



# Drought tolerance in citrus trees is enhanced by rootstock-dependent changes in root growth and carbohydrate availability



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## ABSTRACT

Valencia orange scions grafted on Rangpur lime or Swingle citrumelo were grown under water deficit to evaluate how those rootstocks modulate the non-structural carbohydrate (NSC) availability and the drought tolerance of citrus trees. Additionally, the importance of young mature leaves as possible sources of carbon in citrus trees was studied. Herein, young mature leaves are those ones fully expanded and developed during water deficit. After 30 days under water limiting conditions, plant growth, leaf water status, photosynthetic rate and carbohydrate availability in old mature and young mature leaves, branches and roots were evaluated. Water deficit reduced the leaf water potential and caused diffusive limitation of photosynthesis in both rootstocks. Drought-induced decrease in total NSC content occurred only in plants grafted on Swingle. While plant growth on Swingle citrumelo was severely reduced by water deficit, plants grafted on Rangpur did not exhibit impairment of dry matter accumulation. The lower sensitivity of plant growth on Rangpur lime was associated with the enhanced root growth, the maintenance of the total carbohydrate pool and to a large shift in the carbohydrate partitioning, with the roots accumulating carbohydrates under water deficit. Regarding the young mature leaves, they exhibited higher photosynthetic rates than the old mature leaves after 30 days of treatment, regardless of the water conditions. As possible sources of carbohydrates, young mature leaves have equal importance as compared to branches under well-watered conditions.

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## 1. Introduction

Drought is considered the most constraining environmental factor, limiting crop yield and development and significantly impairing photosynthesis (Parry et al., 2005; Passioura, 2007; Chaves et al., 2009). As photosynthesis is the primary source of carbohydrates, imbalances in the carbon metabolism of citrus trees are expected under water shortage. The early effects of water stress on citrus photosynthesis are mediated through partial stomatal closure, causing low CO<sub>2</sub> availability at carboxylation sites (Erismann et al., 2008). Under more severe conditions, the biochemistry of photosynthesis is affected, as the activity of ribulose-1,5-bisphosphate (RuBP) carboxylase/oxygenase (Rubisco) and the regeneration of RuBP are reduced (Vu and

Yelenosky, 1988; Damour et al., 2008). Photochemistry is also affected under water shortage, with citrus plants showing low quantum efficiency of photosystem II (PSII) and reduced electron transport rates in thylakoid membranes (García-Sánchez et al., 2007). As another consequence of drought stress, shoot respiration may increase to maintain metabolic activity and then decrease carbohydrate reserves in storage organs (Meltcafe et al., 2010).

Under severe carbon starvation induced by water deficit, physiological adjustments to balance the supply and demand of energy and carbon occur, with plants frequently presenting a reduction in growth rates (Smith and Stitt, 2007) or changes in shoot/root ratio (Shao et al., 2008). Roots and branches in tree species are well-known storage organs, where significant amounts of starch may be found and remobilized to supply plant demand. Under constraining conditions, sucrose synthesized in photosynthetic organs such as leaves or originated from starch degradation in roots and branches must be used to maintain plant metabolic activity (Dickson, 1991). Increases in leaf concentration of soluble carbohydrates and reductions in starch concentration are observed under moderate water deficit, whereas there are reductions in

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both soluble and starch fractions under severe water deficit (Vu and Yelenosky, 1989; Chaves et al., 2009). These changes in carbon availability are probably consequences of both low photosynthesis and high mobilization of leaf reserves for maintaining physiological activity and plant growth under moderate water deficit. Plants may use the carbohydrates stored in leaves, branches and roots to overcome stressful conditions, as low photosynthetic rates are not adequate to supply the plant metabolic demand (Dickson, 1991). As citrus trees may maintain shoot growth under moderate water deficit, the importance of young mature leaves for plant carbon balance is unknown as compared to old mature ones.

Citrus rootstocks have differential capacities for supplying shoot tissues with water and carbon, improving resistance to biotic and abiotic stresses and affecting plant water status and photosynthesis (Barry et al., 2004; Romero et al., 2006; Rodríguez-Gamir et al., 2010; Machado et al., 2013). Water relations have been well studied in citrus trees, showing that rootstocks alter the physiological performance under water deficit through variations in plant hydraulic conductance, leaf water potential and stomatal conductance (Romero et al., 2006; Magalhães Filho et al., 2008; Rodríguez-Gamir et al., 2011). However, the importance of rootstock as source of carbohydrates is poorly reported. Recently, Bueno et al. (2012) showed that increases in shoot growth rate occurred in parallel with the consumption of starch stored in roots, which was more abundant in citrus trees grafted on Rangpur lime than in those grafted on Swingle citrumelo. Rangpur lime is an important rootstock in Brazilian citriculture, improving crop yield under water limiting conditions (Davies and Albrigo, 1994). On the other hand, Swingle citrumelo is an alternative rootstock that induces tolerance to low temperatures, with increasing importance due to its resistance to some citrus diseases (Davies and Albrigo, 1994).

To improve our understanding of citrus carbon metabolism under water deficit, we hypothesized that (i) rootstocks modulate the non-structural carbohydrate availability in citrus trees, affecting the carbon reserves and plant growth; and (ii) young mature leaves are important sources of carbon for citrus trees. This study was carried out with Valencia sweet orange scions grafted on Rangpur lime and Swingle citrumelo grown under water deficit, revealing an interesting modulation of plant carbohydrate availability through rootstocks and the relevance of young mature leaves for the plant carbohydrate pool.

## 2. Materials and methods

### 2.1. Plant material

Valencia sweet orange [*Citrus sinensis* (L.) Osbeck] plants were grafted on 10-months old Rangpur lime (*Citrus limonia* Osbeck) or Swingle citrumelo [*Citrus paradisi* Macf × *Poncirus trifoliata* (L.) Raf.] rootstocks. The experiment began four months after grafting. Plants were grown in plastic pots (7 L) containing a commercial organic substrate composed of pine bark and vermiculite (Multiplant Citrus, Terra do Paraíso Ltda., Holambra, SP, Brazil) under greenhouse conditions. Inside the greenhouse, air temperature varied between 15 and 35 °C and the maximum photosynthetically active radiation (Q) reached about 700  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at tree canopy. Plant nutrition was supplied using a commercial nutrient solution (Brennfeed®, Brenntag Química Brasil Ltda., São Paulo, SP, Brazil), and plants were irrigated and fertilized frequently until the beginning of the water deficit treatment.

### 2.2. Growth conditions and water deficit

Plants of similar size (height, leaf area and number of sprouting shoots) were selected. At this time, the biometry and the

dry matter partitioning of three plants of each rootstock was evaluated to characterize the initial condition. The leaf dry matter of plants grafted on Swingle and on Rangpur was  $3.2 \pm 0.3$  and  $2.7 \pm 0.5$  g, respectively. For branch dry matter, plants grafted on Swingle presented  $9.7 \pm 1.0$  g while those ones grafted on Rangpur had  $6.8 \pm 0.9$  g. Regarding root dry matter, plants grafted on Rangpur and on Swingle had  $7.6 \pm 0.9$  and  $10.9 \pm 1.3$  g, respectively. Plant height was around  $48.5 \pm 4.1$  and  $46.9 \pm 2.1$  cm on Swingle and Rangpur, respectively. The stem diameter varied between 0.7 and 0.8 cm on both rootstocks. The total leaf area was  $442 \pm 77$  ( $14 \pm 1$  leaves) and  $529 \pm 33$   $\text{cm}^2$  ( $9 \pm 1$  leaves) in plants grafted on Swingle and Rangpur, respectively.

Selected plants were transferred to a growth chamber (PGR15, Conviron, Winnipeg MB, Canada) and subjected to a thermal regime of 35/20 °C (day/night). The temperature regime of 35/20 °C was chosen to improve citrus growth and obtain high shoot growth rates. Recently, we reported the improvement of citrus growth under warm conditions, with full leaf expansion and physiological maturity achieved within 20–30 days (Bueno et al., 2012; Ribeiro et al., 2012). The other environmental conditions inside the growth chamber were: photosynthetically active radiation (Q) of 800  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , the air vapor pressure deficit (VPD) lower than 1.5 kPa, and the photoperiod of 12 h (7:00–19:00 h).

Plants were grouped into two lots: one lot with three plants of each scion/rootstock combination was maintained at 80% of the maximum water storage capacity of substrate and the other lot also with three plants of each scion/rootstock combination was subjected to water deficit by maintaining substrate moisture at 40% of the maximum water storage capacity throughout the experimental period (30 days). The level of 80% was chosen because there is water enough to reach the demand of citrus plants and to avoid low oxygen concentration and any undesired effect on nutrient availability due to lixiviation. Firstly, we determined the water holding capacity of each pot filled with the commercial substrate. Then, a fraction of this capacity (80% or 40%) was set as the water treatment. As we knew the plant fresh mass, we estimated the initial weight target of each water treatment. Irrigation was stopped and the pots (substrate and plant) were weighed daily until reaching the weight target. Afterwards, water was supplied to compensate the mass variation between two consecutive weightings in intervals of two days. The substrate moisture varied between 35% and 45% of maximum holding capacity in the water deficit treatment and between 75% and 85% in the reference treatment (well-watered).

### 2.3. Plant growth

After 30 days of water deficit, plants were harvested, and the dry matter was determined for old mature leaves (LDM), branches (BDM) and roots (RDM). Dry matter of young mature leaves and branches developed during the experimental period were also evaluated, summed and named as shoot dry matter (SDM). The entire plant dry matter (TDM) was calculated as the sum of LDM, BDM, RDM and SDM. The plant organs were separated and dried in an oven with forced air circulation (MA032, Marconi, Piracicaba, SP, Brazil) at 60 °C until constant weight. The young leaf area (LA) was assessed using a digital planimeter (LI-3000, LI-COR, Lincoln, NE, USA). The length of young shoots (SL) was evaluated using measuring tape. The growth rates were calculated for LDM, BDM, RDM, SDM, TDM, LA and SL during the experimental period.

### 2.4. Leaf water potential

The leaf water potential ( $\Psi$ ) was measured using a pressure chamber model 3005 (SoilMoisture, Santa Barbara, CA, USA) on leaves similar to those used for the evaluation of leaf gas exchange. Measurements were obtained during the initial characterization

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