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Physiological responses of citrus to partial rootzone drying irrigation

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ABSTRACT

The effect of partial rootzone drying (PRD) on whole plant water use efficiency (WUE_{wp} = tree growth per water applied) and physiological responses of two-year-old split-root potted grapefruit trees was studied in a greenhouse. Four treatments were applied through above and below tree evapotranspiration (ET_c) requirements for 12 weeks: optimum PRD (100% ET_c applied on one split rootzone, no water on the other side), excess PRD (200% ET_c applied on one side, no water on the other side), deficit PRD (50% ET_c applied on one side, no water on the other side), and control (50% ET_c on both pots). Optimum PRD and deficit PRD trees used 18% and 79% less water than control trees, respectively, while excess PRD trees used 70% more water than control trees. Deficit PRD trees, imposing severe water stress by the end of the experiment, had the highest WUE_{wp}, however, decreased efficiency of photosystem II, impaired stomatal conductance, increased concentrations of ABA in leaf tissues, and reduced tree growth. Both optimum PRD, imposing mild water stress, and excess PRD had similar physiological responses, growth, and leaf ABA concentration to control trees. Excess PRD trees did not increase growth with excess water application compared to the other treatments, resulting in drastically reduced WUE_{wp}. On the other hand, optimum PRD trees increased growth allocation to roots over shoots without decreasing growth compared to control trees. Thus, optimum PRD resulted in water-savings without impairing growth or any physiological parameters.

1. Introduction

Citrus are commercially grown in more than 80 countries (Chang, 1992) and the worldwide annual revenues account for more than $9.5 billion (FAO, 2013). The major growing regions include arid, semi-arid, humid subtropical and tropical areas. Some of the major producers are included among the arid and semi-arid subtropical areas, for instance California, Texas and Arizona in the US, countries in the Mediterranean Basin such as Spain, Italy, Greece, Egypt, Turkey or Morocco, and other producing regions such as Australia and northern South Africa (Davies, 1997). In many of these regions, water availability is the most limiting factor and yield reduction can be caused by water stress. Citrus yields heavily depend on irrigation in these areas due to: (a) annual rainfall is lower than crop evapotranspirative needs (ET_c); or (b) an erratic distribution of rainfall does not satisfy seasonal demands during fruit growth.

Partial rootzone drying (PRD) is a strategy based on the irrigation of half of the root system while the other half is left under dry soil; the roots under dry soil trigger a root-to-shoot signaling mechanism based on chemical signals such as abscisic acid (ABA) that are transported to the leaves through transpiration and hydraulic signals (Zhang et al., 1987; Zhang and Davies, 1987, 1989, 1990; Liang et al., 1997; Yao et al., 2001). ABA induces a partial stomatal closure (Zhang and Davies, 1989) and the expression of a group of genes that increase drought tolerance (Bray et al., 1999). As a result of the partial stomatal closure, leaf transpiration decreases without limiting CO_2 assimilation (Jones, 1992), reducing transpiration losses (Davies and Zhang, 1991) without affecting photosynthesis and consequently increasing water use efficiency (WUE; Dry et al., 1996; Stikic et al., 2003).

PRD can be applied either in drip irrigation or in surface irrigation (furrow irrigation) systems although most of the studies have been developed using drip irrigation. PRD has successfully been used in grapevine (Dry et al., 1996; Dry and Loveys, 1998; Stoll et al., 2000; de la Hera et al., 2007), pear (Kang et al., 2002), peach (Goldhamer et al., 2002), olive (Fernández et al., 2006), mango (Spreer et al., 2007) and apple (Leib et al., 2006; Talluto et al., 2008)

Abbreviations: ABA, abscisic acid; ET_c, crop evapotranspiration; PRD, partial rootzone drying; SWP, stem water potential; TPDW, total plant dry weight; VWC, volumetric water content; WUE, water use efficiency; WUEwp, whole plant water use efficiency.

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trees. Nevertheless, PRD has been scarcely studied in citrus (Dzikiti et al., 2008; Melgar et al., 2010); overall, there is a lack of knowledge on the growth response of citrus to PRD and on its effect on basic plant physiological processes. Thus, the objective of this work was to study the physiological responses of citrus trees to PRD strategies.

2. Materials and methods

2.1. Plant material and growth conditions

The study was conducted in a greenhouse at the Texas A&M University-Kingsville Citrus Center, located in Weslaco, TX (USA). Trees were grown in a greenhouse, where the average day/night temperatures were 35/20 °C, the relative humidity varied between 40 and 100% and there was a natural photoperiod of about 14 h.

Two-year-old grapefruit trees (*Citrus paradisi* Macf. cv. Rio Red) grafted on C-146 (*Sunki mandarin* × *Swingle trifoliate orange*) were used. All trees came from our nursery at the Texas A&M University-Kingsville Citrus Center, and only trees of uniform size were selected for this experiment. Each tap root was split with a knife up to the soil line while the shoot remained intact (Gowing et al., 1990; Davies et al., 2000; Loveys, 1991). Then, each half of the root system was allowed to establish separately in two adjacent 2.4 L pots that were taped together. All pots were filled with soil potting mixture (Metro-Mix 300, Sun Gro, Bellevue, WA) containing vermiculite, composted pine bark, Sphagnum peat moss, coarse perlite, bark ash, starter nutrient charge and slow release nitrogen, and Dolomitic limestone. All trees were well-watered daily (soil was kept at field capacity) for 10 days so that trees recovered from the stress of splitting the roots and transplanting.

Whole plant ET_c was gravimetrically calculated every week by determining the weight loss of each pair of attached pots. Eight replicate split-root trees were established in each of the four irrigation treatments: (i) Control; well-watered trees with 50% of the daily ET_c needs applied to each pot; (ii) optimum PRD, with 100% of the ET_c needs were always applied to one pot while the other pot was allowed to dry; (iii) excess PRD, with 200% of the ET_c needs were applied to one pot, zero to the other one [to simulate flood irrigation; flood irrigation is still the primary irrigation system used in different regions, for instance Texas in the U.S. (80%; Nelson, 2013) or traditionally grown citrus in countries in the Mediterranean Basin such as Spain (20%), MAGRAMA, 2012]; and (iv) deficit PRD, with 50% of the ET_c needs applied to one pot while the other pot was not irrigated; this treatment could be defined as a combination of PRD and deficit irrigation (with water applications below the ET_c requirements; García-Tejero et al., 2007). The experiment lasted for 12 weeks. At the end of the experiment, the accumulated ET_c was calculated. Lixiviation was considered (when occurred) for a more exact determination of the volume of water to be applied.

2.2. Soil moisture content

Soil moisture content was measured once a month by time domain reflectometry. At the beginning of the experiment, a soil moisture probe FieldScout TDR 300 with 20 cm rods (Spectrum Technologies Inc., Plainfield, IL) was calibrated for this type of soil by plotting a calibration curve to determine the volumetric water content (VWC, %). Three measurements per each pot were taken using a soil moisture probe: at the beginning of the experiment (week 2), in the middle of the experiment (week 5) and close to the end of the experiment (week 10).

2.3. Chlorophyll fluorescence

Chlorophyll fluorescence was measured with a pulse-modulated fluorometer (OS1p, Opti-Sciences, Hudson, NH) to determine changes in the efficiency of light utilization for electron transport. Measurements were performed every two weeks until the end of the experiments and were taken on one dark-acclimated leaf per tree. Leaves were acclimated to dark by using light exclusion clips (Opti-Sciences, Hudson, NH). The maximum quantum efficiency of photosystem II (F_v/F_m) was calculated as $F_v/F_m = (F_m - F_0)/F_m$, where F_m and F_0 were maximum and minimum fluorescence of dark-acclimated leaves, respectively (Maxwell and Johnson, 2000).

2.4. Gas exchange and water relations

Stomatal conductance (g_s) was measured every two weeks in one young adult leaf per tree since the beginning of the experiment. Measurements were taken with a porometer (SC-1, Decagon Devices Inc., Pullman, WA) between 9:00 and 11:00 h to avoid the high temperatures and low relative humidity of the afternoon that can cause a high leaf-to-air vapor pressure deficit that close stomata (Hu et al., 2009; Jifon and Syvertsen, 2003). Tree water status was determined every two weeks by measuring midday stem water potential (SWP) in one leaf per tree using a Scholander-type pressure chamber (PMS Instrument Co., Albany, OR; Scholander et al., 1965). Leaves were previously introduced in plastic bags covered with duct tape that avoided light penetration, minimized transpiration and equilibrated leaf and stem water potential (SWP; McCutchan and Shackel, 1992). Measurements were taken at least 2 h after leaves were covered, normally starting at 13:00 h.

2.5. ABA: extraction and determination

At the end of the experiment, samples of 1 g fresh weight (FW) of leaves per tree were collected for determination of the ABA concentration, according to the method described by Norman et al. (1990). Briefly, samples were frozen in liquid N, and kept at −20 °C until analysis. Samples were suspended in 20 ml of 80% acetone, 100 mg L^{-1} BHT (2.6-di-tert-butyl-methyl phenol) and 500 mg L^{-1} citric acid. This suspension was constantly stirred for 16 h at 4 °C. Extracts were vortexed and a 12.5 μL of the supernatant was diluted to 0.5 mL with cold TBS buffer (50 mM Tris, 1 mM $MgCl_2$, 150 mM NaCl, pH 7.8). Duplicate samples were analyzed and ABA was quantified using the indirect enzyme-linked immunosorbent assay (ELISA) method with the Phytodetek® ABA immunoassay test kit (Agdia, Elkhart, IN). All this process was performed in darkness to avoid sample ABA degradation. ABA concentration was calculated by interpolation with the logit transformation of the ABA standard curve (Quarrie et al., 1988).

2.6. Growth

Tree growth was determined at the end of the experiment. Leaves, stems and roots were separated, and leaf area, stem and root length were measured. Leaf area was measured using a Li-3100C (Li-COR Inc., Lincoln, NE). Then, leaves, stems and roots were dried in an oven at 70 °C for between two and five days, and dry weight (DW) of each part was measured. With the value of leaf DW, specific leaf area was calculated as leaf area/leaf DW. Total plant dry weight (TPDW) was calculated as the sum of all the dried parts. Whole plant water use efficiency (WUE_{wp}) was calculated as TPDW/total volume of water used.

2.7. Experimental design and statistical analysis

Duplicate samples were used for the ABA analyses, and ABA concentration was calculated by interpolation with the logit transformation of the ABA standard curve (Quarrie et al., 1988). Data from each experiment were analyzed separately as completely