Journal of Elementology ISSN 1644-2296

Hamurcu M., Khan M.K, Pandey A., Avşaroğlu Z.Z., Elbasan F., Gezgin S. 2020. *Boron stress exposes differential antioxidant responses in maize cultivars (Zea mays* L.*).* J. Elem., 25(4): 1291-1304. DOI: 10.5601/jelem.2020.25.3.1970

RECEIVED: 7 March 2020
ACCEPTED: 9 August 2020

ORIGINAL PAPER

BORON STRESS EXPOSES DIFFERENTIAL ANTIOXIDANT RESPONSES IN MAIZE CULTIVARS (*ZEA MAYS* L.)*

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Abstract

Boron stress is largely influencing the growth and yield of crop plants all around the world. In this scenario, identification of the genotypes that are tolerant to boron stress, understanding the mechanisms behind the tolerance and their application in the breeding programs can open new pathways towards dealing with this global stress. Focusing on this, we compared the differences in the physiological and biochemical responses of two hybrid maize (*Zea mays* L.) cultivars, boron tolerant RX 770 and boron susceptible TTM 8119. Both genotypes were subjected to four different B treatments, 0, 2.5, 25 and 50 mg L^{-1} B. Samples were collected before the application, after 5 days of treatments and 10 days of treatments. Root shoot lengths, dry weights, malondialdehyde (MDA), proline content and activity of antioxidant enzymes were evaluated for different harvest periods. The aim of the study was to determine the role of antioxidant enzymes in providing tolerance to maize genotypes towards B stress. Based on the results, it can be concluded that the activity of SOD, APX, POX and GR enzymes may have a significant role in providing resistance to the maize cultivar RX 770 towards B toxicity, especially at the early stages of plant development. The comparison of the physiological and biochemical mechanism of the tolerant maize genotype with the susceptible one in the presence of the boron stress may provide deep understanding useful for the development of new B tolerant maize cultivars.

Keywords: antioxidant, boron stress, maize, biochemical analysis, susceptible, tolerant.

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* Project was financially supported by TÜBİTAK, Turkey (Project Number 110T260) and Selcuk University BAP Project, Turkey (Project Number 09401073).

INTRODUCTION

Maize plantations rank third after wheat and rice in the world and provide the greatest percentage of calorie intake in the diet in more than 22 countries (Macauley, Ramadjita 2015, Wu et al. 2019). However, the yield still needs to be increased to fulfill the future food demand (Ray et al. 2013). Therefore, it is of great importance to enhance the yield and quality of the maize crop. Boron stress is one of the most serious problems globally, affecting the development, yield and quality of maize (Kumar et al. 2018, Lordkaew et al. 2011). Boron toxicity causes metabolic disorders in the ribose parts bound to ATP, NADH and NADPH due to its damage to the cell wall in plants. It leads to injuries in the dividing and developing cells produced by RNA, free glucose or ribose bonds in plants. Boron accumulating in a large amount in the leaves of plants also has unwanted effects, like the upsetting of the osmotic order in the direction of the transpiration flow (Nable et al. 1997, Brown et al. 2002, Stangoulis and Reid 2002, Reid et al. 2004, Matthes et al. 2018). Boron deficiency leads to the development of necrotic spots with wrinkled leaf tips. It also causes shriveling of anthers, which often lack pollen, consequently affecting the plant yield (Lordkaew et al. 2011).

A study conducted by a team of researchers (Gezgin et al. 2002) in the Central Anatolia Region of Turkey showed that 26.6% of cultivated soils had boron deficiency (<0.5 mg kg^{-1}), while 18% had boron toxicity (>3.0 mg kg^{-1}). Hence, in order to develop crops with tolerance towards B deficiency and B toxicity stress, it is crucial to determine the effect of both stresses on the growth and development of different major crops. Both boron deficiency and toxicity are known to damage plants by the development of reactive oxygen species (Karabal et al. 2003, Choudhary et al. 2020). However, plants develop an efficient scavenging system comprising antioxidants in order to protect themselves from oxidative damage (Gunes et al. 2006, Cervilla et al. 2007, Ardic et al. 2009, Choudhary et al. 2020). Thus, the genotypes with greater activity of antioxidants in B stress can be more tolerant. Although studies have been conducted to evaluate the effect of B stress on the morphological and reproductive development of maize genotypes (Vaughan 1977), experiments on determining their influence on ROS and antioxidant system, especially of maize shoots, have been limited (Esim et al. 2013). Maize is a major crop of Turkey, which encouraged us to obtain the information about the changes in the reactive oxygen species (ROS) and the antioxidant responses of two maize genotypes, RX 770 and TTM 8119 grown under different boron supply conditions. In some of the previous studies, RX 770 and TTM 8119 genotypes have been respectively determined as tolerant and susceptible towards B toxicity on the basis of the growth parameters and B content (Çetin, Gezgin 2011). Thus, determining the differences in the antioxidant activity of the two cultivars in B stress may highlight the mechanism lying behind the B stress tolerance in specific cultivars.

MATERIAL AND METHODS

In this study, two hybrid maize genotypes, RX770 and TTM 8119, were used for treatments. Seeds were initially disinfected with 5% sodium hypochlorite and after germination were incubated with 0.5 mM $CaCl_2$ at 25°C in dark. Later, germinated seedlings were transferred to 1/5 Hoagland solution (pH 6.0) in controlled hydroponic conditions, where humidity, temperature, light intensity and photoperiod were set to 45-55%, 21±1°C, 14000 lux/day and 16/8 hrs day/night, respectively. At three-leaf stage, plants in six replicates were supplied with 1/5 Hoagland solution containing 0, 2.5, 25 and 50 mg L^{-1} B. Samples were collected at the zero day (just before treatment), and on the 5^{th} day and 10^{th} day after boron treatment, and stored at -80°C.

Growth parameters

Roots and shoots of harvested maize genotypes at zero day, 5^{th} day and 10^{th} day were separated from each other and root-shoot length and fresh weight were measured. After drying the samples at 70°C for 72 hrs, root--shoot dry weights were measured.

Boron analysis

Around 0.5 g root/shoot samples was desiccated at 70°C and processed with concentrated HNO_3 in a microwave system (CEM, Mars 5). Further, Inductively Coupled Plasma Atomic Emission Spectrometry (ICP-AES, Varian, Vista) was employed to measure the boron concentration in the supernatant. The measurement of the elemental concentration was checked by the certified values of the B element in the reference leaf material provided by the National Institute of Standards and Technology (NIST, Gaithersburg, MD, USA).

Enzymes analysis

Around half gram of frozen leaf samples was crushed with 50 mM sodium phosphate buffer (pH 7.8) consisting of 1 mM disodium-EDTA and 2% (w/v) polyvinylpolypyrrolidone (PVPP). After centrifugation at 14,000 rpm for 40 min at 4°C, supernatants were used for the enzyme activity assays.

Employing bovine serum albumin as standard, the total soluble protein contents of the enzyme extracts were estimated following the method of Bradford (1976). The spectrophotometric measurements were done using a Shimadzu (UV 1600) spectrophotometer. The activity of Superoxide dismutase (SOD; EC 1.15.1.1) was estimated by its capacity to prevent the photochemical reduction of nitrobluetetrazolium (NBT) at 560 nm (Beauchamp and Fridovich 1971). At 25°C, 3 mL of a reaction mixture comprising 0.033 mM NBT, 10 mM L-methionine, 0.66 mM EDTA Na_2, and 0.0033 mM riboflavin in 0.05 mM sodium phosphate buffer (pH 7.8)

were incubated for 10 min under 300 μmol m^{-2} s^{-1} irradiance. The non-irradiated reaction mixture was kept as control. A unit of SOD activity was considered as the amount of SOD necessary to lead to 50% inhibition of NBT, and the specific enzyme activity was mentioned as units mg^{-1} protein. Catalase (CAT; EC 1.11.1.6) activity was evaluated using a mixture containing 0.05 M Na-phosphate buffer (pH 7.0) with 0.1 mM EDTA and 3% H_2O_2 (Bergmeyer 1970). The initial rate of decomposition of H_2O_2 was estimated at 240 nm and 1 μmol H_2O_2 decomposed per min was considered as one unit of CAT. Peroxidase (POX; EC 1.11.1.7) activity was measured employing the Herzog (1973) method. The absorbance of the reaction mixture was measured at 465 nm. A unit of POX activity was considered as μmol ml^{-1} H_2O_2 decomposed per min. The activity of Ascorbate peroxidase (APX; EC 1.11.1.11) was estimated by Nakano and Asada (1981) method. The decrement in the absorbance of the reaction mixture containing oxidized ascorbate at 290 nm was monitored. A unit of APX activity was considered as μmol ml^{-1} oxidized ascorbate per min. Glutathione reductase (GR; EC 1.6.4.2) activity was evaluated according to Foyer and Halliwell (1976) method. NADPH oxidation was followed at 340 nm. The NADPH oxidation in the assay medium was observed at 340 nm and the activity was measured employing the extinction coefficient of NADPH (6.2 mM^{-1} cm^{-1}). A unit of GR activity was considered as μmol ml^{-1} oxidized GSSG per min. The specific enzyme activities were mentioned as units mg^{-1} protein for all the studied enzymes.

Lipid peroxidation

Malondialdehyde (MDA) formation indicates the level of lipid peroxidation and thiobarbituric acid was used to estimate the MDA content (Rao, Sresty 2000). The differences in the absorbance at 532 nm and 600 nm were used to calculate the MDA content.

Proline analysis

Free proline content was measured according to Bates et al. (1973) method. The absorbance of the reaction mixture was estimated at 520 nm and proline content was provided as μmol proline g^{-1} fresh weight.

Statistical analysis

All analyses were conducted using one-way analyses of variance (ANOVA) (Minitab 16.0). The data were the mean of four replicates (n=4), and the differences between mean values at P<0.01 were considered to be significantly different.

RESULTS

The effects of different doses of boron (0, 2.5, 25, and 50 mg L^{-1}) on the shoot dry weight values were examined on the 5th and 10th day of boron application. It was found that in RX 770 on 5th day, the shoot dry weight values significantly decreased at all doses as compared to the control (P<0.01). In the case of TTM 8119, shoot dry weight increased by 19% at the 25 mg L^{-1} of boron dosage on the 5th day, but the difference was non-significant. On the 10th day, RX 770 showed an 18% increase at 25 mg L^{-1} boron dosage, while TTM 8119 showed a decrease at all doses with reference to the control (Figure 1). Similarly, the root dry weight values of RX 770 decreased by 11%, 16%, and 26% in 2.5, 25, and 50 mg L^{-1} B treatment, respectively; however, in TTM 8119, it increased by 2% and 7% at the B doses of 2.5 and 25 mg L^{-1}, respectively, but decreased by 10% at the dose of 50 mg L^{-1} on the 5th day (Figure 1). On the 10th day, root dry weight of RX 770 increased as compared to the control at the doses of 2.5 and 25 mg L^{-1} of B, while it decreased at 50 mg L^{-1} B dosage. In the case of TTM 8119, root dry weight decreased at all doses as compared to the control.

The shoot length significantly increased at the dose of 50 mg L^{-1} of B in RX 770 maize cultivar, while in the case of TTM 8119, it significantly

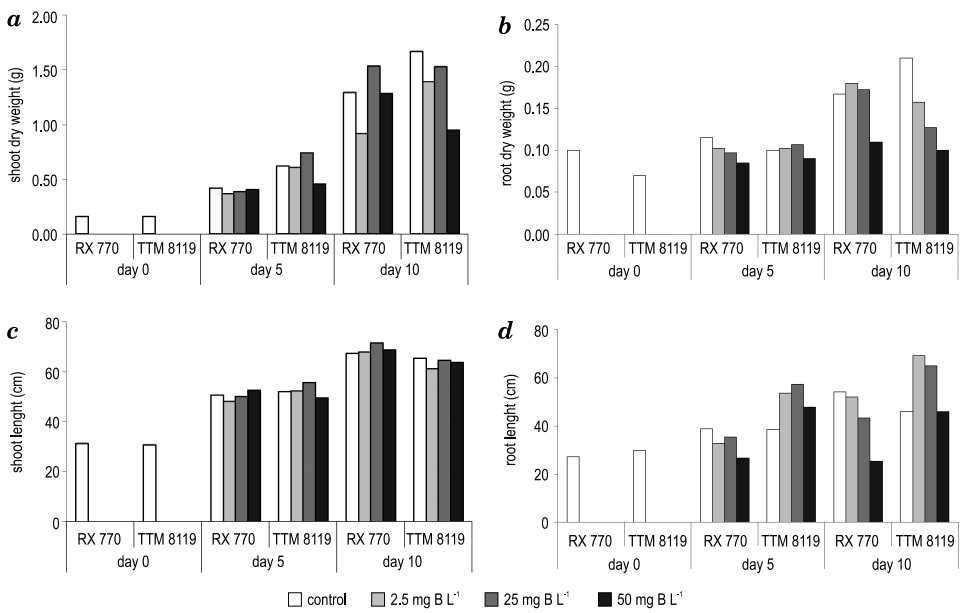

Fig. 1. Effect of different B treatments (0 control, 2.5, 25, 50 mg L^{-1} of boron) on (*a*) shoot dry weight (*b*) root dry weight (*c*) shoot length and (*d*) root length of two maize cultivars; the tolerant one, RX 770 and the susceptible one, TTM 8119 before the B application, 5 days after B application and 10 days after B application

increased by 7% at the dose of 25 mg L^{-1} of B on the 5th day as compared to the control (P<0.01). On the 10th day, shoot length increased by 1%, 6%, 2% and decreased by 2%, 3%, 17% at the doses of 2.5, 25, 50 mg L^{-1} of boron in RX 770 and TTM 8119 respectively, but the differences were non-significant (Figure 1). Similarly, the effects of boron application on root lengths varied between the maize cultivars with a significant decrease in RX 770 at the doses of 2.5 and 50 mg L^{-1} of boron and a significant increase in TTM 8119 at all doses on the 5th day. However, on the 10th day, 50 mg L^{-1} of B dosage caused a decrease in root length of TTM 8119 similar to RX 770 (Figure 1); in the case of RX 770, the difference was significant (P<0.01).

On the zero day of application, shoot boron concentrations of two maize cultivars were similar (11.94 and 12.19 mg L^{-1}). However, on the 5th day, the highest shoot boron concentration (2,423.90 mg L^{-1}) was recorded in TTM 8119, and the rates of increase were also higher depending on the doses of boron applied as compared to the control. On the 10th day at 50 mg L^{-1} B, the highest shoot boron concentration (4,216.30 mg L^{-1}) was detected in RX 770 with a higher rate of increase as compared to TTM 8119 (Figure 2). The root boron concentration was higher in RX 770 than in TTM 8119 on 0th day. Additionally, the boron concentration values for RX 770 and their rates of increase were also higher than those of TTM 8119 in the sampling on the 5th and 10th day (Figure 2).

On the 5th day, the significant increase in proline content as compared to control was higher in RX 770 than TTM 8119 at 25 and 50 mg L^{-1} B dose (P<0.01). On the 10th day, however, an increase in proline content of both cultivars was observed with increasing B dosages, although it was non-significant (Figure 3).

The lipid peroxidation values for the maize cultivars used in the research were computed according to the changes in the amount of malondialdehyde. In the sampling of RX 770 on the 5th day, there was a 7% significant decrease in the MDA content at the 2.5 mg L^{-1} of B dose as compared to the control, whereas it significantly increased by 82% and 28% at the doses

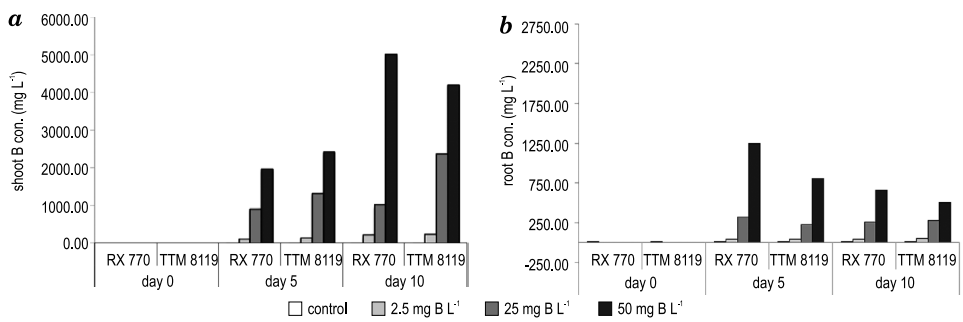

Fig. 2. Effect of different B treatments (0 – control, 2.5, 25, 50 mg L^{-1} of boron) on (*a*) shoot B concentration (*b*) root B concentration of two maize cultivars; the tolerant one, RX 770 and the susceptible one, TTM 8119 before the B application, 5 days after B application and 10 days after B application

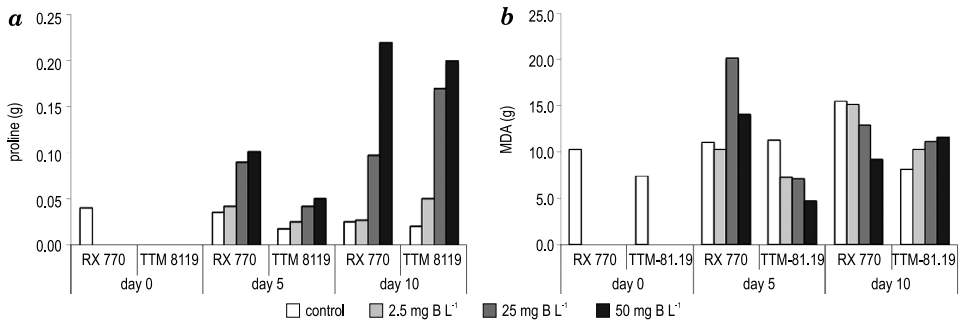

Fig. 3. Effect of different B treatments (0 – control, 2.5, 25, 50 mg L^{-1} of boron) on (*a*) proline and (*b*) MDA content of two maize cultivars; the tolerant one, RX 770 and the susceptible one, TTM 8119 before the B application, 5 days after B application and 10 days after B application

of 25 and 50 mg L^{-1} of B, respectively. On the 10th day, MDA values significantly decreased by 17%, and 40% in RX 770 at 25 and 50 mg L^{-1} B dose, respectively, with reference to control; however, MDA significantly increased by 27%, 37%, and 43% in TTM 8119, respectively (P<0.01) – Figure 3.

It was determined that the SOD activity levels varied between the maize cultivars depending on the doses of B. It significantly increased by 22%, 27%, and 35% at the doses of 2.5, 25, and 50 mg L^{-1} of B, respectively in RX 770 as compared to the control treatment on the 5th day (P<0.01). SOD values significantly increased by 17% at 2.5 mg L^{-1} of B but decreased by 6% and 15% at 25 and 50 mg L^{-1} of B in TTM 8119. On the 10th day of boron application, it significantly decreased by 21%, and 16% in RX 770, at the doses of 2.5 and 50 mg L^{-1} of B respectively; whereas it significantly decreased by 5% and 21% at the doses of 2.5 and 25 mg L^{-1} of B in TTM 8119 (Figure 4).

According to the results, on the 5th day, the POX activity values for the maize cultivars significantly increased by 16%, 12%, and 20% at all doses in RX 770 as compared to the control depending on the increase in the boron doses; whereas it increased by 5% at the dose of 2.5 mg L^{-1} of B but decreased by 19% and 35% at the doses of 25 and 50 mg L^{-1} of B in TTM 8119, respectively. On the 10th day, it significantly decreased by 14% and 5% at the doses of 2.5 and 50 mg L^{-1} of B in RX 770, respectively, while it increased by 13% at the dose of 50 mg L^{-1} of B in TTM 8119 (Figure 4).

On the 5th day, the CAT activity values significantly increased by 95% and 109% at the doses of 25 and 50 mg L^{-1} of B as compared to the control in RX 770, respectively. However, it significantly increased by 129%, 363%, and 159% in TTM 8119 depending on the increase in the doses of boron (P<0.01). In the samples taken on the 10th day, CAT activity values significantly increased by 51% and 106% at the doses of 25 and 50 mg L^{-1} of B in RX 770, respectively. However, in TTM 8119, it significantly increased by 79%, and 194% at 2.5 and 50 mg L^{-1} of B doses, respectively (P<0.01) – Figure 4.

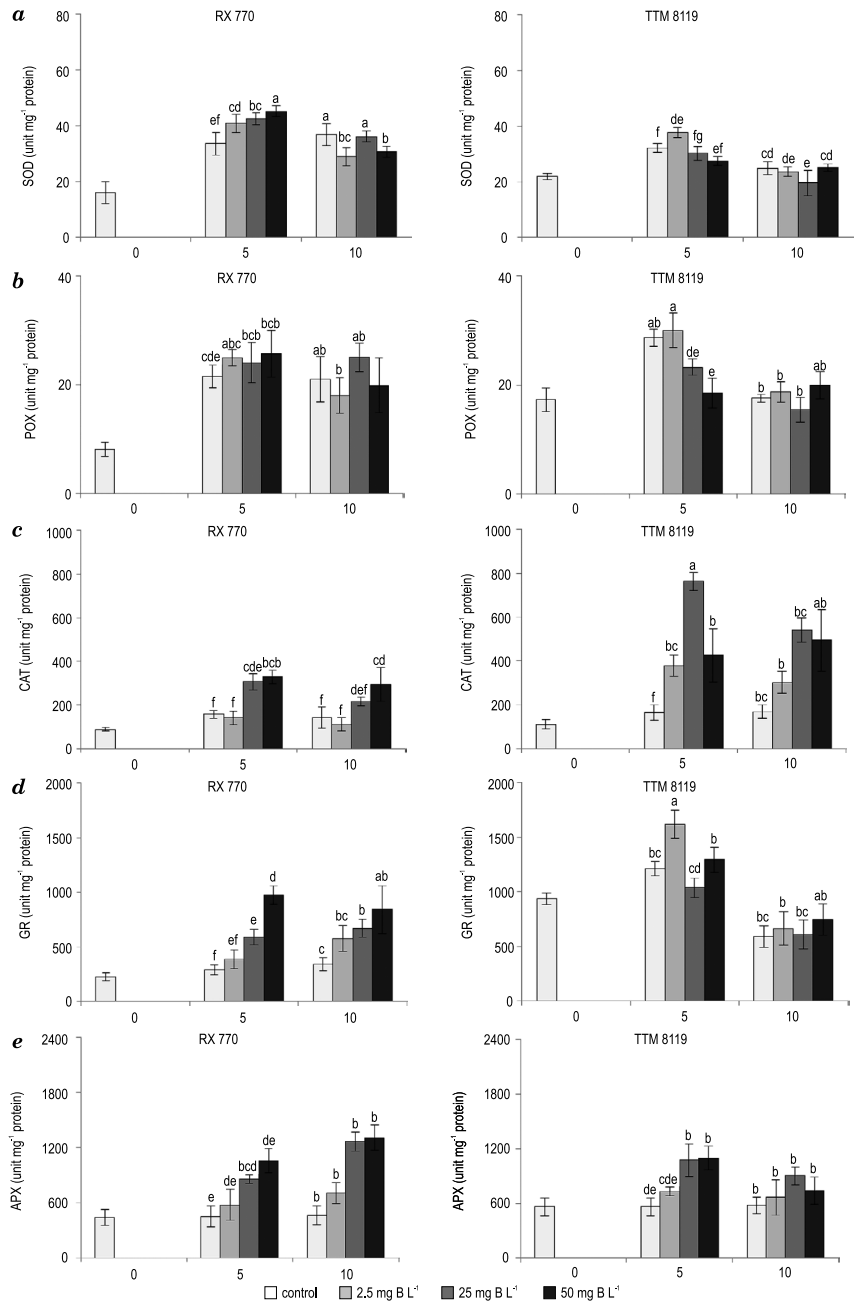

Fig. 4. Effect of different B treatments (0 – control, 2.5, 25, 50 mg L^{-1} of boron) on (*a*) SOD, (*b*) POX, (*c*) CAT, (*d*) GR and (*e*) APX of two maize cultivars; the tolerant one, RX 770 and the susceptible one, TTM 8119 before the B application, 5 days after B application and 10 days after B application. The data points are mean of four replicates. Parameter values with the same letters in the same group are not significantly different at $P<0.01$

The GR activity values were much higher in TTM 8119 than in RX 770 in 5th day samples. However, it was established that the rates of increase at 50 mg L^{-1} of B were much higher in RX 770 in samples taken on the same day. As a result of the analyses, it was determined that the GR activity values significantly increased by 33%, 103%, and 236% at the doses of 2.5, 25, and 50 mg L^{-1} of B in RX 770, respectively as compared to the control (P<0.01). The GR activity values significantly increased by 34% at the dose of 2.5 mg $L^{-1}$of B but decreased by 14% at the dose of 25 mg L^{-1} of B in TTM 8119. In samples collected on the 10th day, the GR activity values significantly increased in RX 770 with the increasing doses of boron. However, in the case of TTM 8119, GR activity significantly increased at 2.5 and 50 mg L^{-1} of B as compared to control (P<0.01) – Figure 4.

On the 5th day the APX activity values significantly increased by 28%, 91%, and 135% as compared to the control at all doses of boron in RX 770, respectively, and also increased by 30%, 91%, and 95% in TTM 8119 depending on the increase in the doses of boron, respectively (P<0.01). On the 10th day, although the APX activity values increased in both cultivars, the differences were not significant (Figure 4).

DISCUSSION

Based on the basis of the results, we can conclude that excess boron caused serious damage in plants by blocking the metabolic pathways of the growth metabolism in maize cultivars and the results of our study resembled the results obtained by several other researchers (Paull et al. 1988, Mahalakshmi et al. 1995, Lee et al. 1996, Karabal et al. 2003, Sotiropoulos et al. 2003, Ardic et al. 2009, Esim et al. 2013, Konuşkan et al. 2019). When root/shoot dry weights of maize cultivars under 50 mg L^{-1} of boron supply, which is a toxic level for plants, were compared with the 0 mg L^{-1} of B treatment group, 10th day samples of TTM 8119 showed highest rates of decrease. Similar to previous studies, there were great differences in sensitivity towards B toxicity among the two maize genotypes (Paull et al. 1988, Huang, Graham 1990, Nable 1991). In the field studies on cereals concerning B nutrition in plants (Alkan 1998, Torun et al. 2006), it has been determined that the cultivars display substantial differences in their responses to boron. The amount of B required by plants is rather small. An excessive amount of B, although being very slightly more than the amount of boron required, negatively affects the development of a plant, as in B deficiency, and stops the plant development.

Our results showed greater B accumulation in shoots of the maize genotypes under different boron treatments as compared to the roots. Moreover, the highest boron concentration between the maize cultivars was at the dose of 50 mg L^{-1} B. Although TTM 8119 showed greater values in 5th day sam-

ples, RX 770 yielded greater values on the 10th day. This shows that there were also differences in the B uptake between the two maize cultivars, as in previous studies (Paull et al. 1988, Huang, Graham 1990, Nable 1991, Kaur, Nelson 2015). In a greenhouse study on bread and durum wheat under different B applications, Alkan (1998) concluded that the development of toxicity symptoms, their concentrations and B contents varied depending on a cultivar type. It is thought that dry weight values have a greater role in developing the variation in boron concentrations of root/shoot or different plant cultivars.

In plants, boron deficiency and toxicity lead to oxidative damage apart from causing damage to the plant growth, development, cellular membrane permeability, etc. (Bray 2000, Karabal et al. 2003, Esim et al. 2013). To control the physiological production of reactive oxygen species (ROS), plants have well-developed enzymatic and non-enzymatic antioxidant mechanisms. Therefore, resistance to boron stress partially depends on the increase in the antioxidant compounds and antioxidant enzymes. ROS are produced in both unstressed and stressed cells. However, defense systems in plants enable the elimination of ROS besides limiting their formation. Under unstressed conditions, the formation and elimination of ROS are in balance. Nevertheless, under stressed conditions, the defense system fails to react towards the increase in ROS and is unsuccessful to eliminate the increasing enzymatic or non-enzymatic antioxidants.

SOD is a key antioxidant enzyme for aerobically respiring cells which is responsible for scavenging superoxide radicals (Asada 1999). In our study, it was determined that there were differences in the SOD activity of the two maize cultivars depending on the boron application. The SOD activity of RX 770 increased at all doses on the 5th day of B stress and decreased in the 2.5 and 50 mg L^{-1} of B applications on the 10th day of boron application. Moreover, it increased at the dose of 2.5 mg L^{-1} of boron on the 5th day of B application in TTM 8119 maize cultivar. Like in our study, Ardic et al. (2009) applied a toxic level of boron to chickpea cultivars and revealed that the SOD values for the cultivars increased and decreased depending on toxicity and the type of cultivars. Similar results were also obtained by Ermiş (2002), Karabal et al. (2003) and Esim et al. (2013).

Antioxidant enzymes like CAT, APX, POX, SOD and GR scavenge reactive oxygen species and play a role in the regulation of the production of H_2O_2 at the intracellular level. However, CAT, APX, POX and GR are among the most important ones. In plants, APX is the most important peroxidase that converts H_2O_2 into water and plays a crucial role in the elimination of toxicity (Foyer, Halliwell 1976, Noctor, Foyer 1998). In our study, APX enzyme activities of the maize cultivars increased depending on the boron applications and increases were at closer rates between the cultivars on the 5th day of application. The APX activity values and the rates of increase were higher in RX 770 than in TTM 8119 on the 10th day of application. The increases in the levels of ascorbate for the maize cultivars

in our research were also in agreement with the previous studies (Cakmak et al. 1993, Ermiş 2002, Karabal et al. 2003, Ardic et al. 2009).

CAT is one of the most effective antioxidant enzymes that play a role in preventing cellular damage (Scandalios 1993). It converts strong oxidant H_2O_2 into H_2O and molecular oxygen in peroxisomes. The catalase activity of the maize cultivars used in our research increased depending on the boron applications, and these increase rates were higher in TTM 8119 at both the sampling times. The results obtained resembled those in studies by Karabal et al. (2003) and Ardic et al. (2009).

POX not only supports the elimination of produced H_2O_2 but also facilitate the processes concerning growth and development (Dionisio-Sese, Tobita 1998). They use oxygen as a hydrogen acceptor and catalyze reactions for the removal of hydrogen from the substrate. It was found that the POX activities of the maize cultivars increased in RX 770 but decreased in TTM 8119 on the 5th day. Our results differ from some of the studies that showed only increases in POX activities (Lopez et al. 1996, Renard, Guerrier 1997), but resemble a few reports indicating decreases in the amount of POX (Ermiş 2002, Ardic et al. 2009, Esim et al. 2013).

As a metabolic regulator and an antioxidant, the GR enzyme catalyzes the conversion of oxidized glutathione (GSSG) resulting from the reduction of hydrogen peroxides again into reduced glutathione, GSH (Noctor, Foyer, 1998). The reduction of oxidized glutathione (GSSH) to GSH is performed by the GR enzyme depending on NADPH. As a result, either the hydroxyl radical decreases or its formation is prevented in the medium (Rao, Sresty 2000). The GR activity values varied between the two maize cultivars and were much higher in TTM 8119 than in RX 770 in 5th day samples; however, the values were similar in both the genotypes on the 10th day of application.

Proline functions as an osmolyte, whose production increases in plants particularly under stress conditions. It is a free radical scavenger, which stabilizes water stress by regulating cytoplasmic pH, and ensures the stability of proteins (Jain et al. 2001). In our study, the proline contents of the maize cultivars increased according to the increase in the boron dosages and these rates of increase at 50 mg L^{-1} were higher in both genotypes at 10th day of sampling as compared to the 5th day of sampling. The results of our study were similar to the results obtained by Karabal et al. (2003) and Ardic et al. (2009).

Another important indicator of the oxidative stress which increases as a result of stress in plants is the peroxidation of the membrane lipids, and it is determined according to the amount of malondialdehyde (MDA) in the medium. In samples collected on the 5th day, MDA values of RX 770 increased and that of TTM 8119 decreased as compared to the control in 25 and 50 mg L^{-1} treatments. However, in 10th day samples, the situation was completely opposite, with an increase in the MDA values of RX 770 and a decrease in TTM 8119 following the increasing B doses. It means that

on the 10th day of sampling, the lipid peroxidation in RX 770 genotype was decreased with the increasing B doses. The antioxidant enzymes activities may have contributed to this decrease in the MDA value in the tolerant genotype. Our results were not in accordance with the study conducted by Esim et al. (2013), where antioxidant enzymes activities were not able to protect the maize roots from the oxidative stress.

CONCLUSION

Based on the results, it can be concluded that the activity of SOD, APX, POX and GR enzymes can play a significant role in providing resistance to the maize cultivar RX 770 towards B toxicity, especially at the early stages of plant development, as compared to TTM 8119. This conclusion was drawn from the fact that SOD and APX enzymes were higher in RX 770 than in TTM 8119. The POX activity was higher in RX 770 in the first stage of development of the plant. The higher rates of GR activity in RX 770 than in TTM 8119 were also correlated with the increase in the level of APX. which is quite effective in the scavenging of ROS in the ascorbate – glutathione cycle. The aim of this study was to determine whether the antioxidants contribute to the tolerance level of genotypes or not. RX770 has already been determined as a B tolerant maize genotype and TTM 8119 as a susceptible one based on the growth parameters and B concentrations determined in the previous studies. An increase in the MDA values with the increasing B dosages in RX 770 genotype on 5th day of sampling showed that the plant was suffering from oxidative stress. However, a decrease in the MDA values with the increasing B dosages on the 10th day of sampling confirmed that the lipid peroxidation in RX 770 genotype decreased due to the increased activities of antioxidant enzymes, thereby making it more tolerant towards the B stress. Thus, it can be concluded that antioxidants have a potential role in providing tolerance to maize genotypes against the boron stress. The comparison of the physiological and biochemical mechanism of the tolerant maize genotype with the susceptible ones in the presence of the boron stress may provide deep understanding useful for the development of new B tolerant maize cultivars.

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