintain a optimal physiological status (Dichio et al. 2006). Integrating knowledge of water relations with whole-plant hydraulics information could contribute to improve irrigation strategy and management (irrigation frequency, volume and method) in order to maximise the environmental and economic performance of these crops.

The evolutionary pattern has led *Olea* and *Actinidia* plants to differ also in terms of daily oscillation of leaf water potential, and consequently of the maximum hydrostatic pressure gradient (ΔP) which drives the catenary process of plant water transport. For example, well-irrigated olive trees are able to lower the midday leaf water potential down to −2.5 to −3 MPa while kiwifruit reaches ∼−0.7 to −1.0 MPa (Xiloyannis et al. 2003; Dichio et al. 2006; Montanaro et al. 2009). Vessel density and diameter affect the conductance of the conduits as predicted by Hagen–Poiseuille's law (Tyree and Ewers 1991). Efficiency of xylem also affects plant performance (i.e. transpiration, carbon gain and growth) to the extent that the *status* of xylem pipes affects water and xylem-borne nutrient transport (Tyree 2003).

Laboratory measurements of stem segment hydraulic conductivity have been assumed to be a proxy for the whole-plant conductance (K_{plant}), however, a whole-plant approach that takes account of hydraulic architecture could help to make the dynamics of plant water flow clearer (Tyree 1988; Becker et al. 1999). Direct measurements of K_{plant} have begun to reveal the adaptive significance of plant hydraulic architecture across species (Meinzer et al. 2001), moreover, they could integrate current knowledge on water relations and contribute to elucidate species-specific differences in water use strategies.

Based on our knowledge, although information on sap flow and xylem conductance in olive and kiwifruit are accessible (Lo Gullo and Salleo 1990; Fernández et al. 2001; Froux et al. 2002; Clearwater and Clark 2003; Martínez-Vilalta et al. 2003; Clearwater et al. 2004; Raimondo et al. 2009), few studies have been designed to simultaneously explore the in vivo whole-plant hydraulics of that species growing under the same environment. There is evidence that the some environmental variables (e.g. irradiance, soil water and nutrient availability) can influence whole-plant and component water transport in combination with vessel features (Tyree 2003; Raimondo et al. 2009; Sellin et al. 2011) contributing to amplify (or mask) species-specific differences (Tyree et al. 1998). Based on this background, this study was aimed at concurrently comparing both the whole-plant water transport and stem hydraulics and vessel anatomy in olive and kiwifruit plants growing under the same Mediterranean environmental conditions.

Taking into account that olive trees has a high root-to-canopy ratio and a high soil–plant pressure gradient (Dichio et al. 2003, 2006), we hypothesised that water supply per unit leaf area is higher in *Olea* than *Actinidia* plants. This in turn would cause the whole-plant conductance to be lower in *Olea* than *Actinidia* because of the higher ΔP in *Olea* plants. To test these hypotheses, we measured the diurnal whole-plant water supply as sap flow and leaf water potential in 2-year-old potted olive and kiwifruit plants under open-door conditions. We concurrently determined the leaf-specific conductivity in the laboratory in combination with stem anatomy and classical hydraulic parameters on 1-year-old shoots.

Because of the simultaneous measurement of component (laboratory) and whole-plant hydraulics (out-door experiment) results may contribute to integrate current knowledge on different strategies amidst *Olea* and *Actinidia* plants to cope with soil water availability in Mediterranean climates.

Methods

Plant material and experimental design

The trials were conducted at the 'Pantanello' experimental farm in Metaponto (Southern Italy—N 40° 24′, E 16° 48′) on 2-year-old own-rooted *O. europaea* L. (cv. 'Coratina') and *A. deliciosa* (cv. 'Hayward') plants which had similar leaf area (∼40 dm^{-2} $plant^{-1}$). Plants were grown uniformly outdoors in 0.016 m^3 pots filled with a 3:1 mixture of field soil (73 % sand, 13 % silt and 14 % clay) and peat. Pots were wrapped with plastic film and aluminium foil in order to avoid evaporation from the soil surface and to minimise temperature increase inside the containers. Plants were grown under optimal water availability conditions during their growing season. The soil water content of pots was maintained close to 85 % of water holding capacity by replenishing in the evening 100 % of the daily water loss determined by weighing.

Air temperature and relative humidity were monitored by a standard weather station located within 500 m from the experimental plot. The air vapour pressure deficit (VPD) was then calculated from the records of air temperature and relative humidity, according to Goudriaan and van Laar (1994).

Wood sampling and stem hydraulic measurements

In June, one-year-old wood segments (∼0.16 m length) with 5 (olive) and 2 (kiwifruit) nodes were excised (20 replicates) under water from the plants (10 replicates per species) early in the morning, when VPD is generally low.

Thereafter, they were wrapped in humid cloth and enclosed in a polyethylene bag, in order to minimise the dehydration of tissues, and promptly transferred to the laboratory. To avoid that excised segments contain vessels cut open at both ends, the length of segments to be used in this experiment was established based on preliminary observations carried out following the paint method (Zimmermann and Jeje 1981).

For each segment, the length and the basal, medial and apical diameter were measured using a digital calliper and averaged to calculate the mean radius. The cross-sectional area of segments (A_{stem}, mm^2), including phloem, xylem, bark and pith, was calculated from the mean radius assuming the cross-section of the segment to be a circle. The leaf area sustained by each segment (A_{leaf}, m^2) was measured with a LI-3100 leaf area metre (LI-COR, Lincoln, NE, USA).

Immediately before hydraulic conductivity determination, segments were cut again slantwise in distilled water, and the stem extremities were debarked. The flow through the segments was measured by following the methodology of Sperry et al. (1988) with some modifications. Since segments were collected in the early morning and because the assessment of cavitation vulnerability was behind the scope of this study, stems were not flushed with degassed water (Melcher et al. 2012). The liquid employed and forced through the stem segments was a 0.05 M ascorbic acid solution, used to prevent microbial growth. A constant pressure of 0.005 MPa was applied using a compressed nitrogen tank. Before entering the segments, the solution was filtered with a 0.2 µm filter (Millipore, Billerica, MA, USA) and degassed with an agitator connected to a vacuum pump.

The flow rate through the stem was determined gravimetrically with a 3-point electronic balance (Sartorius A 120AS, Goettingen, Germany) interfaced with a computer programmed to output the values of stem hydraulic conductivity (k). The conductivity was calculated as flow rate passing through a given length of sample per unit of applied pressure gradient (ΔP) according to Sperry et al. (1988)

$$k = \frac{F \times \mathrm{SL}}{\Delta P}\ (\mathrm{kg\,m\,s^{-1}\,MPa^{-1}}), \tag{1}$$

where F is the flow rate (kg s^{-1}, assuming a water density of 1 g cm^{-3} at a room temperature of 25 °C), SL is the stem length and ΔP (expressed in MPa) is the hydrostatic gradient.

For each stem segment, at least 40 measurements of k values were recorded at 15-s intervals in a period of 10 min. The values obtained were plotted versus the time-course weight determination in order to establish the occurrence of the steady-state. The mean k was calculated by averaging at least 15 measurements in the flat and stable part of the graph under the assumption that the whole xylem was functional.

Stem hydraulic conductivity was subsequently used to calculate stem-specific conductivity (k_{stem}) by dividing k by stem cross-sectional area A_{stem} (k_{stem}, kg m^{-1} s^{-1} MPa^{-1}). The xylem hydraulic conductivity (k_{xyl}, kg m^{-1} s^{-1} MPa^{-1}) was determined by dividing k by the xylem area (A_{xyl}), while the vessel hydraulic conductivity (k_{ves}) was calculated by dividing k by the total vessel lumina area (A_{ves}) of each segment section (k_{ves}, kg m^{-1} s^{-1} MPa^{-1}). Leaf-specific conductivity (k_{leaf}) was also determined by dividing k by the 'supported leaf area' of each segment (A_{leaf}, see above) (Zimmermann 1978). This approach follows that used by Tyree and Ewers (1991).

Anatomical determination

From each segment, 3-mm-long portions were cut with a scalpel and fixed in FAA (90 % ethanol, 5 % acetic acid and 5 % formaldehyde), dehydrated in ethanol series and then embedded in paraffin. Ten sub-sections (5 proximal and 5 distal) of 15 µm in thickness were obtained from each portion by a MICROM 400R microtome (Microm International GmbH, Walldorf, Germany). The sub-sections were stained with safranin and fast-green (Jensen 1962) and successively examined at 20× magnification under a confocal laser scanning microscope (LSM Axiophot, Zeiss, Oberkochen, Germany). Image study was carried out with a shareware image-analysis software (Image Tool v3.0).

Phloem (A_{phl}, mm^2) and pith area (A_{pith}, mm^2) were calculated assuming these tissues as circles whose radius was determined through microscopy analysis and image study (Fig. 1).

Total xylem area (A_{xyl}, mm^2), i.e. the area of the xylem ring measured between the cambium and the innermost

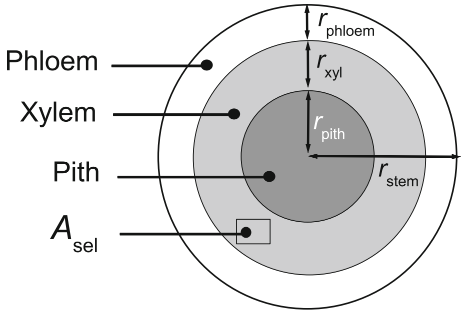

Fig. 1 Schematic representation of the anatomical partitioning adopted: r_{stem}, stem cross-sectional radius; r_{phl}, phloem thikness; r_{xyl}, xylem thikness; r_{pith}, pith thikness; A_{sel}, selected area of the xylem

ends of tracheary elements, was determined from the following equation:

$$A_{\mathrm{xyl}} = A_{\mathrm{stem}} - A_{\mathrm{phl}} - A_{\mathrm{pith}}(\mathrm{mm}^2) \tag{2}$$

Total vessel lumina area (A_{ves}) was calculated using

$$A_{\mathrm{ves}} = \sum A_{\mathrm{lum}} \times A_{\mathrm{xyl}}\ (\mathrm{mm}^2) \tag{3}$$

where (ΣA_{lum}) is the sum of all the values of single lumen area measured in 1-mm^2 selected areas (20×) of xylem image (A_{sel}; Fig. 1).

Vessel diameters were analysed for their frequency in 5 μm diameter classes and the hydraulically weighted mean diameter (D_{h}) was calculated according to Sellin et al. (2008).

Whole-plant hydraulic conductance

The whole-plant hydraulic conductance (K_{plant}) was determined on ten plants per species from measurements of whole-plant sap flux (heat balance method) according to the following equation (Phillips et al. 2002; Reid et al. 2005):

$$K_{\mathrm{plant}} = \frac{F_{\mathrm{sap}}}{\Delta P}\ (\mathrm{kg\,m\,s^{-1}\,MPa^{-1}}), \tag{4}$$

where F_{sap} represents the rate of sap flow passing through the whole-plant and ΔP the hydrostatic pressure gradient between soil and leaf. Values of ΔP at a given time (t) of the day (ΔP_t) were calculated as the difference between the leaf water potential (Ψ_{w}) measured at pre-dawn ($\Psi_{\mathrm{w-PD}}$) and that measured at time t ($\Psi_{\mathrm{w}-t}$) under the assumption that $\Psi_{\mathrm{w-PD}}$ of leaves had equilibrated with bulk soil water potential by pre-dawn (Raimondo et al. 2009; Black et al. 2011)

$$\Delta P_t = \Psi_{\mathrm{w-PD}} - \Psi_{\mathrm{w}-t}(\mathrm{MPa}) \tag{5}$$

Leaf water potentials were measured by a pressure chamber (model 600; PMS Instrument Co., Corvallis, OR, USA) pressurised with N_2. Four fully expanded leaves were selected from each plant along the median segment of new-growth shoots.

The sap flow (F_{sap}) was measured by a Dynagage Sap Flow system using 10 probes (model SGA13, Dynamax, Houston, TX, USA). Sensors were connected to a data logger (CR10, Campbell Scientific Inc., Logan, UT, USA) programmed to measure sap flow at 1-min intervals and to compute and record the average flow at 30-min intervals. Prior to starting with sap flow measurements, in order to adjust each sensor at zero flow, the sensors were installed for some clear days on a 20-cm long defoliated olive/kiwifruit trunk having a diameter similar to that of plants used for the experiment. Each sensor was installed on the trunk at 15–20 cm above ground, and covered with aluminium foil to minimise sensor warming. A couple of measurement days were spent to properly set for each gauge the thermal conductance constant at zero. The sap flow was scaled to plant leaf area (see below) and expressed as $F_{\mathrm{sap,LA}}$ (g m^{-2} h^{-1}).

According to Becker et al. (1999), the whole-plant conductance (Eq. 4) was normalised by leaf area (A_{L}, m^2; subscript LA) and the leaf-specific whole-plant conductance determined ($K_{\mathrm{plant,LA}} = K_{\mathrm{plant}}/A_{\mathrm{L}}$, kg m^{-2} s^{-1} MPa^{-1}). At the end of the experiment, on each of the ten plants used for sap flow measurements the plant total leaf area A_{L} was measured (LI-3100 leaf area metre, LI-COR, Lincoln, NE, USA).

Results

Hydraulic conductivity of wood segments

All the anatomical and morphological traits measured were significantly higher in kiwifruit than olive twigs except for the mean vessel density, namely the values A_{xyl} and A_{ves} in kiwifruit were approximately twofold of those in olive ones (Table 1). The average area of leaves supplied by a ~0.16-m long segment (A_{leaf}) in *Actinidia* was about tenfold greater than the olive one. The number of vessels per mm^2 of the conductive tissue in *Olea* was more than sixfold higher than *Actinidia* and the mean value of D_{h} was up to threefold that of the *Olea* (Table 1). The distribution of diameters greatly differed between *Olea* and *Actinidia* vessels. Olive vessels were roughly normally distributed and the most of xylem transport was attributable to the vessels 25–30 μm in diameter (Fig. 2a), while in kiwifruit ~45 % of vessels belonged to the 35–60 μm diameter class and smoothly declined with increasing diameter (Fig. 2b).

Table 1 Mean stem and hydraulically weighed vessel diameter (D_{h}), total xylem area (A_{xyl}), total vessel lumina area (A_{ves}), vessel density measured in sections of olive and kiwifruit one-year-old wood segments

	Stem diameter (mm)	D_{h} (μm)	A_{xyl} (mm^2)	A_{ves} (mm^2)	$A_{\mathrm{ves}}/A_{\mathrm{xyl}}$ (%)	Vessel density (n, mm^{-2})	A_{leaf} (m^2) × 10^{-2}
Olea	4.40* ± 0.71	30.5* ± 4.1	7.29* ± 1.20	0.92* ± 0.17	12.6	302* ± 62	2.94* ± 0.82
Actinidia	6.61 ± 0.12	97.0 ± 19.0	13.83 ± 2.83	2.25 ± 0.36	16.3	46 ± 9	22.19 ± 11.32

A_{leaf} is the leaf area supplied by the twig analysed. Each data point represents the mean (±SD) of 20 measurements. Values with the asterisk are significantly different between olive and kiwifruit segments ($P = 0.05$, Student's t test)

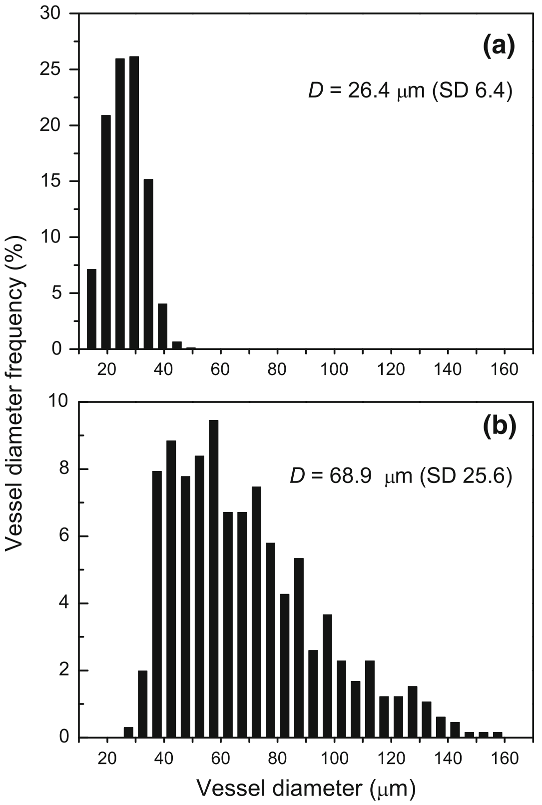

Fig. 2 Frequency distributions (%) of vessel lumen diameters in **a** *Olea* and **b** *Actinidia* segments ($n = 1{,}715$ and 656 for olive and kiwifruit, respectively; *D* mean diameter, *SD* standard deviation)

The stem hydraulic conductance (k) of *Actinidia* segments was significantly higher ($P = 0.05$, Student's t test) than *Olea*. The conductivity related to the stem cross-sectional area (k_{stem}), to the xylem area (k_{xyl}) and to the lumina area of vessels (k_{ves}) were similarly significantly high (Fig. 3). By contrast, the mean k_{leaf} was significantly higher in olive than kiwifruit segments (Fig. 3).

Whole-plant conductance

During the measurement day, VPD had a typical pattern with a maximum value (~2.2 kPa) recorded between 11:00 h and noon (Fig. 4a). The VPD slowly declined in the early afternoon till 17:00 h, thereafter it sharply declined toward the minimum values.

The lowest values of Ψ_w were reached during the central part of the day (12:00–14:00 h) ~1 h later the highest VPD value was reached, when the midday minimum Ψ_w was lower for olive leaves (~−3.0 MPa) than kiwifruit (−0.7 MPa) (Fig. 4b).

The daily variations of $F_{\mathrm{sap,LA}}$ followed those of VPD, showing a sudden increase in the early part of the day up to the maximum value of about 200 g h^{-1} m^{-2} for both species. However, during the early hours of the day (07:00–10:00 h) and in the late afternoon (17:00–20:00 h) sap flow was significantly higher in *Olea* than *Actinidia* plants (Fig. 5a).

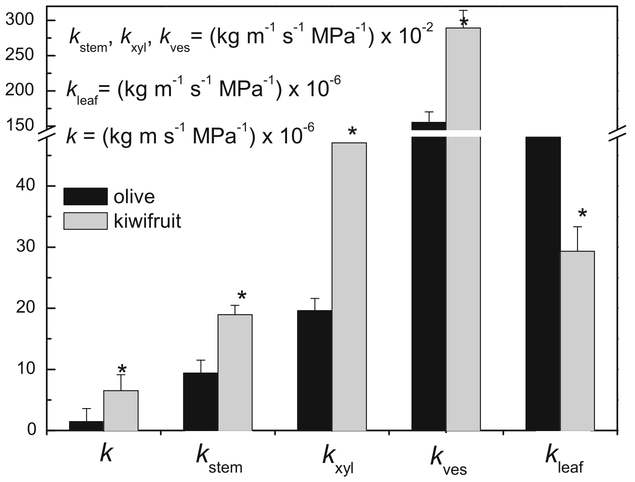

Fig. 3 Stem hydraulic conductivity (k), stem-specific hydraulic conductivity (k_{stem}), xylem hydraulic conductivity (k_{xyl}), vessel hydraulic conductivity (k_{ves}), and leaf-specific conductivity (k_{leaf}), measured in ~0.16 m wood segments of one-year-old olive and kiwifruit stems. Each column represents the mean (±SD) of 20 measurements. Comparing species in each parameter * indicates significant difference ($P = 0.05$, Student's t test). Note that the *Y*-axis is broken from 48 to 145

Early in the morning (08:00 h), values of $K_{\mathrm{plant,LA}}$ were similar in both the compared species (i.e. 4.1×10^{-5} kg m^{-2} s^{-1} MPa^{-1}) (Fig. 5b). Thereafter, $K_{\mathrm{plant,LA}}$ of *Olea* plants tends to decrease toward the minimum value at midday, in the afternoon $K_{\mathrm{plant,LA}}$ progressively increased reaching in the evening (19:00 h) a value similar to that recorded in the morning (Fig. 5b). On the contrary, *Actinidia* plants showed a sharp increase in $K_{\mathrm{plant,LA}}$ during the morning and peaked at ~10×10^{-5} kg m^{-2} s^{-1} MPa^{-1} from 10:00 to 14:00 h; in the afternoon it transiently peaked at 11.3×10^{-5} kg m^{-2} s^{-1} MPa^{-1}, in the evening it was again at values comparable to those of the morning (Fig. 5b).

Discussion

Kiwifruit vines exhibited lower water supply (i.e. sap flow per unit leaf area, $F_{\mathrm{sap,LA}}$) and higher leaf-specific whole-plant conductance ($K_{\mathrm{plant,LA}}$) which is attributable to the combined effect of the lesser pressure gradient and some anatomical features of conduits (i.e. higher vessel size). In general, higher $K_{\mathrm{plant,LA}}$ is expected for those species with larger conducting vessels, such as woody lianas, and species adapted to environments with high soil water availability, which exhibit slight Ψ_w fluctuations during the day and, in turn, a lower hydrostatic gradient between leaves and roots (Sperry et al. 1987; Dünisch and Morais 2002; Clearwater and Clark 2003). In this study, the mean

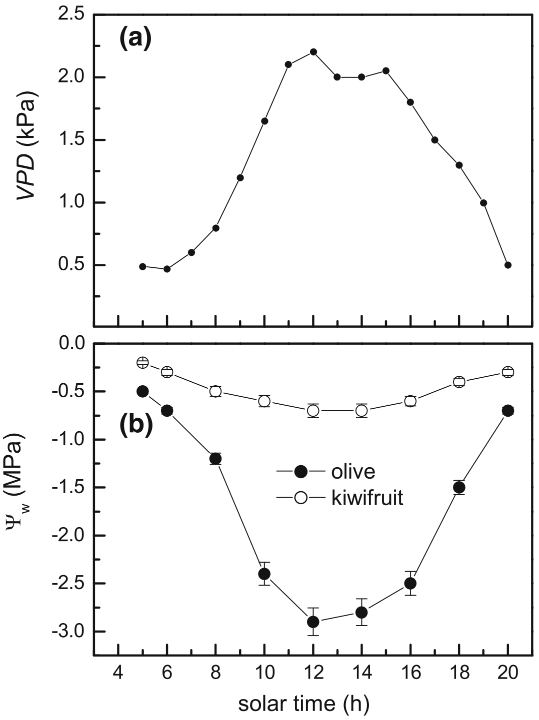

Fig. 4 Daily variations of **a** vapour pressure deficit (VPD, kPa) and **b** leaf water potential (Ψ_w, MPa) during the day of measurement

diameter of vessel lumina in 1-year-old kiwifruit stem was 2.6-fold of that in olive twigs (see Fig. 2) while the ΔP was smaller compared with the olive one (Fig. 4b). Features of conductive tissue (vessel density and diameter) found in kiwifruit were similar to those reported for other woody lianas species of the same age (e.g. *Vitis vinifera*) (Salleo et al. 1985), while Condon (1992) reports a larger vessel diameter (up to 500 µm) for stems of mature kiwifruit vines. Anatomical results on *Olea* plants are in agreement with Trifilò et al. (2007). However, Lòpez-Bernal et al. (2010) report a larger vessel diameter for mature olive trees. Age-related changes in xylem development (Takemoto and Greenwood 1993) may help to explain narrower vessel diameter detected in this experiment compared with published results for both olive and kiwifruit.

Different requirements between species for mechanical support (structural tissue) and transport tissue could interfere with the appraisal of stem hydraulic conductivity (k) especially when scaled to cross-sectional area of the stem (k_{stem}) (Salleo et al. 1985). The xylem area (A_{xyl}) represented 48 and 40 % of the total stem cross-sectional area in *Olea* and *Actinidia* plants, respectively, while the lumen area of vessels (A_{ves}) was 13 % (olive) and 16 % (kiwifruit) of A_{xyl} (Table 1). The larger conductive efficiency calculated for kiwifruit stems (i.e. higher D_{h}) seems to balance the lower vessel density (Table 1) (Sellin et al. 2008). However, the overall plant supply (i.e. sap flow) remained lower than that in olive plants (Fig. 5a and discussion below).

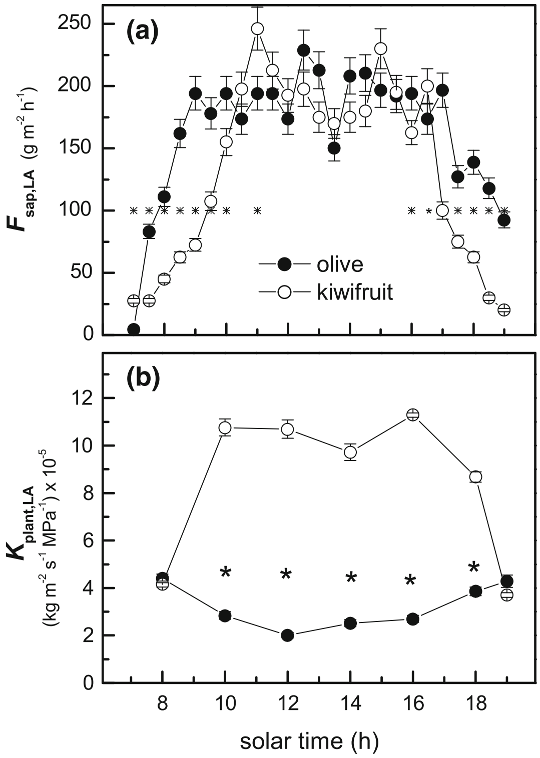

Fig. 5 Diurnal oscillations of **a** sap flux per unit leaf area ($F_{\mathrm{sap,LA}}$, g m^{-2} h^{-1}) and **b** leaf-specific whole-plant conductance ($K_{\mathrm{plant,LA}}$, kg m^{-2} s^{-1} MPa^{-1} × 10^{-5}) in olive (*closed circle*) and kiwifruit (*open circle*) plants. Each data point represents the mean (±SD) of ten measurements. *Significant difference between olive and kiwifruit at $P = 0.05$ probability level (Student's *t* test)

Differences in size and density of vessels led shoot hydraulic conductivity (k) in kiwifruit segments to be fourfold higher than that in olive segments. This is in accordance with physical principles establishing that k is proportional to the size of vessels and to the conductive area which were significantly greater than in kiwifruit stems (see mean vessel area and A_{ves} in Table 1). Additionally, lower k observed in olive twigs was likely related also to the higher resistance of the flowing sap within xylem of olive stems due to the presence of higher constriction zones (5 nodes against 2 in kiwifruit, see "Methods" section) (Tyree and Ewers 1991).

The lower k detected in olive twigs is in line with the evidence that a lower stem hydraulic conductivity is directly related to a lower active xylem area (Tyree and Ewers 1991; Sperry et al. 2003); it may be concluded that k_{ves} can give more accurate comparative information on hydraulic capacity of transport system than the k_{stem}. Based on this approach, it appears that hydraulic conductivity of shoots of *Olea* plants is ~41 and 49 % of that of *Actinidia* plants when scaled to the xylem (k_{xyl}) and stem cross-sectional (k_{stem}) areas, respectively (Fig. 3). While, when

k is scaled to the vessels area (k_{ves}), that percentage rises to a value close to 54 % (Fig. 3), confirming the need for such a parameter to yield more accurate information (Salleo et al. 1985). Leaf-specific conductivity (k_{leaf}) is considered the hydraulic capacity of the stem to supply leaves with water (Sterck et al. 2008). Figure 3 shows that olive stems had k_{leaf} 65 % higher than the kiwifruit ones indicating a better potential capacity of olive shoots to supply water per unit leaf area.

In olive plants, in addition to the vessel size (narrower) and architecture (constricted twig regions localized in the nodes) (Salleo et al. 1985), a high k_{leaf} may represent a tool contributing to minimising the occurrence of cavitation and diffusion of emboli which could be interpreted as an adaptive trait to dry environments (Zimmermann and Jeje 1981; Bacelar et al. 2007). By contrast, in kiwifruit the lower k_{leaf} as combined with the large vessel size could be responsible for the more frequent occurrence of embolism and cavitation also at a relatively low xylem water potential (i.e. −0.5 MPa) (Froux et al. 2002; Sperry et al. 2003; Clearwater and Clark 2003). However, differences in cavitation vulnerability among three *Acer* species have been attributed to differences in frequency of the leakiest pits rather than vessel size (or pit number) (Christman et al. 2009), hence determination of such a frequency in *Olea* and *Actinidia* species would be desirable.

The observed higher value of k_{leaf} in olive segments is mainly due to the smaller leaf area per unit of length of the analysed twigs (A_{leaf}) compared to the kiwifruit (Table 1). This again may reflect some evolutionary adaptation driven by differences in the environment of origin (i.e. humid or dry). Additionally, diurnal fluctuation of Ψ_{w} in olive plants was significantly higher than in kiwifruit leading the maximum soil–plant ΔP to be 2.4 (olive) and 0.5 MPa (kiwifruit), respectively, (Fig. 4b). This behaviour conceivably reflects the higher tissue capacitance of olive trees than *Actinidia* plants, helping to establish a higher hydrostatic gradient between leaves and roots (Nuzzo et al. 1997; Xiloyannis et al. 2003).

The water potential gradient existing between soil and leaves drives the water flow across the plant to replace the water transpired by leaves. In general, high transpirational fluxes from leaves can only be sustained by producing a large soil–leaf pressure gradient, or a highly conductive (i.e. lowly resistive) hydraulic system (Brodribb 2009). Laboratory measurements showed that olive twigs were significantly less conductive (i.e. lower k values) than kiwifruit (Fig. 3). However, the water supply per unit leaf area ($F_{\text{sap,LA}}$) tends to be higher than the kiwifruit, particularly during the morning and afternoon (Fig. 5a). That is, integration of the $F_{\text{sap,LA}}$ values shows that the *Actinidia* crown was fed by 3.3 kg m^{-2} sap a day (06:00–20:00 h) while *Olea* by 4.1 kg m^{-2}. Much of such a difference was gained by olive plants when VPD was relatively low (i.e. in the early morning and late afternoon) under a ΔP significantly higher than the kiwifruit plants. Brodribb (2009) reviewed the hydraulic/photosynthetic coordination suggesting that under non-limiting conditions the water supply could be interpreted as the link between hydraulics and plant performance (e.g. carbon gain). Hence higher amounts of water transport recorded in irrigated olive trees suggest a higher photosynthesis/transpiration ratio for that species. In addition, the higher water transport of olive plants compared with kiwifruit ones documented in the out-door experiment is in line with the higher k_{leaf} detected under controlled conditions (Fig. 3) which can be interpreted as an adaptive trait to the Mediterranean environment.

The overall higher $F_{\text{sap,LA}}$ in *Olea* plants is consistent with Darcy's Law, which predicts that sap transport through xylem conduits is proportional to their conductance and to the resulting hydrostatic pressure gradient which was approximately five times than that of kiwifruit plants. Under certain stress conditions (e.g. root severance), also in kiwifruit vines the pressure gradient between soil and canopy may increase in order to warrant adequate water supply to the canopy (Black et al. 2011).

Leaf-specific plant conductance ($K_{\text{plant,LA}}$) of olive plants are in the magnitude of those reported for *O. oleaster* (estimated through the evaporative flux method) having ∼−2.2 MPa midday leaf water potential (Lo Gullo et al. 2003). However, our results on $K_{\text{plant,LA}}$ seem to differ from recent findings in *Olea* plants which show considerably higher values of K_{plant} (close to 8×10^{-5} kg m^{-2} s^{-1} MPa^{-1}) (Raimondo et al. 2009). Differences could be explained considering the less negative minimum leaf water potential reached in that study (i.e. −1.2 MPa), and possible morpho-anatomical differences (vessel density or A_{L}) related to the variety. Furthermore, in Raimondo et al. (2009) plant conductance was calculated using the leaf transpiration as flux, while in this study we measured the sap flow.

Estimations of whole-plant leaf-specific conductance here presented for kiwifruit are comparable with those of four mature *Actinidia* spp. vines that oscillate from 4.5 to 6.9×10^{-5} kg m^{-2} s^{-1} MPa^{-1} (in the range of −0.8 to −0.6 MPa leaf water potential) (Clearwater et al. 2004). Also, we observed that $K_{\text{plant,LA}}$ oscillated during the day in sympathy with VPD oscillation (i.e. a rise during the morning and a decline in the afternoon) (Figs. 4a, 5b). This apparently contrasts with Clearwater et al. (2004) who did not observe any daily changes of $K_{\text{plant,LA}}$. However, in that work K_{plant} measurements started at 10:00 h when the initial rise of conductance (and Ψ_{w} early morning decline) was conceivably finished, while we measured water potentials also in the middle of that ascending stage (08:00 h) and the $K_{\text{plant,LA}}$ increase was documented.

Based on the hydraulic-centred view of plant functioning proposed by Brodribb (2009), high K_{plant} determines high stomatal conductance and photosynthetic capacity. However, during drought as the pipes that constitute the xylem pathway begin to cavitate or collapse, high K_{plant} may result in high vulnerability to cavitation. According with this view, higher $K_{plant,LA}$ observed in *Actinidia* plants which is partially due to the higher k and lower ΔP (see Figs. 3, 4) provides further evidence of the high vulnerability of this Mediterranean non-endemic species to embolism (Lo Gullo et al. 1995; Sperry and Saliendra 1994; Froux et al. 2002). Additionally, differences in vessel diameters suggest a possible different dynamic of embolism repair in xylem which would be slower in *Actinidia* (lower vessel density and higher vessel size, Table 1) than *Olea* plants. Based on recent in vivo observations of the refilling flux in embolised vessels of *Vitis vinifera* (Brodersen et al. 2010) and the mean vessel diameter presented (Fig. 2), it could be estimated that about 8 and 3 h would be required to refill the empty lumen of *Actinidia* and *Olea* vessels, respectively.

In summary, the two experiments reported here showed markedly greater leaf-specific conductivity (k_{leaf}) and lower leaf-specific whole-plant conductance per unit leaf area ($K_{plant,LA}$) in *Olea* than *Actinidia* plants. This study compared the hydraulics of *Olea* and *Actinidia* grown under the same environment, results may contribute to explain their different strategies to cope with soil water availability in Mediterranean climates. When soil water is available, the *Actinidia* plants have high rates of photosynthesis and transpiration, but under limited water they suffer large reductions in leaf conductance and photosynthesis rate (Montanaro et al. 2009). By contrast, olive trees use water more sparingly when it is available without restraint and has a more gradual decrease of photosynthesis and stomatal conductance under prolonged water shortage (Dichio et al. 2006). This vision is consistent with the lower $K_{plant,LA}$ observed in olive trees that may increase water use efficiency and water conservation, which is advantageous in Mediterranean ecosystems.

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