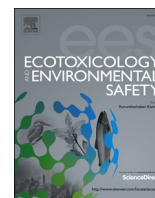




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Response of three citrus genotypes used as rootstocks grown under boron excess conditions



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ABSTRACT

In citrus, the effects of an excess of boron (B) are conditioned by the type of rootstock. In the present work, the morphological, physiological and biochemical responses of seedlings from three citrus genotypes, commonly used as rootstocks in citriculture. In particular, Citrange Carrizo (CC), *Citrus macrophylla* (CM) and sour orange (SO) seedlings were treated with an excess of B (10 mg L^{-1}) in the nutrient solution in order to determine the relative tolerance and to understand the possible mechanisms that make a rootstock more tolerant than the others. To assess these responses, different parameters were measured in plants, such as vegetative growth, B concentration in leaves, stems and roots, gas exchange and chlorophyll fluorescence, the concentration of osmolytes and the activity of enzymes related to the antioxidant system. The results showed, according to the growth parameters, that the SO rootstock was the most tolerant to an excess of B; while CC was the most sensitive. This result was due to the fact that SO plants accumulated less B in leaves, as its roots have a great capacity of restricting the uptake and transport of B towards the aerial part. Moreover, SO is suggested to diminish B toxicity risk through its antioxidant system, since it presented high activity of ascorbate peroxidase (APX) and superoxide dismutase (SOD), as well as high accumulation of quaternary ammonium compounds (QACs).

1. Introduction

Boron (B) is a micronutrient that is needed by higher plants for their main physiological functions involved in their growth and development. However, toxicity caused by an excess of this nutrient can be found in arid or semiarid regions, in which waters high in B concentration are used (Dorta-Santos et al., 2016). The addition of water from seawater desalinating plants and urban wastewater treatment plants is common in areas with a Mediterranean climate, where good-quality water resources are scarce. These non-conventional water sources can have excessive concentrations of B for sensitive crops, such as in the case of citrus plants, where a concentration above 0.3 mg L^{-1} is considered to be the threshold of toxicity (Grattan, 2013). With the use of this type of water for irrigation, phytotoxicity problems can arise, which give way to the loss of good agronomic performance of the crops (Sotiropoulos et al., 1999; Gunes and Alpaslan, 2000).

The most common symptom found in plants exposed to high concentrations of B, for crops that have a low B mobility (e.g. citrus), is the appearance of the chlorosis and/or burns on the edges and tips of the

more mature leaves (Gimeno et al., 2012). Tolerance to B has been associated, among other factors, to the ability of the plant to restrict B uptake through the roots, and its subsequent transport to the aerial parts of the plant (Reid, 2010), which allows for the maintenance of a B concentration that is below its toxic values. The absorption of B through the roots is regulated by three transport mechanisms across the plasma membrane: passive diffusion of boric acid, facilitated diffusion of boric acid via channels, and export of the borate anion via passive and/or active transporters. (Yoshinari and Takano, 2017). Under boron-limiting conditions, boric acid channels and borate exporters function in the uptake and translocation of B to support growth of various plant species, while borate exporters act under conditions of excess B. Once the B enters the roots, it is transported by the transpiration stream towards the upper part of the tree (Papadakis et al., 2004a; Chatzissavvidis and Therios, 2011), so that all the factors that influence transpiration (weather conditions, genotypes, etc.) will play an important role in the crop's tolerance to B. On the other hand, besides the concentration of B that accumulates in the tissues, the different plant's tolerances to B is determined by the toxic effects this element exerts at

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the cellular, vascular, physiological and metabolic levels, as described by Princi et al. (2016). This toxicity can be dampened by different factors such as the compartmentation of B into the vacuole, the insolubilization and deposition of B in the cell wall, and/or the induction of antioxidant systems (Princi et al., 2016). When plants experience some type of stress, such as B toxicity, the creation of reactive oxygen species (ROS) can occur. The effects of ROS can be diverse, such as the inhibition of enzymes, degradation of photosynthetic pigments, lipid peroxidation of cellular membranes, and DNA fragmentation (Das and Roychoudhury, 2014). The ROS produced within cells can be eliminated by diverse antioxidant systems, through the action of enzymes such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), and the ascorbate-glutathione cycle (ASA-GSH). One of the parameters used to evaluate the damage caused by the oxidative stress is malondialdehyde (MDA) concentration. In addition, the compatible solutes (proline, quaternary ammonium compounds, and carbohydrates) have also an important role in the adaptation mechanism of the plants to abiotic stresses, including boron toxicity, where its functions vary from species to species and even within plants species (Siddiqui et al., 2013; Chen et al., 2012). This is due to compatible solutes can lower or balance the osmotic potential within cells and it can also act as an antioxidant and a source of energy (Marco et al., 2015; Rejeb et al., 2014).

In citrus, rootstock genotypes play a fundamental role in the tree's tolerance to abiotic stresses, including drought, cold, salinity and alkalinity. Among common commercial citrus rootstocks, sour orange (*C. aurantium* L.; SO) is considered salt and drought tolerant relative to Citrange Carrizo (*Citrus sinensis* × *Poncirus trifoliata*; CC) which is considered sensitive; while *Citrus macrophylla* (CM) is considered to have an intermediate tolerance between SO and CC (Syvertsen and Garcia-Sanchez, 2014; Ribeiro et al., 2014). The greater tolerance of SO and CM to salinity and drought as compared to CC is mainly due to the former having a high water use efficiency (WUE) and a greater capacity for restricting the entrance and transport of Cl⁻ and/or Na⁺ from the root to the aerial part of the plant (Balal et al., 2012; Fernandez-Ballester et al., 2003; Syvertsen et al., 2010). As for the responses of these rootstocks to B, they have hardly been studied. Thus, the objective of the present study is so evaluate the morphological, physiological and biochemical responses of seedlings of the citrus rootstocks Citrange Carrizo (CC), *Citrus macrophylla* (CM) and sour orange (SO) to an excess of B (10 mg L⁻¹), in order to identify the more tolerant rootstock, as well as the mechanisms/effects that determine this tolerance. More specifically, the relationship between absorption and transport of B from the root to the aerial part of the plant and the concentration of B in the leaves will be studied, as well as the toxic effects provoked by B on the physiological and biochemical processes of these plants.

2. Materials and methods

2.1. Plant materials and experimental conditions

In this study, three-month old plants of the rootstocks Citrange Carrizo (*Poncirus trifoliata* [L.] × *Citrus sinensis* [L.]), *Citrus macrophylla* and sour orange (*Citrus aurantium* L.) were used, which were acquired from a commercial nursery (Viveros Torreblanca S.L.). The seedlings were grown in 7 L pots with a fine-grained universal substrate (a mix of white and black peat, coconut fiber and perlite, 5:4:1; Projar, Spain). The experiment was conducted in a multi-tunnel-type greenhouse, with the following climatic conditions: maximum photosynthetically-active radiation (PAR) of 1000 mmol m⁻² s⁻¹, day/night temperature of 35/18 ± 3 °C, day/night relative humidity of 65/85 ± 5% and a 16-h photoperiod. The plants were watered 3 times per week, with enough water to produce a drainage of 15% of the total volume applied. The plants were irrigated with a complete nutrient solution with the following composition of macronutrients (mM): 20 N, 0.75 P, 4.2 K and 6 Ca; and micronutrients (µM): 23 B, 2 Mn, 2 Zn, 0.5 Cu, 0.5 Mo and 20

Fe. Two months after the plants were transplanted to the greenhouse pots, they were divided into two groups per rootstock. One of the groups was watered with the previously-mentioned nutrient solution. The 0.25 mg L⁻¹ B concentration was considered to be the control, as this was an adequate B concentration for normal plant growth (Hoagland and Arnon, 1950). The other group of plants was watered with nutrient solutions containing 10 mg L⁻¹ of B (equivalent to 925 µM). In any treatment, B was applied as boric acid (H₃BO₃). The B treatments were applied for 120 days during August–November (2015), after which, the plants were harvested. For each rootstock and B treatment, there were 12 randomly-distributed seedlings in the greenhouse, in a surface area of 30 m².

2.2. Plant growth analysis, and boron transport and uptake

In the days 0, 45, 90 and 120 after starting the experiment, three plants per treatment were harvested, and the leaves, stem and roots were separated and weighed. The tissues were briefly rinsed with deionized water, oven-dried at 60 °C for at least 48 h, weighed and ground to a fine powder.

The dry masses of the leaves, stem and roots were used to calculate the total plant dry mass and the relative growth rate (RGR; Evans, 1972). The RGR is the increase in dry weight per unit of initial dry weight, and was calculated by the following equation (Fernandez-Ballester et al., 2003):

$$RGR = \frac{LnW_2 - LnW_1}{t_2 - t_1}$$

where W_1 and W_2 are the dry mass of the plants harvest times t_1 and t_2 , respectively, expressed in g g⁻¹ day⁻¹. The RGR is factored into two components: the mass-based net assimilation rate, NAR_m (mg g⁻¹ day⁻¹), which is the increase in plant biomass per unit leaf mass and time, and the leaf mass fraction, LMF (g g⁻¹), which is the ratio between leaf mass and the plant dry weight.

$$RGR = NAR_m \times LMF$$

$$= \left(\frac{(W_2 - W_1)(LnLw_2 - LnLw_1)}{(t_2 - t_1)(Lw_2 - Lw_1)} \right) \left(\frac{\left(\frac{Lw_1}{w_1} \right) + \left(\frac{Lw_2}{w_2} \right)}{2} \right)$$

Where Lw_1 and Lw_2 are the dry mass of the leaves harvest times t_1 and t_2 , respectively. The relationships between the various growth parameters and RGR were tested with GRC_x (Poorter and van der Werf, 1998). The growth response coefficients (GRC) value of a growth parameter is calculated as the ratio between the changes in that growth parameter and RGR. This is a simple way to express the relative importance of each of the underlying growth parameters (X = NAR_m or LMF) covarying with the variation in RGR.

$$GRC_x = \frac{Ln(X)_{control} - Ln(X)_B}{Ln(RGR)_{control} - Ln(RGR)_B}$$

GRC_x equals to 1 if a proportional change in RGR is only due to a similar proportional change in growth parameter X, and zero if X remains constant and the change in RGR is only due to changes in other growth parameter.

In all plant tissues, the B concentration was determined by inductively coupled plasma emission optical spectrometry (Iris Intrepid II, Thermo Electron Corporation, Franklin, USA) after an acid digestion in HNO₃:H₂O₂ (5:3 by volume) in a microwave that reached 190 °C in 20 min and held this temperature for 2 h (CEM Mars Xpress, North Carolina, USA). From this, net uptake rate and transport (µmol g_{root DW}⁻¹ day⁻¹) to the shoot were calculated as described by Pitman (1988):

$$Nutrient\ uptake = \left[\frac{LnR_2 - LnR_1}{R_2 - R_1} \right] \times \left[\frac{C_{T2} - C_{T1}}{t_2 - t_1} \right]$$

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