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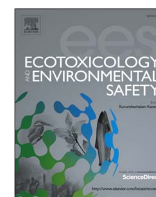

Deficiency and toxicity of boron: Alterations in growth, oxidative damage and uptake by citrange orange plants

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A B S T R A C T

Boron (B) deficiency and toxicity are the major factors that affect plant growth and yield. The present study revealed the effect of B deficiency and toxicity on plant growth, morphology, physiology, and cell structure. A hydroponic culture experiment was conducted with five B levels, B deficient (B0), sufficient (B20, B10, B40) and toxic (B100). Our results show that both B deficient as well as excess level inhibit plant growth. In B deficiency, the major visible symptoms were appeared in roots, while B excess burned the leaf margin of older leaves. The antioxidant enzymes including superoxide dismutase (SOD), peroxidase (POD), catalase (CAT) and ascorbate peroxidase (APX) decreased at B deficiency and also decreased up to some extent at B excess, while in sufficient treatments, the higher antioxidant enzymes were found at B20. In addition, the MDA concentration decreased at B deficiency and increased with B concentration. Moreover, the photosynthetic rate, transpiration rate, stomatal conductance, leaf gas exchange and intercellular CO_2 were reduced at both B deficiency as well as excess and higher at sufficient B20 treatment significantly. The chlorophyll and carotenoid content increased at B20 treatment, while decreased at B deficiency and excess. The middle lamellae of cell wall were found thick at B excess and normal at B20. The current study revealed that B deficiency as well as excess concentration affect plant growth and various morpho-physiological processes.

1. Introduction

Boron (B) is an important micronutrient necessary for the plant growth and development (Tanaka and Fujiwara, 2008). Although the requirement of B varies in different crops but the optimum value of B content for most crops is about 20 mg/kg^{-1} The availability of B concentration in proper amount in soil is necessary for plant growth, development and yield. In the earth crust B content availability ranges from 20 to 200 µg g^{-1}, and B available in soils ranges between 0.4 and 5 µg g^{-1}. The average B content in plant tissues is to be found about 2 µmol g^{-1} (20 µg g^{-1}) of dry weight. Plants uptake B as an un-dissociated boric acid (Hänsch and Mendel, 2009; Mengel and Kirkby, 2001; Tewari et al., 2010). The range of B between deficiency and excess, both is very narrow producing toxic symptoms that affect crop yield and production (Camacho-Cristóbal et al., 2008). B deficiency is a nutritional disorder which vary from high B soils and high rainfall areas all over the world (Marschner, 2012). Plants which grow in B deficient soil must show B deficiency symptoms in initial stage, such as abnormal growth of the apical growing region. Later on, plants show retarded growth, because B deficiency affect physiological, biochemical and molecular processes and resulted in decreased yield (Tewari et al., 2010). Root growth is also sensitive to B deficiency, primarily as a result of disturbing cell wall plasticity and additionally due to the inhibition of root meristem functioning (Herrera-Rodríguez et al., 2010).

In addition to other plants, Boron deficiency and excess also affect citrus growth and productivity. For example, in southern part of China B deficiency negatively affect citrus quality and productivity as well (Jiang et al., 2009; Wang et al., 2011). B deficiency can be removed through the B application by various ways. Many previous studies showed that B application improved yield and fruit quality (Boaretto et al., 2011). In addition to B fertilizers, B deficiency can also be controlled by using different rootstocks to absorb B efficiently from the soil by citrus (Boaretto et al., 2008). On the other side, B excess also results in plant toxicity and also damage the plant growth and productivity. The primary symptoms exhibit by plants exposed to B toxicity are burning of older leaves margins or tips i.e., chlorosis and necrosis and

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reduce vigor. Later on, it delay development, inhibit plant growth and decrease weight, number and size of fruits (Herrera-Rodríguez et al., 2010; Reid and Fitzpatrick, 2009). It is well known from the previous studies that B toxicity increases oxidative stress (Aftab et al., 2010; Cervilla et al., 2007; Landi et al., 2014). For instance, it has been described that excess of B from contaminated soil causes oxidative stress in sunflower (*Helianthus annuus* L.) (Giansoldati et al., 2012; Tassi et al., 2011).

Citrus belong to the genus *Citrus L*. of the family Rutaceae. It is subtropical evergreen fruit tree that are mostly cultivated on acid soils in humid and sub humid of tropical, subtropical, and temperate areas of the world. Citrus count as one of the important commercial crops in China as well as all over the world. The annual production of citrus is about 102 million tons (Mehl et al., 2014). Citrus fruits are highly accepted and appreciated by consumers throughout the world because of their pleasant flavors, attractive color and aroma. With the increase in production, improvement in storage, processing techniques and year-round supply, citrus fruits became an important commercial fruit and dietary source of nutrients for people all over the world. Previous reports showed that B deficiency commonly observed in China, and is responsible for significant loss of citrus fruit productivity and quality (Han et al., 2009; Jiang et al., 2009; Xiao et al., 2007).

In order to adapt their self in harsh environmental conditions, citrus plants evolved various processes to cope with numerous stresses including B deficiency and excess. Antioxidant enzymes are one of these strategies that tolerate plant against multiple stresses including B deficiency and toxicity (Juan et al., 2005). As in most environmental stresses, B toxicity leads to the formation of reactive oxygen species (ROS) which cause oxidative damage of cellular membranes and finally the cell death may occur (Cervilla et al., 2007). In order to reduce cellular damage produced by ROS, plants have developed the scavenging systems composed of antioxidant enzymes, such as superoxide dismutase (SOD), peroxidase (POD), ascorbate peroxidase (APX) and catalase (CAT) (Chen et al., 2005), and non-enzymatic scavenging system like ascorbate, glutathione, alpha -tocopherol (Blokhina et al., 2003; Miller et al., 2008) and osmoprotective solutes like proline (Cervilla et al., 2012). It has been well reported that under B deficiency plants display antioxidant enzymes to scavenge ROS (Karabal et al., 2003; Gunes et al., 2006; Molassiotis et al., 2006; Han et al., 2008; Tewari et al., 2010).

The present work was conducted to study the effects of B toxicity and deficiency on the growth of citrange orange plant. In addition, B concentrations in leaf, stem and root were also determined. Moreover, lipid peroxidation (MDA), proline and H_2O_2 content, and antioxidant enzyme (SOD, POD, CAT and APX) activities were also checked to determine the optimum concentration required for citrange. This study was designed to provide a basis for developing strategies to reduce the risks related to B deficiency and toxicity and maintain and/or increase citrange production.

2. Material and methods

2.1. Plant materials, growth conditions and treatments

Hydroponic conditions were used for this study. Six month-old Citrange plants with uniform size were brought from a commercial plant market. To remove surface contaminants, seedlings were washed three times with distilled water and soaked in tap water for two days. The resultant seedlings were transplanted in black pots containing three liter of nutrient solution. Black foam board with holes for seedling were used to fix the seedlings and put in an illuminated greenhouse with relative humidity of 60–80%, a constant temperature of 26 °C, and a photoperiod of 14 h/10 h light/dark (300–320 μmol m^{-2} s^{-1} photosynthetic photon flux density). The greenhouse, where experimental plants were placed, is located in Huazhong Agricultural University, Wuhan, China. Before the experimental treatments, modified form of Hoagland and Arnon (0.5 mM KNO_3, 0.6 mM $Ca(NO_3)_2$, 0.5 mM $MgSO_4$, 0.07 mM Na_2HPO_4, 0.16 mM NaH_2PO_4, 2.2 μM $MnCl_2$, 0.4 μM $ZnSO_4$, 0.08 μM $CuSO_4$, 0.09 μM Na_2MoO_4, 14.4 μM EDTA-Fe) were provided for two weeks. Meanwhile, two-week-old seedlings grown in the same conditions were kept as control. The experiments were started on April 2016, and lasted 75 days.

2.2. Plant growth parameters

The primary root length was measured with the help of a ruler from the top of the hypocotyls along the taproot to the root tip. In addition, plant height was measured by a ruler from the bottom of the epicotyls along the stem to shoot tips.

2.3. Leaf gas exchange

The leaf gas exchange parameters such as the photosynthetic rate (Pn; lmol CO_2 m^{-2} s^{-1}), intercellular CO_2 concentration (Ci; mmol mol^{-1}), stomatal conductance (gs; mmol H_2O m^{-2} s^{-1}), and transpiration rate (E; mmol H_2O m^{-2} s^{-11}) were measured by using the Li 6400 portable photosynthesis system (LI-COR Inc., Lincoln, NE, USA) at the end of the experiments. Measurements were conducted on the basal leaves of plant which are located between the middle and the base of the scion's shoots. These parameters were measured from 09:00 a.m. to 12:00 p.m. under balanced light intensity of 1000 lmol m^{-2} s^{-1} with 385 ± 10 llL^{-1} CO_2 concentration and 28–30 °C temperature.

2.4. Plant morphology and B uptake by citrange

The root scanning analyzer (WinRHIZO2009) was used to observe the root morphology. All the plant parts i.e., root, stem and leaves were washed consecutively with tap water and deionized water for at least three times. The corresponding samples were dried in an oven at 70 °C for 3 days. After recorded fresh and dry weight of samples, the subsequent dry samples were then grounded to fine powder and stored for further analyses.

To determine the B concentration in root, stem and leaves, 0.2 g grounded powder of each part were ashed at 550 °C in porcelain crucibles and followed by dissolution of 10 ml 0.1 M HCl. Sheng et al. (2009) was further followed to determine the B concentration in citrange.

2.5. Antioxidant enzyme activity

To evaluate the enzymes activities in shoots of different B treatments, freshly washed above ground part (0.5 g) were ground in liquid N_2 and homogenized in 5 ml of 0.2 mol L^{-1} sodium phosphate buffer (pH 7.8). The homogenate was then centrifuged at 12,000 rpm for 15 min at 4 °C, and the supernatant was collected for the determination of enzymes activities.

SOD activity was evaluated by the method of Beauchamp and Fridovich (1971). CAT activity was assessed by using the method of Aebi and Bergmeyer (1983). POD activity was checked by using the guaiacol oxidation method as illustrated by Li (2000). APX activity was evaluated by the method of Nakano and Asada (1981). Lipid peroxidation was measured by determination of the MDA contents as described by Heath and Packer (1968).

2.6. Microscopy

For (Transmission Electron Microscope) TEM study, the samples were fixed in 2.5% glutaraldehyde solution in 50 mM potassium phosphate buffer (pH 6.8) and kept overnight at room temperature. After that, samples were washed three times, for 15 min each, with 50 mM sodium cacodylate buffer (pH 6.9) and ultimately diluted (1:1) with 50 mM sodium cacodylate buffer (pH 6.9) (Sandalio et al., 2001).

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