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Effects of water deficits on whole tree water use efficiency of orange

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ABSTRACT

To study the effects of water deficits on water use efficiency (WUE) of citrus trees, whole tree transpiration and CO_2 assimilation were measured in a semi-arid environment during the summer of 2012. Young orange trees "Valencia Late", either water stressed (DI) and well-irrigated (C), were monitored in selected days using a gas exchange chamber. Tree transpiration was also measured on a continuous basis with sap flow sensors. The water restriction reduced the transpiration of the DI treatment down to 60% of the maximum potential (treatment C) during the peak of water stress. The instantaneous WUE ranged between 1.7 and 79 g CO_2 L^{-1} H_2O and was tightly related to the vapour pressure deficit. Differences in instantaneous WUE due to water stress were insignificant. On a daily basis, WUE ranged between 4.9 (7 August) and 8.8 (7 June) g L^{-1} for the daytime period; and between 4.0 and 8.2 g L^{-1} for the 24 h period. As water stress was imposed on the DI treatment, a trend of increasing WUE in DI relative to C was observed, reaching, in the maximum stress period, a difference, of 13–15% (daytime) and 20–22% (24 h) although not statistically significant. Partial rewatering returned the WUE to similar values in both treatments. An analysis of the differences in the diurnal patterns of transpiration suggests that the increase in WUE due to water stress in citrus is achieved indirectly by shifting the overall carbon assimilation towards the morning hours of lower evaporative demand.

1. Introduction

Most citrus species originated in the sub-humid, subtropical areas of south-eastern Asia (Scora, 1975; Spiegel-Roy and Goldschmidt, 1996) where drought episodes are infrequent but, over the centuries, the crop has adapted to the arid and semi-arid zones of the world. In these areas, citrus are normally grown under irrigation and water scarcity is often the norm, thus requiring that water is used as efficiently as possible. Assessing the efficiency of water use in crop production has been based on quantifying the water use efficiency (WUE), broadly defined in agronomy as the ratio between crop production and water used (Hsiao et al., 2007). It has long been known that for a given crop and climate, WUE is relatively constant, either under ample or deficient water supply (De Wit, 1958).

From the physiological standpoint, WUE is defined as the ratio of CO_2 assimilation to transpiration and is often termed transpiration efficiency (TE). For methodological reasons, measurements of TE are carried out at the single leaf scale and studies characterizing the TE of citrus are no exception (e.g. García-Sánchez et al., 2007; Habermann et al., 2003; Nebauer et al., 2013; Ribeiro et al., 2009; Syvertsen et al., 1997, 2003). Scaling up TE measurements obtained on single leaves to determine the WUE of whole trees or canopies carries a high degree of uncertainty due to the variations in radiation levels and in the microclimate around trees. If whole tree measurements could be performed, they should be much more meaningful for scaling up to the behaviour of canopies. The use of gas-exchange chambers or canopy bags (Corelli-Grappadelli and Magnanini, 1993) to measure carbon assimilation, transpiration or both simultaneously in whole plants has been expanding progressively in different species: for example apple (Dragoni et al., 2005; Lakso et al., 1996), grapevine (Dragoni et al., 2006; Intrigliolo et al., 2009) and olive (Pérez-Priego et al., 2010; Villalobos et al., 2012).

The strong theoretical and experimental evidence of the relative constancy of WUE under water deficits (De Wit, 1958; Steduto et al., 2007; Tanner and Sinclair, 1983) contrasts with the reports at the physiological level indicating that TE in leaves increases under water deficits. Such an increase is based on an analysis of the resistance analogues to CO_2 and H_2O fluxes (Jones, 1993), and on experimental evidence at the leaf level in various species (reviewed by Chaves and Oliveira, 2004). In citrus, a review of the early

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literature (Kriedemann and Barrs, 1981) indicated that there were conflicting reports about the effects of soil water deficits on TE (with some increase or decrease under water stress relative to what was observed under ample supply), and concluded that further work was desirable to clarify this issue.

Deficit irrigation is a practice that has been recommended for citrus (Ballester et al., 2012; González-Altozano and Castel, 2000) but the tolerance mechanisms that operate during the water deficits periods have not been uncovered. If the WUE of whole trees increase under water deficits, this could be one of the mechanisms contributing to the positive response that deficit irrigation elicits in several citrus species, such as orange (Castel and Buj, 1990) and mandarin (Ballester et al., 2011). We conducted an experiment to measure the whole-tree transpiration water use efficiency (henceforth WUE) of whole young orange trees under ample and deficient water supply, to ascertain the fate of tree WUE as it undergoes water stress and during recovery, at different time scales.

2. Materials and methods

2.1. Site description and experimental setup

The experiment was conducted at Cordoba (south-western Spain; 37.8°N, 4.8°W, 110 m altitude), at the Institute for Sustainable Agriculture of the Spanish Research Council (CSIC) during summer 2012. The soil is a Typic Xerofluvent of sandy loam texture easily penetrable by roots beyond 2 m. The upper (field capacity) and lower (wilting point) limits of available water are 0.23 and 0.09 $m^3\ m^{-3}$, respectively.

The experimental plot consisted of a small orchard (nine rows with five trees per row) of 4-year old orange [*Citrus sinensis* (L.) Osbeck 'Valencia Late IVIA126'] trees, grafted on 'Volkamer' lemon (Citrus volkameriana Tan. and Pasq.), planted at a distance of 4 × 4 m. The plot was fertilized with 75 kg ha^{-1} of N, 50 kg ha^{-1} of P, and 50 kg ha^{-1} of K in spring.

Trees were irrigated by the drip method, with a different combination of emitter number and discharge rate to match the target irrigation treatment. Control trees had four emitters per tree placed on a single drip line near the tree. Two 4 L h^{-1} emitters were located 0.5 m away from the trunk, and two 2 L h^{-1} emitters were placed one m apart from the other two, on each side of the tree. The deficit treatment was irrigated with two, 2 L h^{-1} emitters placed 0.5 m on each side of the tree trunk, that were sided by other two 4 L h^{-1} emitters from 28 August to ensure the recover the deficit irrigated trees. Prior to planting the orchard, vertical plastic sheets of 150 μm thickness were placed between the trees down to 1.2 m depth to isolate their root systems. This allowed the use of individual trees as experimental units without the need for adjacent trees acting as borders.

Six trees in two different water regimes were used for the experiment:

- three individual trees received a control treatment (C), where irrigation fully replenished the estimated crop evapotranspiration (ET). No water deficits were allowed throughout the experiment. The irrigation season lasted from 16 May to 25 September;
- three individual trees received a deficit irrigation treatment (DI), with the same start and ending dates as C, received the following amount of irrigation;
- 33% of the full water requirements, from 16 May until 15 July;
- 16.5% from 16 July to 27 August;
- 100% from 28 August to 6 September, to study the recovery from stress;
- 33% from 8 September to 25 September (end of the season).

During the irrigation season the two irrigation treatments supplied 2221 L $tree^{-1}$ (138 mm) to the control trees and 804 L $tree^{-1}$ to the DI treatment (50.3 mm).

For irrigation scheduling, the full water requirements were calculated as ET-rainfall, where ET was calculated using crop coefficients for citrus trees corrected for canopy size and the Penman–Monteith mean monthly reference evapotranspiration or ET_0 (Allen et al., 1998) for Cordoba, obtained from 30-year historical data series.

2.2. Gas-exchange chamber

A transitory-state chamber was designed and built at IAS-CSIC for simultaneous measurements of CO_2 and water vapour exchange. The chamber was based on previous prototypes (see Pérez-Priego et al., 2010 for description and drawing), and consisted of a rectangular prism with a base of 1.2 × 1 m, and a height of 2 m, giving an overall volume of 2.16 m^3. The walls were made with four sections of rigid aluminium frames and were fit together with simple screws. This particular prototype has no moving windows and is placed as a cap over the tree; it fits on fixed stainless steel frames acting as a base, firmly anchored in the soil around the base of each experimental tree. The bottoms of the base frames are sealed with a thick polyethylene panel, thus fluxes from the soil are excluded from the measurements. Leaks are avoided by placing a soft rubber gasket along the junctions between the chamber and the support frame. The top and the sides of the chamber are covered with clear bi-axially-oriented polyethylene terephthalate (BoPET) film of 75 μm thickness, stretched and fixed to the aluminium frames. The chamber contains four 10 W fans of 15 cm diameter, mixing the air inside the chamber while it is closed (which under normal operating conditions lasts around 3 min). A vacuum pump circulates the air through the sampling circuit: the air is taken from inside the chamber through many intake points, spatially distributed along the chamber and is then returned to it. A sample of 1 L min^{-1} of this airflow is sniffed by a small pump and diverted to a CO_2/H_2O infrared gas analyzer (IRGA) (model LI-COR LI-840, Lincoln, NE, USA) which measures CO_2 and water vapour concentrations simultaneously at 1 Hz sampling rate; the output is recorded by a datalogger (model CR23X, Campbell Scientific, Logan, UT, USA). The IRGA, datalogger and small pump were powered by 12 V batteries. The vacuum pump and the fans are powered using a small portable A/C generator. An infrared thermometer (model IRR-P, Apogee, Logan, UT, USA) is mounted on the centre of the chamber top, facing downwards, to measure the temperature of the canopy. The sensor has a 44° field of view, and can be aimed and adjusted in height for optimal foliage targeting. The canopy temperature variation is checked at post-processing time to ensure that the disturbance in foliage thermal conditions is negligible. The air temperature and relative humidity were also measured inside the chamber with a combined probe (model HMP45AC, Vaisala, Helsinki, Finland) placed near the top of the chamber into a radiation shield.

Two operators are needed for the opening and closing action. At the time of measuring, the chamber is put on the steel frame, closed and the fans are turned on. The CO_2 and water vapour concentrations, measured by the IRGA, change steadily after a short lag time. The concentrations of both gases are recorded at a 1 Hz sampling frequency. After completing a measurement, the chamber is lifted up to the open position away from the tree, with the fans off.

The IRGA was operated in the range of 0–2000 μmol mol^{-1} for CO_2 and 0–80 mmol mol^{-1} for water vapour. A two-point calibration procedure was carried out in the laboratory before measurement operations.

The fluxes were calculated by fitting a second order polynomial model to the gas concentration time series, after removing the lag