Exogenous aminolevulinic acid protects wheat seedlings against boron-induced oxidative stress

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Abstract
The present study was carried out in order to elucidate whether exogenous ALA treatment mitigates the stress damages in wheat under boron toxicity. Three different concentrations (5, 10 and 20 mg L⁻¹) of ALA were applied to the 9-day-wheat leaves and then boron (5 mM) was added to the nutrient solutions for 3 days. Boron toxicity severely reduced root and shoot lengths as well as the level of soluble protein and photosynthetic pigments. In a similar manner, it caused a marked decrease in the activities of antioxidant enzymes including superoxide dismutase, guaiicol peroxidase, catalase, ascorbate peroxidase and glutathione reductase. As a result, boron toxicity led to increment in the level of oxidative stress indicators such as superoxide anion, hydrogen peroxide, and lipid peroxidation. ALA application significantly mitigated the boron-induced reductions in the growth parameters and antioxidant defence system. The values of oxidative stress indicators were lesser in ALA-applied seedlings that were associated with higher activities of antioxidant enzymes as well as higher protein level. A significant correlation was recorded between boron and/or ALA-induced protein content and protein profile observed at SDS-PAGE. On the other hand, while boron application caused to a marked increase in boron amounts in roots, ALA treatments reduced considerably the boron uptake from roots. These data clearly revealed that ALA improves boron toxicity in wheat seedlings by increasing antioxidant activity and by modulating boron uptake and/or transportation.

Keywords: Aminolevulinic acid, boron toxicity, wheat, oxidative stress, antioxidant system

1. Introduction
Boron is an essential microelement having important roles for many metabolic processes of plants. Its optimal concentration for plant growth and development is very close to its toxic level. Boron level in the media, therefore, is very important for plants. Its excess amounts which results from boron-containing irrigation water and groundwater in especially arid and semi-arid regions cause to toxic impacts on growth, development and the other metabolic pathways of plants [1].

Boron is taken from roots with a passive process and transported to the leaves through xylem. The passive transportation process is due to high permeability of lipid layers against boric acid [2]. While boron is transport ed easily in xylem, it is immobile in phloem. Therefore, it is accumulated in the leaves and ultimately causes characteristic symptoms such as chlorosis and necrosis [3]. Moreover, boron toxicity reduces significantly the rate of photosynthetic efficiency. It leads to deterioration on structure of thylakoid membranes [4], reduction in
chlorophyll contents[5], disorganization on the construction of mesophyll cells[6], decline in electron transport rate[7] and activities of enzymes which serve CO₂ assimilation[8]. It has been considered that toxic effects of boron are resulted from disruptions in many metabolic processes which boron causes by binding to free ribose or ribose inside RNA, ATP, NADP, and NADPH as well as disruption in cell wall structure[9]. Eventually, boron in toxic levels brings about oxidative stress by increasing formation of reactive oxygen species (ROS)[1].

Plants have antioxidant defence system which consists of enzymatic and non-enzymatic compounds to protect themselves against various stress factors[10-15]. These compounds are capable of ROS scavenge. There are a lot of reports on boron-induced changes in activities of especially antioxidant enzymes such as catalase (CAT), ascorbate peroxidase (APX), guaiacol peroxidase (GPX), superoxide dismutase (SOD), and glutathione reductase (GR)[1, 10]. In these reports, it was determined that antioxidant system was affected in different ways depending on concentration and application time of boron, and species and development stage of plants.

To improve plant resistance against environmental stressors including boron toxicity, many substances like plant growth regulators (PGRs) such as plant hormones, steroids, vitamins, and various chemicals have been applied exogenously to plants via spraying, watering, and fertilizing. These applications improved the resistance of plants up to a certain degree[16, 17]. In recent years, aminolevulinic acid (ALA) is being used to increase growth and development of plants and to improve their stress tolerance. ALA is an essential precursor for tetrapyrrolys such as chlorophyll and heme[18]. Prior reports demonstrated that exogenous application of ALA resulted in significant increases in growth and development in various plants. In addition, its application enhanced plant tolerance ability against different stress factors such as drought stress[19], low light and cold stress[20], salt stress[21] and cadmium toxicity[22]. However, the effects of ALA on boron toxicity, one of the common environmental stresses, remain unclear.

In this study, it was aimed to elucidate the effects of exogenously-treated ALA on some morphological (root and shoot development), physiological (boron uptake and pigment content), biochemical (ROS formation, membrane damage, and antioxidant defence responses), and molecular (protein profile) parameters in wheat seedlings exposed to boron toxicity.

2. Material and Methods

2.1. Plant materials and treatments

Seeds of wheat (Triticum aestivum cv. Doğu88) were obtained from East Anatolian Agricultural Research Institute. The seeds were sterilized with 5% NaOCl for 5 min and then carefully washed with distilled water five times. The seeds were planted in pots filled with hydroton. The pots were embedded in hydroponic systems containing Hoagland nutrient solution. The hydroponic systems were continuously aerated with an air pump. Wheat seedlings were grown for 12-day in a controlled climate room at 24 ± 2°C temperate, 50% relative humidity and 16 h photoperiod. 5-ALA at various concentrations (5, 10 and 20 mg.L⁻¹) was applied to aboveground organs of nine day seedlings and simultaneously 5mM boron (H₃BO₃) was added to the Hoagland nutrient solution. The 5 mM concentration of boric acid has been predetermined with preliminary studies. Distilled water was sprayed to the aboveground organs of control groups. The pH of hydroponic growth mediums was adjusted to 6.0. After 3 day of treatments, root and shoot of wheat seedlings was harvested for morphological, biochemical analyses.
2.2. Pigment and soluble protein contents, protein profile and antioxidant enzymes activities

Chlorophyll and carotenoid contents were measured according to Witham & al.[23]. The soluble protein content was determined according to the method of Bradford [24]. Superoxide dismutase (SOD) activity was determined by the method of Agarwal and Pandey [25]. Catalase (CAT) activity was based on the method described by Gong & al. [26]. Peroxidase (GPX) activity was measured according to Yee & al. [27]. Glutathione reductase (GR) activity was determined according to Foyer and Halliwell [28]. Ascorbate peroxidase (APX) was determined according to the method described by Nakano and Asada [29]. Protein profiles of leaves samples were assayed according to method of Laemmli [30].

2.3. Superoxide anion, hydrogen peroxide, lipid peroxidation and boron contents

Superoxide formation rate was assayed by the modified method as described by Elstner and Heupel [31]. Hydrogen peroxide content was determined according to the method of Junglee & al. [32]. The lipid peroxidation level was expressed by estimating the amount of MDA according to Heath and Packer [33]. Boron levels in roots were analysed by inductively coupled plasma mass spectrometry after microwave digestion with HNO₃ and H₂O₂ [34].

2.4. Statistical analysis

The experiment was a completely random design with three replications with four parallel. All data were analysed with a one-way analysis of variance (ANOVA) and the mean differences were compared by Duncan test at the 95% (p<0.05) confidence using SPSS 20. The standard errors were shown at all tables.

3. Results

3.1. Changes of growth parameters

Upon exposure to boron stress, root and shoots lengths of wheat decreased severely when compared to their control (Figure 1). On the other hand, 5, 10 and 20 mg.L⁻¹ ALA treatments increased significantly values of these growth parameters as compared to boron treatment. Boron treatment causes to decrease by 16 and 9.98% at the root and shoot lengths, respectively. As compared to only boron stress, the highest increment rates of the parameters were obtained with 10 mg.L⁻¹ ALA treatment. The treatment increased by 15.7% the root length and by 6.9% the shoot length.

![Figure 1](image)

**Figure 1.** Effects of boron and ALA treatments on root and shoot lengths of 12-day-old wheat seedlings.

(5 ALA; 5 mg.L⁻¹ ALA, 10 ALA; 10 mg.L⁻¹ ALA, 20 ALA; 20 mg.L⁻¹ ALA)

3.2. Changes in protein profiles and soluble proteins contents

Soluble protein content of wheat leaves decreased by 8.5% with boron treatment. As compared to boron treatment, all of the exogenous ALA treatments increased soluble protein
content. The increment rates at 5, 10 and 20 mg.L\(^{-1}\)ALA treatments compared to boron treatments were by 2.2, 6.4 and 0.6% respectively (Table 1). Protein profile determined in SDS-PAGE supported enhanced soluble protein content with ALA treatments. The boron decreased density of protein bands, whereas the 10 mg.L\(^{-1}\)of ALA treatments stimulated intensity of protein band with particularly between 48 and 58 kD (Figure 2).

### 3.3. Changes in chlorophyll and carotenoid contents

Leaf pigments contents were decreased markedly exposure to boron stress. Chlorophyll \(a\), chlorophyll \(b\), total chlorophyll and carotenoid contents were decreased by 14.3%, 9.5%, 13% and 22.9% respectively with the 5 mM boron treatment. As compared to only boron treatment, combined treatments of boron and ALA increased significantly these pigment contents. The highest increment at these pigment contents was recorded with 10 mg.L\(^{-1}\)ALA treatments. Obtained increment rates in this treatment compared to boron treatment were by 18.8% in Chlorophyll \(a\), 18.8% in chlorophyll \(b\), 18.8% in total chlorophyll and 20.4% in carotenoid contents (Table 1).

![Figure 2. Effects of boron and ALA treatments on total protein profile of 10-day-old wheat leaves.](image)

### 3.4. Antioxidant enzymes

Boron stress caused to serious declines in the activities of antioxidant enzymes containing SOD, GPX, APX and GR and to increment in CAT activities (Table 2). The determined decrease rates of SOD, GPX, APX and GR activities in boron treatment were by 29.5, 22.2, 10.8 and 30.4 %, respectively, compared to those in control groups. The CAT activity increased by 11.4 % with boron treatment. As compared to boron treatment on its

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**Table 1. Effects of boron and ALA treatments on contents of soluble protein, chlorophyll \(a\), chlorophyll \(b\), total chlorophyll and carotene in leaves of 12-day-old wheat seedlings.**

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Soluble protein (mg.g(^{-1}) FW)</th>
<th>Chlorophyll (a) (mg.g(^{-1}) FW)</th>
<th>Chlorophyll (b) (mg.g(^{-1}) FW)</th>
<th>Total chlorophyll (a) (mg.g(^{-1}) FW)</th>
<th>Carotene (mg.g(^{-1}) FW)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>33.07 ± 0.053a*</td>
<td>9.08 ± 0.038ab*</td>
<td>3.65 ± 0.053b</td>
<td>12.73 ± 0.050c</td>
<td>1.25 ± 0.025a</td>
</tr>
<tr>
<td>Boron</td>
<td>30.27 ± 0.131d</td>
<td>7.78 ± 0.071c</td>
<td>3.30 ± 0.022c</td>
<td>11.08 ± 0.091d</td>
<td>0.97 ± 0.012c</td>
</tr>
<tr>
<td>Boron + 5 ALA</td>
<td>30.93 ± 0.199c</td>
<td>9.14± 0.040ab</td>
<td>3.86 ± 0.057a</td>
<td>13.00 ± 0.075ab</td>
<td>1.12 ± 0.021b</td>
</tr>
<tr>
<td>Boron + 10 ALA</td>
<td>32.19 ± 0.111b</td>
<td>9.24 ± 0.063a</td>
<td>3.92 ± 0.065a</td>
<td>13.16 ± 0.119a</td>
<td>1.17 ± 0.018b</td>
</tr>
<tr>
<td>Boron + 20 ALA</td>
<td>30.45 ± 0.163d</td>
<td>9.03 ± 0.050b</td>
<td>3.83 ± 0.052a</td>
<td>12.86 ± 0.054bc</td>
<td>1.15 ± 0.027b</td>
</tr>
</tbody>
</table>

* Different letters in the same column indicate statistically significant differences (P < 0.05).
own, combined treatments of boron and ALA increased all of the antioxidant enzyme activities. However, the highest values in activities of these enzymes compared to boron treatment were measured with 10 mg.L⁻¹ ALA treatments. The obtained increment rates with 10 mg.L⁻¹ ALA treatments compared to the boron treatment were recorded as 31.2 % at SOD, 43.1 % at GPX, 15.9 % at CAT, 11 % at APX and 9.5 % at GR activities.

Table 2. Effects of boron and ALA treatments on the superoxide dismutase (SOD), guaiacol peroxidase (GPX), catalase (CAT), ascorbate peroxidase (APX) and glutathione reductase (GR) activities in leaves of 12-day-old wheat seedlings.

<table>
<thead>
<tr>
<th></th>
<th>SOD (U.mg⁻¹ protein)</th>
<th>POX (U.mg⁻¹ protein)</th>
<th>CAT (U.mg⁻¹ protein)</th>
<th>APX (U.mg⁻¹ protein)</th>
<th>GR (U.mg⁻¹ protein)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>22.82 ± 0.299a</td>
<td>1749 ± 29.35b</td>
<td>18.58 ± 0.272d</td>
<td>15.23 ± 0.202a</td>
<td>20.48 ± 0.621a</td>
</tr>
<tr>
<td>Boron</td>
<td>16.08 ± 0.125e</td>
<td>1360 ± 51.14d</td>
<td>20.70 ± 0.245c</td>
<td>13.58 ± 0.149c</td>
<td>14.25 ± 0.210c</td>
</tr>
<tr>
<td>Boron + 5 ALA</td>
<td>18.80 ± 0.253d</td>
<td>1505 ± 19.36c</td>
<td>21.98 ± 0.309b</td>
<td>14.13 ± 0.063b</td>
<td>14.35 ± 0.250c</td>
</tr>
<tr>
<td>Boron + 10 ALA</td>
<td>21.10 ± 0.292b</td>
<td>1946 ± 20.74a</td>
<td>24.00 ± 0.303a</td>
<td>15.08 ± 0.063a</td>
<td>15.60 ± 0.231b</td>
</tr>
<tr>
<td>Boron + 20 ALA</td>
<td>20.38 ± 0.103c</td>
<td>1762 ± 9.78b</td>
<td>18.13 ± 0.330d</td>
<td>13.95 ± 0.266bc</td>
<td>14.33 ± 0.347c</td>
</tr>
</tbody>
</table>

* Different letters in the same column indicate statistically significant differences (P < 0.05).

3.5. ROS and lipid peroxidation levels

Boron stress caused a marked increase in H₂O₂ amount and superoxide anion formation and the increment values in H₂O₂ amount and superoxide anion formation were by 14.8% and 34.9%, respectively. All of exogenous ALA treatments were decreased ROS amounts compared to only boron treatment. However, the important decrease rates in H₂O₂ and O₂⁻ amounts were recorded with 10 mg. L⁻¹ALA. As compared to boron stress, these decrease rates were 5.6% in H₂O₂ and 16.6% in O₂⁻ amounts.

MDA content, important indicator of lipid peroxidation was seriously increased by boron treatment as compared to control. However, 5, 10 and 20 mg L⁻¹ALA treatments declined the MDA levels by 5.6, 31.9 and 23.3 % respectively, compared to boron stress (Table 3).

Table 3. Effects of boron and ALA treatments on the contents of superoxide anion (O₂⁻), hydrogen peroxide (H₂O₂), and malondialdehyde (MDA) in leaves of 12-day-old wheat seedlings.

<table>
<thead>
<tr>
<th></th>
<th>Superoxide content (µg.g⁻¹ FW)</th>
<th>Hydrogen peroxide content (µg.g⁻¹ FW)</th>
<th>Malondialdehyde content (nmol.g⁻¹ FW)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>21.71 ± 0.040e*</td>
<td>57.47 ± 0.189d</td>
<td>12.44 ± 0.158e</td>
</tr>
<tr>
<td>Boron</td>
<td>29.28 ± 0.083a</td>
<td>65.99± 0.421a</td>
<td>22.65 ± 0.136a</td>
</tr>
<tr>
<td>Boron + 5 ALA</td>
<td>25.56 ± 0.121c</td>
<td>62.77± 0.061c</td>
<td>21.38 ± 0.141b</td>
</tr>
<tr>
<td>Boron + 10 ALA</td>
<td>24.41 ± 0.048d</td>
<td>62.27± 0.152c</td>
<td>15.41 ± 0.082d</td>
</tr>
<tr>
<td>Boron + 20 ALA</td>
<td>27.51 ± 0.156b</td>
<td>64.60± 0.092b</td>
<td>17.31 ± 0.083c</td>
</tr>
</tbody>
</table>

* Different letters in the same column indicate statistically significant differences (P < 0.05).

3.6. Boron content

In this experiment, boron amounts in roots were measured with ICP-MS (Figure 3). Boron amount in roots of wheat increased noticeably upon exposure to boron stress; however, ALA treatments compared to boron treatments caused to important decrease at boron amounts. Boron application raised boron level in the roots approximately 20 fold compared to control seedlings. On the other hand, when compared to boron-applied seedlings alone, 5, 10 and 20 mg.L⁻¹ALA-applications reduced markedly boron levels in the roots by 17.2, 30.2 and 28.4%, respectively.
4. Discussion

The toxic effect of high boron concentrations manifests with marked declines in root and shoot growth [1]. In the present study, it was also determined that boron applications inhibited severely root and shoot elongations in wheat seedlings. This reduction might be resulted from devastating effect of excess boron on cell division stages. Reid & al. [9] notified that excess boron damaged the cell division stages by binding ribose within RNA or free ribose in cytoplasm. To mitigate toxic effect of boron, we carried out exogenous ALA application. According to our knowledge, this is the first report about the effects of ALA on plants exposed to boron toxicity. ALA application decreased significantly boron-induced reductions in lengths of root and shoots. The most ameliorative effect was recorded at 10 mg.L⁻¹ ALA-applied seedlings. To exhibit the mitigating effects of ALA on boron toxicity, in addition to changes in root and shoot lengths, the changes in soluble protein content, chlorophyll content, reactive oxygen species, lipid peroxidation level, and activities of antioxidant enzymes were broadly investigated. Boron toxicity caused a decrease in soluble protein content compared to control plants. This finding was accordance with the data reported in prior studies. Inbaraj and Muthuchelian [35] notified that the excess level of boron diminished soluble protein content in cowpea. The decline in protein content might be associated with inhibition in the mRNA splicing reactions. Shomron and Ast [36] reported that high boron levels inhibited the first step of mRNA splicing reactions. The combined applications of boron and ALA increased protein content as compared to boron application alone. SDS-PAGE gel images confirmed the boron and ALA induced-changes determined in protein content. It can be clearly seen that boron and ALA application caused to distinctive changes in protein profile of wheat leaves. Intensity of the protein bands between 50 and 60 kD containing RuBisCo (Ribulose-1,5-bisphosphate carboxylase/oxygenase) [37], one of the most important enzymes for CO₂ assimilation were visibly impressed by boron alone and combined applications boron and ALA. ALA application resulted in a remarkable increase in intensity of these bands. This increase suggested that ALA application might be associated with high photosynthetic efficiency compared to boron-stressed seedlings alone. We determined that boron toxicity decreased severely levels of photosynthetic pigments containing chlorophyll a, chlorophyll b, total chlorophyll and carotenoid. There are a lot of publications confirming these findings [5,6,8]. The decrease in photosynthetic pigment contents might lead to a decline in the maximum quantum yield of chlorophyll fluoresce ratio (Fv/Fm) [7]. The decline in Fv/Fm ratio increases seriously in minimal chlorophyll fluoresce.
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(Fo), which causes devastation in thylakoid membranes [38]. Also, the decline of $Fw/Fm$ ratio might enhance formation of reactive oxygen species (ROS) by increasing photo inhibition [39]. In the present study, it has been determined that ALA applications caused important increases in photosynthetic pigment contents of wheat under boron stress. Tewari and Tripathy [40] has reported that the under the boron toxicity, decline in pigment amounts results from devastation on structure of ALA a precursor of chlorophyll synthesis. Exogenous ALA application might have prevented this inhibition as an extra precursor for chlorophyll synthesis. We detected that excess boron applications caused oxidative stress in wheat seedlings. Superoxide anion (O$_2^-$) formation and hydrogen peroxide (H$_2$O$_2$) amount in leaves severely raised under the boron toxicity. These findings were consistent with the reported by prior researchers. Esim& al. [41] reported that boron stress raised the ROS formation by enhancing oxidative damage in maize seedlings. It is highly likely that the increase of ROS formation could be result from boron-induced devastation on structure of thylakoid membranes and photo inhibition [39]. Unlike these data and hypothesis, Karabal& al. [42] notified that boron stress did not lead to oxidative stress in barley. This contrasting data with the findings of the present study might be attributed to various effects of boron on different plant species and development stage. As compared boron treatment alone, combine applications of boron and ALA markedly decreased the ROS amount. This ameliorative effect might be related with repairing effect on photosynthetic apparatus or preventing effect on photo inhibition. Boron treatment increased drastically the MDA level, a good indicator of cell membrane damage, as well as ROS formation. These results corroborate with findings of Esim& al.[41] who has shown to increase of MDA and ROS formation in response to excessive boron. These data clearly shows that excess boron levels cause oxidative stress. The combined application of ALA and boron decreased significantly the MDA content as concomitant with the reduction in ROS formation.

It has been well known that the levels of boron above optimal values affect activities of antioxidant enzymes containing SOD, GPX, CAT, APX and GR. However, there are some controversies regarding the effects of boron toxicity on the activities of antioxidant enzymes. Cervilla& al. [15] has reported that boron stress increased activity of SOD enzyme, which is responsible for detoxification of superoxide anion; on the other hand, its high concentrations did not led to any change on the SOD enzyme activity in different cultivars of the same plant. In this study, SOD activity decreased under boron stress. ALA treatments together with boron improved markedly SOD activities as compared to boron treatment alone. ALA-induced increases in the enzyme activities are compatible with decrease in superoxide anion formation. Similarly, the other antioxidant enzymes GPX, CAT, APX and GR, are responsible for H$_2$O$_2$ elimination, were severely affected by boron applications. While the CAT activities increased by boron treatment, the GPX, APX and GR activities decreased markedly as compared to the control. In accordance with these data, Eraslan& al. [43] reported that boron stress increased CAT activity but decreased APX activity. Similarly, it has been informed that boron stress enhanced CAT activities in tomato [15] and tobacco [44]. In the present study, in spite of the increase in CAT activity with effect of boron stress, the hydrogen peroxide amount and MDA level did not decreased. This data demonstrates that the increment in only CAT activity apart from other antioxidant enzymes were insufficient to prevent the oxidative stress arising from boron toxicity. As compared to boron treatment alone, combine treatments of boron and ALA resulted in marked increases in the activities of all antioxidant enzymes. In ALA-applied seedlings, MDA level and ROS formation decreased inversely with the raises in antioxidant enzyme activities. This case can be explained by the fact that ALA treatments repaired distortions in metabolic processes, which are negatively
affected by boron stress, by stimulating antioxidant system. This hypothesis is in accordance with the assumption of Erdaland Dumlupinar [45,46] who notified that low ROS levels can increase tolerance of plants against stress conditions by inducing antioxidant system with their signal roles.

For evaluating the effect of ALA treatments on boron uptake from roots, boron levels in roots were measured with inductively coupled plasma mass spectrometry (ICP-MS). Boron treatment severely increased in the boron levels in roots. The excessive increment in boron level could be due to high permeability against boron of lipid bilayers and passive uptake from roots of boron or inhibition of transportation from roots to leaves [2]. Since boron is immobile in the phloem, it is accumulated in leaves by transporting through xylem [5]. The accumulated boron in the leaves manifests with significant symptoms such as chlorosis and necrosis [6]. In comparison with boron treatment alone, combined applications of ALA and boron caused an important decline in boron level. In light of these observations, it can be said that the mitigating effect of ALA against boron stress might be due to its stimulating effect on antioxidant systems as well as reduction of boron level in root structure. The present study is the first investigation reporting ALA application reduces boron levels in the roots. On the other hand, Ali & al. [22] reported that exogenous ALA treatment can be provide tolerance against Cd toxicity by causing very important ultra-structural changes containing smooth cell wall, developed nucleus and nucleus membrane. In this study, the decrease of boron level with ALA treatment might have resulted from these changes in ultra-structural of wheat roots under boron stress. In addition to this possibility, ALA treatments could be reduced boron uptake by affecting post transcriptional levels of BOR and NIR channels, which are regulated by alteration of boron levels and are responsible for boron uptake and transport [47].

In conclusion, it has been determined that excessive boron concentration reduced root and shoot development and caused oxidative stress in wheat. Furthermore, boron stress led a decline of photosynthetic pigment contents and important raise of boron levels in roots. ALA applications alleviated the growth deficiency, oxidative stress and boron accumulation caused by boron stress. These complex effects of the ALA prove that it can be used to enhance plant resistance against boron toxicity.

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