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The dynamics of radial sap flux density reflects changes in stomatal conductance in response to soil and air water deficit

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ABSTRACT

Water scarcity in semiarid regions of Europe threatens the sustainability of fruit tree orchards unless irrigation water is optimized and scheduled in deficit irrigation strategies. Stomatal conductance (g_s) is one of the best indicators of plant water stress, since it is placed in the crossroad between water and CO_2 fluxes at the leaf level. Unfortunately, it is not possible to measure g_s automatically and continuously, which reduces its potential for irrigation scheduling. In this work we examined the use of sap flux density (J_s) in the outer rings of the sapwood of olive trees as a surrogate of g_s. The working hypothesis was that as olive trees are well-coupled to atmosphere because of their small leaves, the ratio of J_s to air vapor pressure deficit (D) should correlate well with the dynamics of g_s in the canopy. It was also expected that current year, sun exposed leaves were mainly connected to the outer rings of the sapwood, and the oldest, shaded leaves to the inner rings. This was tested by measuring g_s in new, sun-exposed leaves vs g_s in old, shaded leaves. Both hypotheses were contrasted and our results confirmed that g_s can be estimated from J_s/D (R^2 of the relationships were always higher than 0.8). A wide range of estimated g_s values (0.350–0.025 $\mathrm{mol\,m^{-2}\,s^{-1}}$) were derived from J_s measurements in an olive orchard under three different irrigation regimes. Results were satisfactory and open the possibility of applying this method to estimate g_s and use it either as a reliable water stress indicator or in transpiration and photosynthesis models applied to fruit tree orchards under a wide range of water stress conditions.

1. Introduction

Expected climate conditions in the Mediterranean area demand an increasing use of sustainable water use practices in agriculture, such as deficit irrigation (DI). The correct use of the most successful deficit irrigation strategies, such as regulated deficit irrigation (RDI; Chalmers et al., 1981) requires both a good understanding of physiological mechanisms involved in the response of plants to water stress, and the use of reliable and sensitive indicators of water stress (Fernández, 2014a). For the latter, special attention has been paid to plant-based methods, since plant measurements have the advantage of integrating the soil and atmospheric water status, as well as the response of the plant to the surrounding conditions (Jones, 2004). New methods have been developed for non-destructive, automatic and continuous measurements, such as dendrometers, sap flow and turgor-related probes. These new methods have several advantages compared to conventional plant-based methods, e.g. water potential or stomatal conductance, which are commonly destructive and time and labor consuming (Fernández, 2014b).

Stomatal conductance (g_s) is a good plant-based indicator for irrigation purposes. Besides g_s quick response to increasing water stress, stomatal closure limits photosynthesis (Flexas et al., 2013) and thus, it has important implications for plant function, growth and yield (Brodribb, 2009). Indeed, stomatal control is regulated to optimize the outward diffusion of water vapor and the diffusion of CO_2 into the leaf during photosynthesis (Hetherington and Woodward, 2003). However, its use for irrigation scheduling purposes faces a major limitation from the difficulty of being automatically and continuously monitored. Yet g_s can be derived easily from transpiration measurements based on a simplification of the Penman–Monteith equation under certain circumstances, as transpiration proceeds largely at the imposed rate which depends mainly on atmospheric conditions (McNaughton and Jarvis, 1983). Transpiration values can be estimated from sap flow related

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measurements. Sap flow methods work automatically and continuously, and are relatively inexpensive and user-friendly compared to other approaches (Wullschleger et al., 1998). Total sap flow or tree transpiration ($\mathrm{L\,h^{-1}}$) is calculated from upscaling the sap flux density (J_s, $\mathrm{mm\,h^{-1}}$) measured at discrete single points in the sapwood to tree scale (sapwood or leaf area based). However, J_s is very variable both at different azimuthal locations (López-Bernal et al., 2010) and along the radial profile (Swanson, 1994). It has also been observed to change not only in the short-term (Ford et al., 2004b; Poyatos et al., 2007; Hernandez-Santana et al., 2008), but also in the long-term as new xylem forms (Beauchamp et al., 2013). The azimuthal variability is a source of uncertainties in the upscaling to the whole tree transpiration, as several authors have reported (López-Bernal et al., 2010; Vandegehuchte et al., 2012). However, the radial variability provides information about the water status of the plant, useful for irrigation scheduling. Indeed, a number of factors have been reported as responsible for the dynamic radial variation of J_s, including changes in soil water status (Fernández et al., 2001; Nadezhdina et al., 2007 but see Beauchamp et al., 2013), mobilization of water stored in the inner sapwood (Ford et al., 2004a,b) to compensate for cavitation in the outer rings (Granier et al., 1994; Ford et al., 2004b; Poyatos et al., 2007), water uptake from deep roots (Nadezhdina et al., 2007; Čermák et al., 2008), stomatal closure in the exposed leaves in response to evaporative demand (Fernández et al., 2001; Ford et al., 2004b; Nadezhdina et al., 2002; Poyatos et al., 2007; Hernandez-Santana et al., 2008), distribution of foliage in the crown (Fiora and Cescatti, 2008) and changes in the distribution of incident radiation across the canopy (Ford et al., 2004a; Jiménez et al., 2000).

Specifically, quick variations in J_s radial profiles have been proposed to be explained by a differential transpiration between the older leaves, lower in the canopy and thus increasingly shaded, and the younger, better illuminated leaves, in the upper parts of the canopy. The older leaves would be hydraulically connected to older, inner sapwood and the younger to outer sapwood (Dye et al., 1991; Jiménez et al., 2000; Fiora and Cescatti, 2008). Despite all the evidences and hypotheses proposed, however, there has been no direct assessment, to the best of our knowledge, of the link between g_s in sun and shade leaves with differential J_s in younger and older sapwood areas of the same conductive organ, respectively. It is clear that the xylem of leaves produced during a given year is connected preferentially to the stem xylem formed on the same year but little is known on how ageing leaves maintain a connection with the xylem and phloem as the stem grows (Maton and Gartner, 2005). In this study we aimed to assess the links between J_s measured in the trunk of olive trees, at different depths below the cambium, and concomitant g_s measurements in leaves of different age and locations in the canopy. Our objectives were: (i) to determine if there is a robust relationship between g_s measured in the tree canopy and J_s measured in tree trunk, (ii) to assess whether changes in the radial profile of J_s can be attributed to changes in the behavior of g_s of sun-exposed, new leaves (hereafter reported as SUN leaves) vs g_s of shade, old leaves (hereafter SHADE leaves) in response to water stress, and (iii) to determine whether changes in the radial profile of J_s mediated by g_s can be related to changes in soil water deficit and air vapor pressure deficit (D). Our findings could have a great potential in agriculture, because of the usefulness of g_s as water stress indicator to schedule irrigation (Jones, 2004).

2. Materials and methods

2.1. Experimental conditions

Measurements were made at two experimental orchards in different years. A summary of the measurements of each orchard is presented in Table 1. Both orchards are located in an area with Mediterranean climate. Annual average precipitation and potential evapotranspiration are 534.0 mm and 1541.5 mm, respectively, with hardly any rainfall during the summer months. Average maximum and minimum air temperatures in the area are 24.9 °C and 10.7 °C, respectively (period 2002–2012). The hottest months are July and August. Average maximum temperatures over 40 °C are recorded nearly every year, with peak values rarely over 45 °C.

The first set of measurements were conducted in 1998 in the olive orchard of La Hampa, the experimental farm of the Instituto de Recursos Naturales y Agrobiología (IRNAS, CSIC), close to Coria del Río, Seville (latitude 37°17′N, longitude 6°3′W, altitude 30 m). The trees were 30-year-old ‘Manzanilla de Sevilla’ olive trees (*Olea europaea* L.) at 7 m × 5 m spacing (286 trees $\mathrm{ha^{-1}}$). The soil of the orchard is a sandy loam (Xerochrept) of variable depth. Two irrigation treatments were studied: well-watered trees (WW), in which trees were irrigated daily to replace the crop water needs, and rain-fed trees (WS) (see details in Fernández et al., 2003). Irrigation needs (IN) in the WW trees were calculated as $\mathrm{IN} = \mathrm{ET}_c - P_e$, being ET_c the maximum potential crop evapotranspiration calculated with the crop coefficient approach (Allen et al., 1998) and P_e the effective precipitation calculated as 75% of the precipitation recorded in the orchard (Orgaz and Fereres, 2001).

The second set of measurements were made in a commercial hedgerow olive orchard, Sanabria, in southwest Spain (37°15′N, −5°48′W). Trees (*Olea europaea* L., cv Arbequina) were planted in 2007, at 4 m × 1.5 m (1667 trees $\mathrm{ha^{-1}}$), in rows oriented N–NE to S–SW. Measurements were made in the 2012 summer, when trees were 2.40 m tall and the crown was 1.96 m × 1.5 m on average. The studied trees were central individuals located in 12 m × 16 m plots with 24 border trees. We had three irrigation treatments, FI, 60RDI and 30RDI, with four plots per treatment, arranged in a randomized block design. In the FI plots daily irrigation was supplied to replace 100% of IN calculated, once again, with the crop coefficient approach. In the 60RDI and 30RDI plots we applied two regulated deficit irrigation treatments in which total irrigation supplies amounted to 60% and 30% of IN, respectively. In May and June RDI trees were irrigated daily. In July and August, however, trees were irrigated only two days per week in 60RDI and one day per week in 30RDI. Details are given in Fernández et al. (2011).

2.2. Sap flux density measurements

The Compensation Heat Pulse (CHP) method (Green et al., 2003) was used to derive sap flux density (J_s, $\mathrm{mm\,h^{-1}}$) values within the

Table 1
Summary of measurements and sample sizes conducted in the two studied orchards.

	La Hampa		Sanabria	
	No. of trees	No. of leaves	No. of trees	No. of leaves
Sap flow probes	2		9	
Regular stomatal conductance	2		18	18 (1 leaves/tree)
Daily cycles of g_s on SUN-SHADE leaves	2	4	2	8 (4 leaves/tree)