Available online: www.notulaebotanicae.ro
Print ISSN 0255-965X; Electronic 1842-4309
Not Bot Horti Agrobo, 2016, 44(1):250-256. DOI:10.15835/nbha44110136
Notulae Botanicae Horti Agrobotanici Cluj-Napoca
Original Article

Boron Supply and Water Deficit Consequences in Young Paricá (*Schizolobium parahyba* var. *amazonicum*) Plants

Bianca do Carmo SILVA, Pêola Reis de SOUZA, Daihany Moraes CALLEGARI, Vanessa Ferreira ALVES, Allan Klynger da Silva LOBATO, Elaine Maria Silva Guedes LOBATO*

*Universidade Federal Rural da Amazônia, Paragominas, Pará, Brazil; biancadocarmosilva@outlook.com; peolasouza.agro@gmail.com; daihanymc@hotmail.com; vanessa.fealves@gmail.com; allanllobato@ufra.edu.br; elaineguedes1@gmail.com (*corresponding author)*

Abstract

Boron (B) is a very important nutrient required by forest plants; when supplied in adequate amounts, plants can ameliorate the negative effects of abiotic stresses. The objective of this study was to (i) investigate gas exchange, (ii) measure oxidant and antioxidant compounds, and (iii) respond how B supply acts on tolerance mechanism to water deficit in young *Schizolobium parahyba* plants. The experiment employed a factorial that was entirely randomised, with two boron levels (25 and 250 µmol L^{-1}, simulating conditions of sufficient B and high B, respectively) and two water conditions (control and water deficit). Water deficit induced negative modifications on net photosynthetic rate, stomatal conductance and water use efficiency, while B high promoted intensification of the effects on stomatal conductance and water use efficiency. Hydrogen peroxide and electrolyte leakage of both tissues suffered non-significant increases after B high and when applied water deficit. Ascorbate levels presented increases after water deficit and B high to leaf and root. Our results suggested that the tolerance mechanism to water deficit in young *Schizolobium parahyba* plants is coupled to increases in total glutathione and ascorbate aiming to control the overproduction of hydrogen peroxide and alleviates the negative consequences on electrolyte leakage and gas exchange. In relation to B supply, this study proved that sufficient level promoted better responses under control and water deficit conditions.

Keywords: abiotic stress, antioxidant compounds, gas exchange, micronutrient

Introduction

The Paricá plant, *Schizolobium parahyba* var. *amazonicum* (Huber ex. Ducke) Barneby, is a forest species of Amazonian origin, which stands out in forestry and agroforestry plantations (Ohashi *et al*., 2010). This softwood species is used in wood industries for manufacturing plywood blades, as well as in the manufacturing of pulp and paper (Rosa, 2006). Because of this, an expansion of Paricá commercial plantations was observed in Brazil, reaching about 87,901 ha in 2012, mainly in the Amazon (Abraf, 2013).

Boron (B) is an essential micronutrient for higher plants, and it exercises influence on cell functions and metabolism, and inadequate levels can induce physiological and morphological changes, with negative repercussion also on growth and development (El-Hamdaoui *et al*., 2003; Kastori *et al*., 2008; Gupta *et al*., 2014).

Water deficit cause biochemical modifications such as oxidative stress and cell damages (Barbosa *et al*., 2014). Simultaneously, interferences on gas exchange like as stomatal closing and lower photosynthesis and respiration rates are detected (Tahkokorpi *et al*., 2007; Kiani *et al*., 2008).

Tolerance mechanisms are critical to sustain cellular functions and metabolic activities under water deficit conditions (Farooc *et al*., 2009), and to respond how B supply can influence these mechanisms are justified due to this element to have several roles, such as composition of cell wall, plasma membrane permeability and nitrogen fixation (Camacho-Cristóbal *et al*., 2008). Ardic *et al*. (2008) studying *Cicer arietinum* described that the water deficit-sensitive cultivar suffered further because of the high B concentration, suggesting that water deficit can intensify the stress occasioned by high B supply. In other hand, Nunes (2010) described that in *Eucalyptus*, high levels of B in solution inhibited the negative effects of water deficit. However, consequences of the water deficit and/or B supply of form

Received: 06 Oct 2015. Received in revised form: 14 Mar 2016. Accepted: 20 Mar 2016. Published online: 14 June 2016.

isolated or combined have not been described to *S. parahyba* plants.

Therefore, the hypothesis is that sufficient B supply can alleviate the negative effects of water deficit on gas exchange and non-enzymatic compounds of *S. parahyba*. Our research had the aim to investigate gas exchange, oxidants and antioxidant compounds, and tolerance mechanism of young *S. parahyba* plants in response to B supply and water deficit.

Materials and Methods

Location and growth conditions

The experiment was performed in the Campus of Paragominas of the Universidade Federal Rural da Amazônia, Paragominas, Brazil (2°55′S and 47°34′W). Study was conducted in a greenhouse with control to temperature and humidity, the minimum, maximum, and median temperatures were 22 °C, 35 °C, and 26.5 °C, respectively. The relative humidity during the experimental period varied between 70% and 90%, and the photoperiod during study was of 12 h of light.

Seed treatment, container and plant conduction

The seeds of *S. parahyba* var. *amazonicum* were treated with hypochlorite sodium at 1% per 3 minutes, being scarified to accelerate the germination. Subsequently, these seeds were placed to germinate into 1.2-L containers (0.15 m in height and 0.10 m in diameter) filled with substrate mix composed of sand and vermiculite in a 2:1 proportion. For semi-hydroponic cultivation, the containers previously described were equipped with one hole in the bottom and covered with mesh to keep the substrate and the solution, absorbed by capillary action, from being placed into the other container (0.15 m in height and 0.15 m in diameter). The solution contained 500 mL of nutritive solution adjusted to the nutritional exigencies of this species. The ionic force started at 25 %, and it was modified to 50 % and 100 % at regular intervals over three days. After these periods, the nutritive solution remained with the total ionic force. Seedlings received nutritive solution at 100% from 22th until 37th day after experiment implementation.

Experimental design

The experiment employed a factorial that was entirely randomised, with two boron levels (25 and 250 μmol L^{-1}, simulating conditions of sufficient B and high B, respectively) and two water conditions (control and water deficit), totalizing four treatments. This study used five replicates and 20 experimental units, being one plant per container considered one unit experimental.

Nutritive solution, boron and water deficit treatments

During plant conduction, one young plant was maintained in each pot. The plants received macronutrients and micronutrients from the nutritive solution of Hoagland and Arnon (1950) modified containing 5.71 mM KNO_3, 2.85 mM $Ca(NO_3)_2{\cdot}4H_2O$, 1.43 mM $NH_4H_2PO_4$, 3.21 mM $MgSO_4{\cdot}7H_2O$, 0.71 mM KCl, 1.42 mM, KH_2PO_4, 1.42 μM $MnSO_4{\cdot}H_2O$, 1.42 μM $ZnSO_4{\cdot}7H_2O$, 0.35 μM $CuSO_4{\cdot}5H_2O$, 0.35 μM $NaMoO_4{\cdot}5H_2O$, 215 μM NaEDTAFe·$3H_2O$. During the cultivation, the solutions were changed at 07:00 h over 3-day intervals and their pH values were adjusted to 5.0, using HCl or NaOH. To simulate the conditions of sufficient B and high B were used 25 and 250 μmol B L^{-1}, respectively, being applied by 23 days (37th until 60th days after experiment implementation), supplied via H_3BO_3. The water regimes (water deficit and control) were applied by five days (60th until 65th days after experiment implementation), and water deficit was obtained maintained plants without nutrient solution into container. All plants were physiologically measured on the 65th day, and leaf and root tissues were harvested for biochemical analysis.

Leaf gas exchange

The net photosynthetic rate (P_N), stomatal conductance (g_s), transpiration rate (E), and substomatal CO_2 concentration (C_i) were evaluated using an infrared gas analyser (ADC Bioscientific, model LCPro$^+$). Gas exchange of *S. parahyba* were measured in only one day, and leaflets used were removed to determine the leaflet area, with subsequent calculation of variables per unit area (m^2) (Leport *et al.*, 1998). Into chamber were inserted fully expanded leaflets, which are located in the middle of the plant. Previously, a curve of response to P_N and photosynthetically active radiation was constructed to determinate the light saturation point. The equipment chamber was adjusted to measure gas exchange under constant conditions to CO_2 concentration, photosynthetically active radiation, air-flow rate and temperature chamber in 360 μmol mol^{-1} CO_2, 900 μmol photons m^{-2} s^{-1} 300 μmol s^{-1} and 28 °C, respectively, during interval between 11:00 and 12:00 hs. The water use efficiency (WUE) was estimated according to the method of Ma *et al.* (2004), and the instantaneous carboxylation efficiency (P_N/C_i) was calculated using the formula described by Aragão *et al.* (2012).

Leaf water potential

The leaf water potential (Ψw) was measured in fully expanded leaves located in the middle region of the plant and exposed to light, during period between 11:30 to 12:00 h corresponding to midday potential. To determinate the Ψw was used one leaf per plant and five plants per treatment, being measured with an analogue plant moisture system (PMS Instrument Company, model 600). It is based on technical of pressure chamber (Scholander *et al.*, 1964), according to the procedure of Turner (1988).

Extraction of oxidant and antioxidant compounds

Hydrogen peroxide (H_2O_2), total glutathione (GSH), and ascorbate (ASC) were extracted from leaf and root tissues as described by Wu et al. (2006). Extraction mixture was prepared by homogenising 500 mg of fresh matter of leaf and root, being harvested in the middle region of the tissue and mixed in 5 mL of 5% (w/v) trichloroacetic acid. Subsequently, the samples were centrifuged at 15,000 × g for 15 min at 3 °C, and the supernatant was collected.

Hydrogen peroxide determination

Determination of H_2O_2 content was made with 200 μL of supernatant, obtained during extraction procedure, and mixed with 1800 μL of reaction mix prepared with 2.5 mM of potassium phosphate [pH 7.0] and 500 mM potassium iodide, and the absorbance was measured at 390 nm (Velikova *et al.*, 2000).

Electrolyte leakage

Electrolyte leakage (EL) was measured using the method described by Gong *et al.* (1998) with minor modifications. Fresh

matter of leaf and root (200 mg) were harvested in the middle region of the each tissue and it were cut into 1-cm-long pieces and placed in containers containing 8 mL of distilled deionised water. The containers were incubated in a water bath at 40 °C for 30 min, and the initial electrical conductivity of the medium (C_1) was measured using a conductivity meter (QUIMIS, model Q795A, Brazil). The samples were boiled at 95 °C for 20 min to release all the electrolytes. After the samples were cooled, the final electrical conductivity (C_2) was measured. The percentage of EL was calculated using the formula EL (%) = $C_1/C_2 \times 100$.

Total glutathione

For total GSH quantification, 200 µL of supernatant and 1800 µL of reaction mixture (containing 100 mM phosphate [pH 7.6] and 0.60 mM 2-nitrobenzoic acid) were combined, and the absorbance was measured at 412 nm (Wu *et al*., 2006).

Ascorbate

For determining ASC, 200 µL of the supernatant was used with 1800 µL reaction mix, as described by Cakmak and Marschner (1992), with some modifications. The mixture consisted of potassium phosphate pH 7.6, 50% trichloroacetic acid, phosphoric acid, iron chloride III and bipyridyl dissolved in 70% ethanol. The samples were incubated at 37 °C for 60 min, and the absorbance of the resulting coloured solution was measured at 525 nm.

Data analysis

The data were submitted to normality test of Kolmogorov-Smirnov and subsequently subjected to analysis of variance, and when showed significant differences between the means was applied the Scott-Knott test at probability level of 5%. Standard deviations were determined for each treatment. Statistical analyses were performed using SAS software.

Results

B supply influences gas exchange

The PN of plants exposed to B high + control suffered a significant decrease of 21%, comparing with B sufficient + control. The isolated effect of water deficit significantly reduced PN at 77.3% and 78.9% in conditions on the B sufficient and high, respectively (Fig. 1A). To gs, plants under control condition showed a significant reduction of 35.2% due to high B concentration. With the application of water deficit there was also a significant reduction of 28.5% due to increase in the B suply. Plants exposed to water deficit presented decreases of 58.8% and 54.5%, respectively (Fig. 1B), when compared to control + B sufficient and control + B high, respectively. In E, plants under B high + water deficit also showed an increase of 29.8%, comparing with B sufficient + water deficit. In relation to water restriction, significant decreases of 65.3% and 57.1% were observed to B sufficient and high, respectively (Fig. 1C). The Ci, increases of 11.4% and 18.1% were detected after water deficit in plants under B sufficient and high, respectively (Fig. 1D).

The WUE to plants under B high + water deficit showed a decline of 42.1%, compared with B sufficient under equal water regime. The same behaviour was verified when evaluated the isolated effect of water deficit, with a reduction of 35.8% and 50% for B sufficient and high treatments, respectively (Fig. 2A).

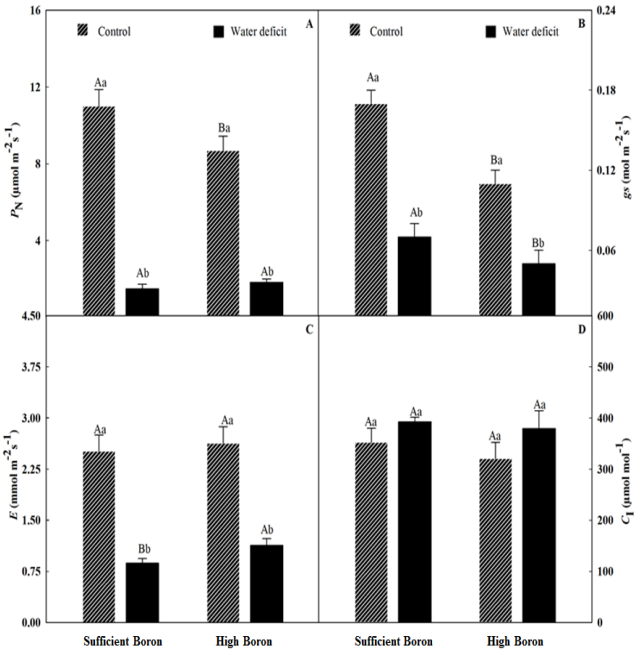

Fig. 1. Net photosynthetic rate (A), stomatal conductance (B), transpiration rate (C) and substomatal CO_2 concentration (D) in young *S. parahyba* plants exposed to two levels of B (B sufficient and B high) and two water regimes (control and water deficit). Different uppercase letters between B levels (B sufficient and B high under equal water regime) and lowercase letters between water regimes (control and water deficit under equal B level) indicate significant differences from the Skott-Knott test ($P < 0.05$). Columns represent the mean values of five repetitions, and the bars represent standard errors.

To PN/Ci, plants under B high + control presented a significant decrease of 33.3%, comparing with B sufficient + control. The water deficit effect promoted a significant reduction of 66.6% and 50%, when were analysed B sufficient and high treatments, respectively (Fig. 2B). In relation to Ψw, control plants presented values of -0.64 MPa to -0.50 MPa, when the B level were increased in the solution. The isolated effect of water deficit caused significant variations of 240% and 252%, when considered B sufficient and high treatments, respectively (Fig. 2C).

The H2O2 of the control and water deficit treatments showed non-significant increases in the leaf and root (Fig. 3A and B) after applications of B high. The isolated effect of water deficit cause also non-significant increases in H2O2 levels in both tissues. In relation to EL was showed similar behavior to leaf and root under B high (Fig. 3C and D), being verified slight increases. When the effect of water deficit was analysed, non-significant increases in the leaf and root were detected.

The total GSH in leaf and root presented reductions under B high to both water regimes, when compared with equal water regimes levels under B sufficient. In relation to leaf, plants subjected to B high + water deficit showed a significant decrease of 43.3%, in comparison with B sufficient + water deficit (Fig. 4A). To root, significant decreases of 55.1% and 50.1% were obtained in B sufficient + water deficit and B high + water deficit, compared with equal B levels under control conditions

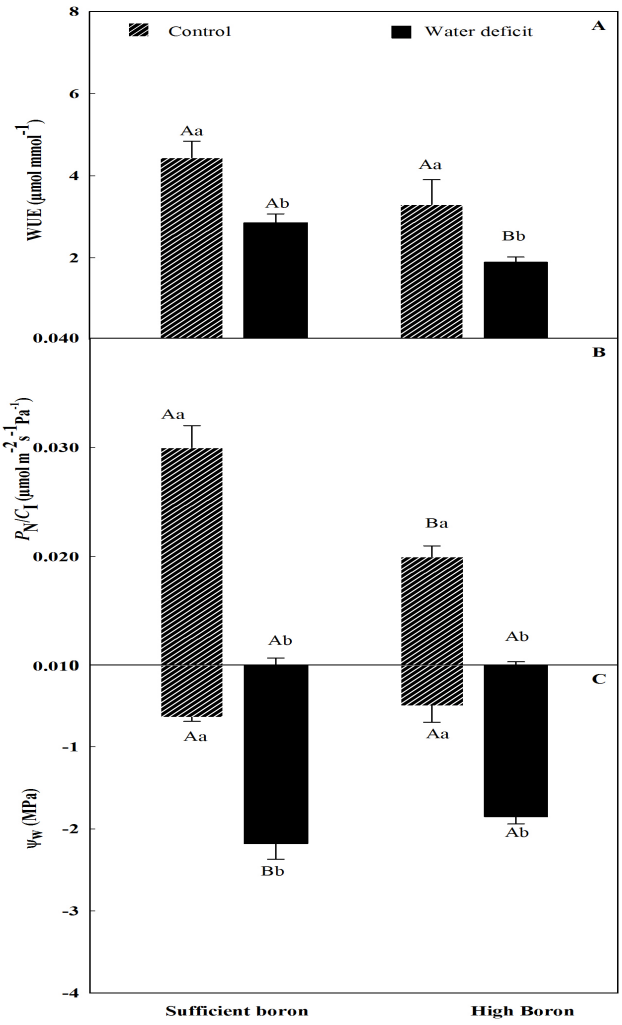

Fig. 2. Water use efficiency (A), instantaneous carboxylation efficiency (B) and water potential (C) in young *S. parahyba* plants exposed to two levels of B (B sufficient and B high) and two water regimes (control and water deficit). Different uppercase letters between B levels (B sufficient and B high under equal water regime) and lowercase letters between water regimes (control and water deficit under equal B level) indicate significant differences from the Skott-Knott test ($P < 0.05$). Columns represent the mean values of five repetitions, and the bars represent standard errors.

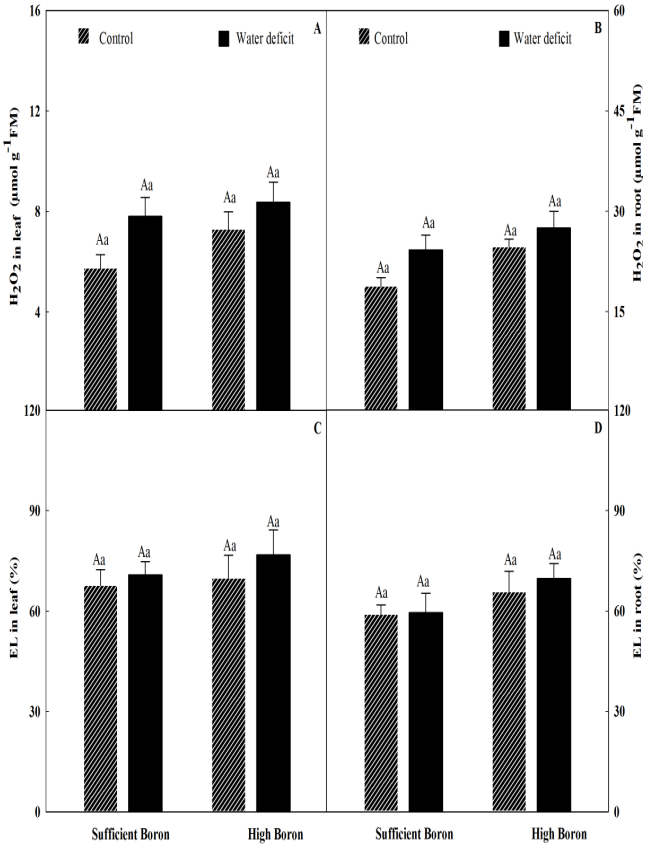

Fig. 3. Hydrogen peroxide in the leaf and root (A - B) and electrolyte leakage in the leaf and root (C - D) in young *S. parahyba* plants exposed to two levels of B (B sufficient and B high) and two water regimes (control and water deficit). Different uppercase letters between B levels (B sufficient and B high under equal water regime) and lowercase letters between water regimes (control and water deficit under equal B level) indicate significant differences from the Skott-Knott test ($P < 0.05$). Columns represent the mean values of five repetitions, and the bars represent standard errors.

(Fig. 4B). To ASC levels in leaf to treatments submitted to water deficit induced significant increases in both B supplies. To leaf, B high + control treatment presented a significant increase of 90.2%, compared with B sufficient under same water regime (Fig. 4C). In the roots, there were significant increases after B high application to control and water treatments (Fig. 4D).

Discussion

Control treatment exposed to B high was detected a reduction to net P_N, being this decrease explained by stomatal limitation (Saibo *et al*., 2009) and confirmed by the lower g_s showed under B high. The reduction in P_N induces a lower of carbon assimilation rate (Chaves and Oliviera, 2004; Machado Filho *et al*., 2006; Sausen and Rosa 2010). Wang *et al*. (2011) obtained similar results in their study of *Pyrus pyrifolia*, and they reported a decrease in the P_N due to increased B levels.

Reduction in g_s was noted when water deficit was applied, and this decrease was influenced by increase in C_i showed in this study, in which it frequently reduces the g_s (Wang *et al*., 2011). In addition, Liu and Stutzel (2002) working with *Amaranthus* plants in water deficit conditions detected a decrease in g_s, as was observed in this study.

The effect of water deficit caused a decrease in the *E*. This result is connected to lower water supply, confirmed by the Ψw of the plants exposed to water deficit treatment (Valadares *et al*., 2014). Ben-Gal and Shani (2002) evaluating *Lycopersicon esculentum* plants showed that the lack of water reduces *E*, corroborating with the data described in this research.

The water deficit caused an increase in C_i. This effect can be explained by a lower diffusion of CO_2 occurring in the

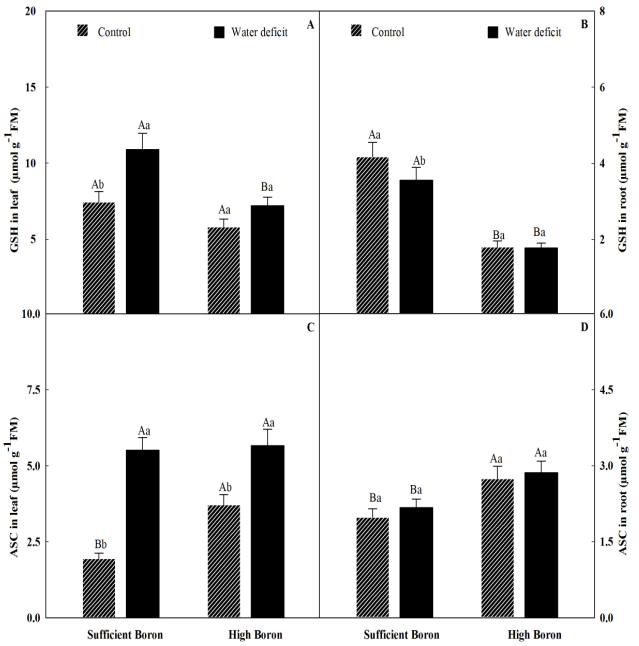

Fig. 4. Total glutathione in leaf and root (A - B) and ascorbate in the leaf and root (C - D) in young *S. parahyba* plants exposed to two levels of B (B sufficient and B high) and two water regimes (control and water deficit). Different uppercase letters between B levels (B sufficient and B high under equal water regime) and lowercase letters between water regimes (control and water deficit under equal B level) indicate significant differences from the Skott-Knott test ($P < 0.05$). Columns represent the mean values of five repetitions, and the bars represent standard errors.

intercellular spaces, this leads to an opposite effect on C_i rate, causing an increase in sub-stomatal conductance (Machado *et al*., 2005). Similar results were observed by Mafakheri *et al*. (2010) working with *Cicer arietinum* under water deficit, where they found an increase in $C_i$rate.

The WUE was reduced by the effects of the B high and also water deficit, and this result occurred due to the water limitation causes severe dehydration in the mesophyll cells with negative consequences on essential processes as photosynthesis and transpiration (Barbosa *et al*., 2014), resulting in a decrease in WUE. Similar results were observed by Silva *et al*. (2013a) working with *Helianthus annuus*, in which the plants showed a decrease in WUE, when in water deficit conditions.

The control plants showed a reduction in the P_N/C_i with increasing B level, being explained by the low P_N combined with higher C_i, promoting smaller P_N/C_i (Kitao *et al*., 1997; Silva *et al*., 2013b). Gomes *et al*. (2004) observed that the effect of water deficit in *Citrus sinensis* plants promoted a decrease of the P_N/C_i, confirming the data described in this study.

The effect of water deficit in plants promoted a drastic reduction of Ψw, this fact was probably due to the low water supply and water losses due to *E*, causing subsequent reduction in cell turgor (Nascimento *et al*., 2011; Oliveira *et al*., 2014). Similar results were found by Gomes *et al*. (2004) analysing *Citrus sinensis*, when in water deficit conditions.

The isolated effect of water deficit caused an increase in the H_2O_2 production in leaf and root tissues, being a response linked to oxidative stress and induced by the superoxide dismutase (SOD), which is an enzyme that acts in mechanism tolerance against the reactive species of oxygen (ROS), dismutating superoxide (O_2^-) to H_2O_2 (Scandalios, 2005; Voothuluru and Sharp, 2013). Similar results on H_2O_2 accumulation were found by Anjum *et al*. (2008) when the leaves of *Vigna radiata* were evaluated, corroborating with the data of this research.

The water deficit caused an increase of EL in leaf and root. This occurred due to an increase in H_2O_2, resulting in membrane disturbs and release of electrolytes, with consequent reduction in permeability of the cell membrane (Gonzalez-Mendoza *et al*., 2009; Demidchik *et al*., 2014; Langaro *et al*., 2014). Masoumi *et al*. (2010) observed an increase in EL in *Kochia scoparia* leaves, corroborating with the data of this study.

In plants subjected to B high and water deficit were verified reductions in total GSH. In relation to decrease promoted by the B, the B high probably blocked the conversion of Cys to GSH (Ruiz *et al*. 2003). Under water deficit, the reduction of the GSH occurred due to reduction of glutathione reductase (GR), that is the enzyme which catalyses the NADPH-dependent reduction of oxidised glutathione (GSSG) to the reduced form (GSH); therefore reducing GR activity will be reduced the production of total GSH (Labudda and Azam, 2014). Similar results were found by Ruiz *et al*. (2003) studying *Helianthus annuus* plants with application of 50 µM H_3BO_3. Pyngrope *et al*. (2013) working with *Oryza sativa* under water stress observed lower total GSH production in the leaves and roots.

The B high and water deficit promoted increases of ASC in both tissues evaluated. These increases detected has the aim to improve the protection of cell structures against B toxicity (Keles *et al*., 2004), and in the case of the isolated effect of water deficit, the ASC accumulation can be explained by the ASC–GSH cycle, which is a predominant mechanism of ROS detoxification (Chakraborty and Pradhan, 2012). Cervilla *et al*. (2007) observed that elevated B concentrations promoted an increase in ASC in study using *Solanum lycopersicum* plants, and Hussein and Khursheed (2014) observed that water deficit caused an increase in ASC of *Triticum aestivum*, corroborating this study.

Conclusions

Water deficit induced negative modifications on gas exchange, being verified repercussions on net photosynthetic rate, stomatal conductance, water use efficiency and instantaneous carboxylation efficiency, while B high promoted intensification of the effects on stomatal conductance and water use efficiency. Hydrogen peroxide and electrolyte leakage of both tissues suffered non-significant increases after B high and when applied water deficit. To total glutathione were detected increases only in leaf after water deficit, but reductions under B high to both tissues. Ascorbate levels presented increases after water deficit and B high to leaf and root. Our results suggested that the tolerance mechanism to water deficit in young *Schizolobium parahyba* plants is coupled to increases in total glutathione and ascorbate aiming to control the overproduction of hydrogen peroxide and alleviates the negative consequences electrolyte leakage and gas exchange. In relation to B supply, this study proved that sufficient level promoted better responses under control and water deficit conditions.

Acknowledgements

This research had financial support Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq/Brasil), Fundação Amazônia Paraense de Amparo à Pesquisa (FAPESPA/Brazil) and Universidade Federal Rural da Amazônia (UFRA/Brazil) to Lobato EMSG.

References

Abraf - Associação Brasileira de Produtores de Florestas Plantadas (2013). Anuário estatístico da ABRAF 2013 ano base 2012. Brasília: ABRAF 148 p.

Anjum NA, Umar S, Iqbal M, Khan NA (2008). Growth characteristics and antioxidant metabolism of moongbean genotypes differing in photosynthetic capacity subjected to water deficit stress. Journal Plant Interactions 3:127-136.

Aragão RM, Silva EN, Vieira CF, Silveira JAG (2012). High supply of NO_3^- mitigates salinity effects through an enhancement in the efficiency of photosystem II and CO_2 assimilation in *Jatropha curcas* plants. Acta Physiologiae Plantarum 34:2135-2143.

Ardıc M, Sekmen AH, Tokur S, Ozdemir F, Turkan I (2008). Antioxidant responses of chickpea plants subjected to boron toxicity. Plant Biology 11:328-338.

Barbosa MAM, Lobato AKS, Pereira TS, Viana GDM, Barbosa JRS, Coelho KNN, Sampaio LS, Santos Filho BG, Silveira JAG (2014). Photosynthesis-involvement in modulation of ascorbate and glutathione in *Euterpe oleracea* plants exposed to drought. Notulae Botanicae Horti Agrobotanici 42:119-127.

Ben-Gal A, Shani U (2002). Yield, transpiration and growth of tomatoes under combined excess boron and salinity stress. Plant Soil 247:211-221.

Cakmak I, Marschner H (1992). Magnesium deficiency and high light intensity enhance activities of superoxide dismutase, ascorbate peroxidase, and glutathione reductase in bean leaves. Plant Physiology 98:1222-1227.

Camacho-Cristóbal JJ, Rexach J, González-Fontes A (2008). Boron in plants: deficiency and toxicity. Journal Integrative Plant Biology 50:1247-1255.

Cervilla LM, Blasco BA, Ríos JJ, Romero L, Ruiz JM (2007). Oxidative stress and antioxidants in tomato (*Solanum lycopersicum*) plants subjected to boron toxicity. Annual Botany 100:747-756.

Chakraborty U, Pradhan B (2012). Oxidative stress in five wheat varieties (*Triticum aestivum* L.) exposed to water stress and study of their antioxidant enzyme defense system, water stress responsive metabolites and H_2O_2 accumulation. Brazilian Journal Plant Physiology 24:117-130.

Chaves MM, Oliveira MM (2004). Mechanisms underlying plant resilience to water deficits: prospects for water-saving agriculture. Journal Experimental Botany 55:2365-2384.

Demidchik V, Straltsova D, Medvedev SS, Pozhvanov GA, Sokolik A, Yurin V (2014). Stress-induced electrolyte leakage: the role of K+-permeable channels and involvement in programmed cell death and metabolic adjustment. Journal of Experimental Botany 65:1259-1270.

El-Hamdaoui A, Redondo-Nieto M, Rivilla R, Bonilla I, Bolanos L (2003). Effects of boron and calcium nutrition on the establishment of the *Rhizobium leguminosarum* - pea (*Pisum sativum*) symbiosis and nodule development under salt stress. Plant, Cell & Environment, 26(7):1003-1011.

Farooq M, Wahid A, Kobayashi N, Fujita D, Basra SMA (2009). Plant drought stress: effects, mechanisms and management. Agronomy for Sustainable Development 29:185-212.

Gomes MMA, Lagôa AMMA, Medina CL, Machado EC, Machado MA (2004). Interactions between leaf water potential, stomatal conductance and abscisic acid content of orange trees submitted to drought stress. Brazilian Journal Plant Physiology 16:155-161.

Gong M, Li YJ, Chen SZ (1998). Abscisic acid-induced thermotolerance in maize seedlings is mediated by calcium and associated with antioxidant systems. Journal Plant Physiology 153:488-496.

Gonzalez-Mendoza D, Quiroz-Moreno A, Medrano REG, Grimaldo-Juarez O, Zapata-Perez O (2009). Cell viability and leakage of electrolytes in *Avicennia germinans* exposed to heavy metals. Zeitschrift für Naturforschung C 64:391-394.

Gupta U, Verma P, Solanki H (2014). Impact of boron concentration on plants. Biolife 2:610-614.

Hoagland DR, Arnon DI (1950). The water culture method for growing plants without soils. Berkeley: California Agricultural Experimental Station 347 p.

Hussein ZK, Khursheed MQ (2014). Effect of foliar application of ascorbic acid on growth, yield components and some chemical constituents of wheat under water stress conditions. Jordan Journal of Agricultural Sciences 10:1-15.

Kastori RR, Maksimoviã IV, Kraljeviã-Balaliã MM, Kobiljski BD (2008). Physiological and genetic basis of plant tolerance to excess boron. Proceedings of the National Academy of Sciences 114:41-51.

Keles Y, Öncel I, Yenice N (2004). Relationship between boron content and antioxidant compounds in *Citrus* leaves taken from fields with different water source. Plant Soil 265:345-353.

Kiani SP, Maury P, Sarrafi A, Grieu P (2008). QTL analysis of chlorophyll fluorescence parameters in sunflower (*Helianthus annuus* L.) under well-watered and water-stressed conditions. Plant Science 175:565-573.

Kitao M, Lei TT, Koike T (1997). Effects of manganese toxicity on photosynthesis of White birch (*Betula platyphylla* var. *japonica*) seedlings. Physiologia Plantarum 101:249-256.

Labudda M, Azam FMS (2014). Glutathione-dependent responses of plants to drought: a review. Acta Societatis Botanicorum Poloniae 83:3-12.

Langaro AC, Nohatto MA, Perboni LT, Tarouco CP, Agostinetto D (2014). Physiological changes in tomato crop due to simulated drift of herbicides. Revista Brasileira Herbicidas 13:40-46.

Leport L, Turner NC, French RJ, Tennant D, Thomson BD, Siddique KHM (1998). Water relations, gas exchange and growth of cool-season grain legumes in a Mediterranean-type environment. European Journal of Agronomy 9:295-303.

Liu F, Stutzel H (2002). Leaf expansion, stomatal conductance, and transpiration of vegetable amaranth (*Amaranthus* sp.) in Response to Soil Drying. Journal of the American Society for Horticultural Science 127:878-883.

Ma CC, Gao YB, Guo HY, Wang JL (2004). Photosynthesis, transpiration and water use efficiency of *Caragana microphylla*, *C. intermedia* and *C. korshinskii*. Photosynthetica 42:65-70.

Machado EC, Schmidt PT, Medina CL, Ribeiro RV (2005). Photosynthetic responses of three citrus species to environmental factors. Pesquisa Agropecuaria Brasileira 40:1161-1170.

Machado Filho JA, Campostrini E, Yamanishi Ok, Fagundes GR (2006). Variação sazonal das trocas gasosas em folhas de mamoeiro cultivado em condições de campo. Bragantia 65:185-196.

Mafakheri A, Siosemardeh A, Bahramnejad B, Struik PC, Sohrabi Y (2010). Effect of drought stress on yield, proline and chlorophyll contents in three chickpea cultivars. Australian Journal Crop Science 4:580-585.

Masoumi A, Kafi M, Khazaei H, Davari K (2010). Effect of drought stress on water status, elecrolyte leakage and enzymatic antioxidants of kochia (*Kochia scoparia*) under saline condition. Pakistan Journal of Botany 42:3517-3524.

Nascimento SP, Bastos EA, Araújo ECE, Freire Filho FR, Silva EM (2011). Tolerance to water deficit of cowpea genotypes. Revista Brasileira Engenharia Agrícola Ambiental 15:853-860.

Nunes, FN (2010). Growth and gene expression in eucalyptus clones influenced by boron and drought. 76 f. Tese (Doutorado em solos e nutrição de plantas). Universidade Federal de Viçosa.

Ohashi ST, Yared JAG, Neto JTF (2010). Variability among *Schizolobium parahyba* var. *amazonicum* (Huber ex Ducke) Barneby provenances planted in the municipality of Colares - PA. Acta Amazonia 40:81-88.

Oliveira EAP, Zucareli C, Prete CEC, Zamuner D (2014). Osmotic potential of the substrate on seeds germination and initial development of seedling sweet corn. Revista Brasileira Ciência Agraria 6:477-482.

Pyngrope S, Bhoomika K, Dubey RS (2013). Reactive oxygen species, ascorbate-glutathione pool, and enzymes of their metabolism in drought-sensitive and tolerant indica rice (*Oryza sativa* L.) seedlings subjected to progressing levels of water deficit. Protoplasma 250:585-600.

Rosa LS (2006). Botanical, anatomical and technological characteristics of parica (*Schizolobium amazonicum* Huber ex. Ducke). Revista Ciência Agrarias 46:63-79.

Ruiz JM, Rivero RM, Romero L (2003). Preliminary studies on the involvement of biosynthesis of cysteine and glutathione concentration in the resistance to B toxicity in sunflower plants. Plant Science 165:811-817.

Saibo NJM, Lourenco T, Oliveira MM (2009). Transcription factors and regulation of photosynthetic and related metabolism under environmental stresses. Annual Botany 103:609-623.

Sausen TL, Rosa LMG (2010). Growth and carbon assimilation limitations in *Ricinus communis* (Euphorbiaceae) under soil water stress conditions. Acta Botanica Brasilica 24:648-654.

Scandalios JG (2005). Oxidative stress: molecular perception and transduction of signals triggering antioxidant gene defenses. Brazilian Journal of Medical and Biological Research 38:995-1014.

Scholander PF, Hammel HT, Hemmingsen EA, Bradstreet ED (1964). Hydrostatic pressure and osmotic potential of leaves in mangroves and some other plants. Proceedings of the National Academy of Sciences 52:119-125.

Silva ARA, Bezerra FML, Lacerda CFL, Pereira Filho JV, Freitas CAS (2013a). Gas exchange in sunflower plants subjected to water deficit at different stages of growth. Revista Ciência Agronomica 44:86-93.

Silva MA, Jifon JL, Santos CM, Jadoski CJ, Silva JAG (2013b). Photosynthetic capacity and water use efficiency in sugarcane genotypes subject to water deficit During early growth phase. Brazilian Archives of Biology and Technology 56:735-748.

Tahkokorpi M, Taulavuori K, Laine K, Taulavuori E (2007). After-effects of drought-related winter stress in previous. Environmental and Experimental Botany 61:85-93.

Turner NC (1988). Measurement of plant water status by the pressure chamber technique. Irrigation Science 9:289-308.

Valadares J, Paula NF, Paula RC (2014). Physiological changes in eucalyptus hybrids under different irrigation regimes. Revista Ciencia Agronomica 45:805-814.

Velikova V, Yordanov I, Edreva A (2000). Oxidative stress and some antioxidant system in acid rain treated bean plants: protective role of exogenous polyamines. Plant Science 151:59-66.

Voothuluru P, Sharp RE (2013). Apoplastic hydrogen peroxide in the growth zone of the maize primary root under water stress. I. Increased levels are specific to the apical region of growth maintenance. Journal of Experimental Botany 64:1223-1233.

Wang JZ, Tao ST, Qi KJ, Wu J, Wu HQ, Zhang SL (2011). Changes in photosynthetic properties and antioxidative system of pear leaves to boron toxicity. African Journal of Biotechnology 10:19693-19700.

Wu QS, Xia RX, Zao YN (2006). Reactive oxygen metabolism in mycorrhizal andnon-mycorrhizal citrus (*Poncirus trifoliate*) seedlings subjected to water stress. Journal Plant Physiology 163:1101-1110.