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Effect of Gamma-Aminobutyric Acid (GABA) Pretreatment on Antioxidant Responses and Alleviation of Salinity Damage in *Prosopis koelziana* Seedlings

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ABSTRACT

Prosopis koelziana belongs to the Fabaceae family (formerly Mimosaceae) and grows in arid and semi-arid regions. It is used for the reclamation of dry forests with low fertility and high salt content. This study was conducted to investigate the effect of gamma-aminobutyric acid (GABA) at concentrations of 0.25 and 0.5 mM on enhancing salinity tolerance in *Prosopis koelziana* seedlings under 400 and 600 mM NaCl. The results showed that salinity stress induced oxidative stress, and malondialdehyde (MDA) content increased in both shoots and roots. Salinity also increased the activities of antioxidant enzymes, including catalase (CAT), guaiacol peroxidase (GPX), and ascorbate peroxidase (APX). However, pretreatment with GABA reduced MDA content and antioxidant enzyme activity. Under 400 and 600 mM salt stress, root sodium (Na^+) content increased by 55% and 62%, and shoot sodium content increased by 73% and 100%, respectively, compared to controls. GABA (0.25 and 0.5 mM) reduced sodium levels in both organs. Salt stress decreased potassium (K^+) content in roots and shoot, whereas GABA pretreatment increased potassium levels. The findings indicate that pretreating plants with GABA significantly reduced membrane lipid peroxidation and lowered the activity of antioxidant enzymes. This stress alleviation appears to be primarily due to reduced sodium uptake and transport into plant tissues, along with increased potassium content. Consequently, antioxidant enzyme activity decreased in GABA pretreated plants under stress conditions.

Keywords: Salinity stress, Gamma Amino-butyric Acid, *Prosopis koelziana,* Antioxidant enzymes

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Introduction

Salinity is a major limiting factor for plant growth and one of the most significant environmental stresses. It is caused by an excessive amount of salt due to high evapotranspiration and a lack of quality water in arid and semi-arid regions (Ahmed and Khalid, 2023). Salty, alkaline soils typically form in these areas, which disrupt

plant growth. Salt stress leads to various problems for plants, primarily resulting from ionic toxicity and osmotic stress (Ali et al., 2023).

Prosopis koelziana is widely used in the restoration of deserts, forests, and degraded soils characterized by low fertility and high salinity (Figure 1). Native to Iran, this species naturally grows in arid and desert regions, where it withstands low rainfall and limited water availability (Bhojvaid and Timmer 1998). Given its native status and its diverse economic and ecological benefits, Iranian Prosopis species represent the optimal choice for conserving biodiversity and protecting the environment in the country's arid and desert areas. Prosopis koelziana is a hardy plant that thrives in dry and saline conditions, making a significant contribution to the improvement and conservation of soil and water resources. Its key roles within its natural habitats include enhancing water supply, preserving biodiversity, protecting soil, and providing positive economic and social impacts on local communities (Zare and Tavili 2011; Emtahani and Elmi 2006; Saadatfar et al., 2023; Mousavi et al., 2025). The preservation and restoration of Prosopis koelziana are crucial for maintaining the natural balance and sustainability of the environment. For this reason, its application in soil stabilization projects is particularly valuable in sandy soil areas, such as deserts (Mousavi et al., 2025; Saadatfar et al., 2023). This approach contributes significantly to sustainable development and effective natural resource management programs.

Figure 1. Image of the Prosopis koelziana plant and the morphology of its leaves.

GABA is a four-carbon (C4) non-protein amino acid having a chemical formula of $C_4H_9NO_2$ and is an important component of free amino acids (Beuve et al., 2004). In plants and animals, GABA is mainly metabolized through a short pathway called GABA shunt, which is able to bypass the two steps of Krebs cycle (Bown et al., 2006). The Shunt pathway consists of the cytosolic Glutamate Decarboxylase (GAD) and mitochondrial enzymes such as Gaba Trans Aminase (GAD) and Succinic Semi Aldehyde Dehydrogenase (SSADH) (Kinnersley and Lin, 2010). This compound has metabolic effects such as, protection against oxidative stress, osmotic regulation, and protection against insects, which is found in Arabidopsis, for instance (Bown et al., 2006; Islam et al., 2024). The impact of the exogenous application of GABA on the increment of plant tolerance to biological and non-biological stresses has been reported in certain studies (Alen et al., 2014). As an example, it has been reported that GABA increases tolerance of peach fruit against the cold stress (Yang et al., 2011) and the tomato plant under the salt stress (Zhang et al., 2011). Furthermore, the exogenous application of GABA has led to an increase in activity of antioxidant enzymes such as catalase and ascorbate peroxidase, and non-enzymatic antioxidants namely, ascorbate and glutathione in rice plant at high temperature (Nayyar et al., 2014). Moreover, it has been

reported that GABA retains the osmotic potential of plants exposed to osmotic stress and prevents the disruption of normal cell activities (Xia et al., 2011). Also, some reports show the effect of exogenous application of GABA on ions absorption (Xing et al., 2007). Given the importance of conserving plant species such as Prosopis koelziana and preventing their extinction, scientific studies are essential to enhance seedling resistance and facilitate the successful transfer of resilient seedlings to natural conditions. Due to the role of gamma-aminobutyric acid (GABA) in increasing tolerance to environmental stresses such as salinity, this study aimed to investigate the potential use of GABA to improve stress tolerance in Prosopis koelziana seedlings. By applying this compound during the early stages of plant development, it may be possible to produce seedlings capable of withstanding salinity and being successfully established in saline environments.

Materials and methods

The seeds used for this experiment were obtained from native Prosopis koelziana plants in Shahdad (Estehkam), located close to the Dasht-E-Lut desert in the Kerman province of Iran (Herbarium number: MIR-4752). This area is not protected, so seed collection is allowed. A small quantity of seeds from this plant was collected for research purposes. The seeds were treated with sulfuric acid for 2 minutes and washed three times with distilled water and soaked in distilled water for 24 hours. After this treatment, the seeds were germinated in petri dishes at 27°C for 24 hours before being planted into plastic pots filled with sand, which had been washed with distilled water prior to use. The seedlings were irrigated daily with half-strength Hoagland solution. After 10 days of growth under a 16/8-hour light/dark photoperiod at 27 °C and 40% humidity, uniform seedlings were selected for treatment. The plants were divided into three groups, each with six replicates (pot) (four plants per pot). Two groups were pretreated with 0.25 mM and 0.5 mM GABA (20 ml of solution per pot), while the control group received only distilled water for five days. On the sixth day, one set of plants that had been treated with GABA solutions and distilled water was exposed to either 400 mM or 600 mM NaCl for six days, while the other set was treated with distilled water only. These NaCl concentrations were optimized in a preliminary experiment. After six days of treatment, the shoots and roots of the plants were harvested, immediately frozen in liquid nitrogen, and stored at -80 for future analysis.

This study was conducted as a completely randomized design (CRD) with three replications. Statistical analyses were performed using SPSS version 23. Treatment effects were evaluated using analysis of variance (ANOVA), and mean comparisons were carried out using Duncan's multiple range test at a 95% confidence level. Graphs were prepared using Microsoft Excel 2019.

Lipid peroxidation

The level of lipid peroxidation, as an indicator of cellular damage, was measured in terms of malondialdehyde (MDA) content according to Heath and Packer (1968). Shoot and root samples (0.1g) were homogenized in 0.1% (w/v) trichloroacetic acid (TCA) and centrifuged at 4000× g for 10 min. The supernatant (0.5 ml) was mixed with 1.5 ml of 20% (w/v) TCA containing 0.5% (w/v) 2-thiobarbituricacid (TBA). The mixtures were heated at 95 °C for 30 min and then quickly cooled in an ice bath. The mixtures were centrifuged at 10000× g for 5 min and their supernatant absorbance was measured at 532nm. The value of non-specific absorption at 600 nm was subtracted from the 532 nm reading. The MDA content was calculated using the Lambert-Beer law, with extinction coefficient of 155 $mM^{-1}cm^{-1}$ and expressed as micromole MDA per g fresh weight.

Enzyme extraction and activity determination

Shoot and root tissues (500 mg) were homogenized in 50 mM potassium phosphate buffer (pH 7.0) containing 1% soluble PVP and 1 mM EDTA. The homogenate was centrifuged at 20,000 × g for 20 min and the supernatant used for assay of the activity of enzymes.

Catalase (CAT) activity (EC 1.11.1.6)

Catalase activity was assayed by measuring the initial rate of H_2O_2 disappearance at 240nm using the extinction coefficient of 40 mM^{-1} cm^{-1} for H_2O_2 (Dhindsa et al., 1981). The enzyme activity was reported as U per milligram of protein (equivalent to 1 µmol of H_2O_2 reduction per minute per milligram of protein).

Guaiacol peroxidase (GPX) activity (EC1.11.1.7)

The GPX activity was determined using the method of Plewa et al., (1999). The oxidation of guaiacol (formation of tetraguaiacol) was assessed by measuring the absorbance at 470 nm one minute after the addition of H_2O_2. The extinction coefficient of tetraguaiacol (25.5 mM^{-1} cm^{-1}) was applied for unit determination. Enzyme activity was expressed as units of enzyme activity per milligram of protein content.

Ascorbate peroxidase (APX) activity (EC 1.11.1.11)

Ascorbate peroxidase was determined spectrophotometrically according to the oxidation of ASA. The reaction solution contained 50mM potassium phosphate buffer (pH 7.0), 0.5mM ascorbate, 0.1mM H_2O_2 and 150µl enzyme extract. H_2O_2-dependent oxidation of ASA was followed by measuring the decrease in absorbance within 1min at 290 (extinction coefficient of 2.8 mM^{-1} cm^{-1}) (Nakano and Asada., 1981). The amount of enzyme that decomposed 1 µmol of ascorbate per minute was defined as one unit (U) of APX activity. The enzyme activity was reported in units per milligram of protein.

Total soluble proteins

Protein content was determined according to the method of Bradford (1976) using bovine serum albumin as standard.

Measurement of K^+ and Na^+ content in root and shoots of plants

Dried samples (100 mg) were digested in 67% (v/v) HNO_3. Samples were maintained overnight in 10 ml HNO_3. The samples were heated for 45 min at 90°C, and then the temperature was increased to 150°C, at which the samples were boiled for at least three h until a clear solution was obtained. Digestion continued until the volume was reduced to about one ml. Finally, these extracts were filtered, diluted with distilled water, and the ion contents were determined using flame photometer. Standard curve was used for the calculation of each ion concentration.

Result

The results showed that the rate of membrane lipid peroxidation, as one of the important stress indicators in the shoot of Prosopis koelziana plants under 400 and 600 mM salt stress, increased by 56% and 70%, respectively in compared to control. This increase and the intensity of stress were greater in the root tissue, such that the rate of membrane lipid peroxidation in the root tissue of plants under 400 and 600 mM salt stress was 2.5 and 5 times that of the control plants, respectively. Under 400 mM salt stress conditions, the application of GABA at concentrations of 0.25 and 0.5 mM in the shoots caused a 23% and 30% reduction in lipid peroxidation, respectively in comparison with control plants. At 600 mM salinity, the application of concentrations of 0.25 and 0.5mM also reduced peroxidation by 28% and 32%. In the roots, GABA application reduced the rate of peroxidation in both salinity treatments, but there was not a significant difference between the different concentrations of GABA (Figure 2). The highest MDA level was observed in plants under 600 mM NaCl stress without GABA pretreatment.

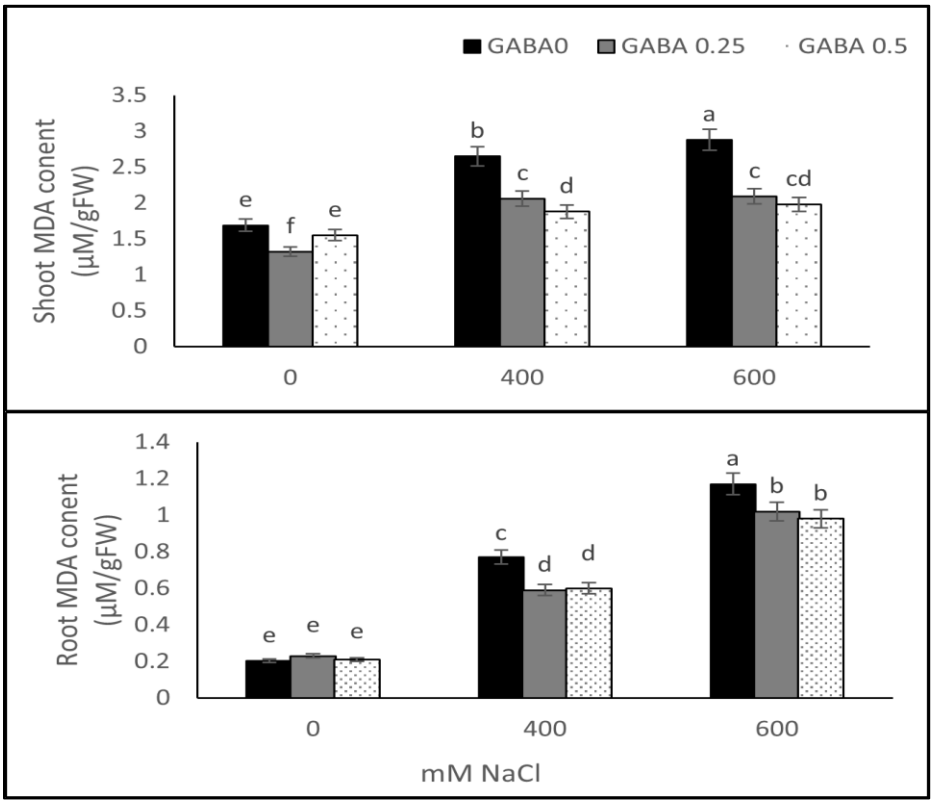

Figure 2. Effect of GABA pretreatment (0, 0.25, and 0.5 mM) on lipid peroxidation of membranes in the shoots and roots of *Prosopis koelziana* seedlings under salinity stress (0, 400, and 600 mM NaCl). Data are means ± SD (n = 3 independent pots). Different lowercase letters above bars indicate significant differences according to Duncan's multiple range test ($p < 0.05$).

The assay of ascorbate peroxidase enzyme showed that salt stress increased the activity of this enzyme in both roots and shoots. The application of 0.25 and 0.5 mM of GABA reduced the activity of this enzyme in the shoot and roots. The results indicated that under 400 mM salinity, the 0.25 mM of GABA was more effective in reducing stress and consequently decreasing enzyme activity; however, under 600 mM salinity, the higher concentration of GABA was more effective (Figure 3). The highest ascorbate peroxidase activity under salinity stress conditions was observed in plants that were not pretreated with GABA.

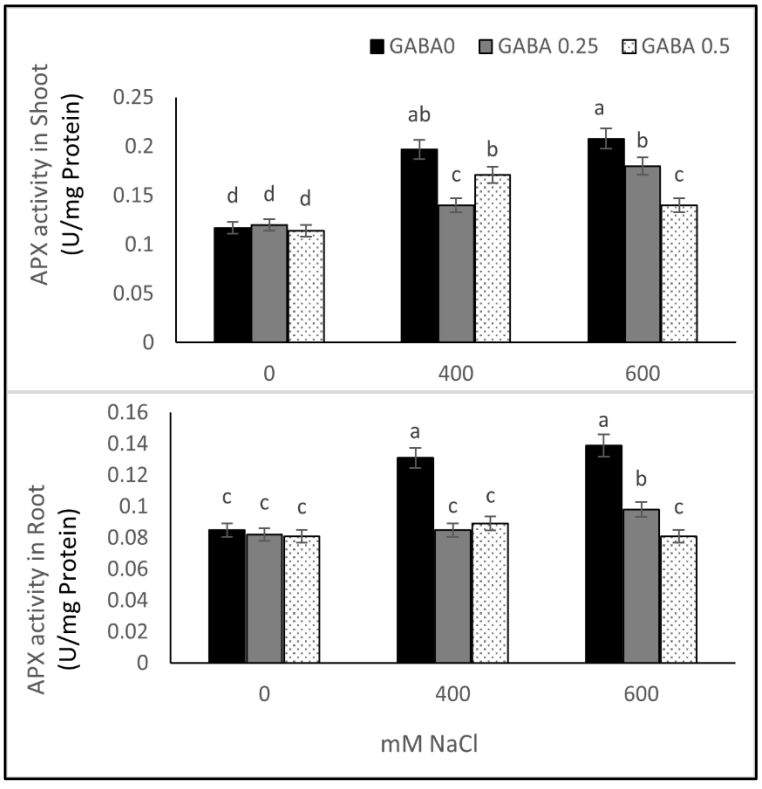

Figure 3. Effect of GABA pretreatment (0, 0.25, and 0.5 mM) on the ascorbate peroxidase activity in the shoots and roots of *Prosopis koelziana* seedlings under salinity stress (0, 400, and 600 mM NaCl). Data are means ± SD (n = 3 independent pots). Different lowercase letters above bars indicate significant differences according to Duncan's multiple range test ($p < 0.05$).

The results of measuring catalase enzyme activity in the roots and shoot of the *Prosopis koelziana* plant showed that this enzyme increased significantly under salt stress, and the application of GABA reduced the activity of this enzyme in both the roots and shoots of the plant. Almost no significant difference was observed between the effects of the two GABA concentrations on the activity of this enzyme, and both concentrations reduced enzyme activity. The application of GABA in the 400 mM salinity treatment did not have a significant effect on catalase enzyme activity in the roots (Figure 4).

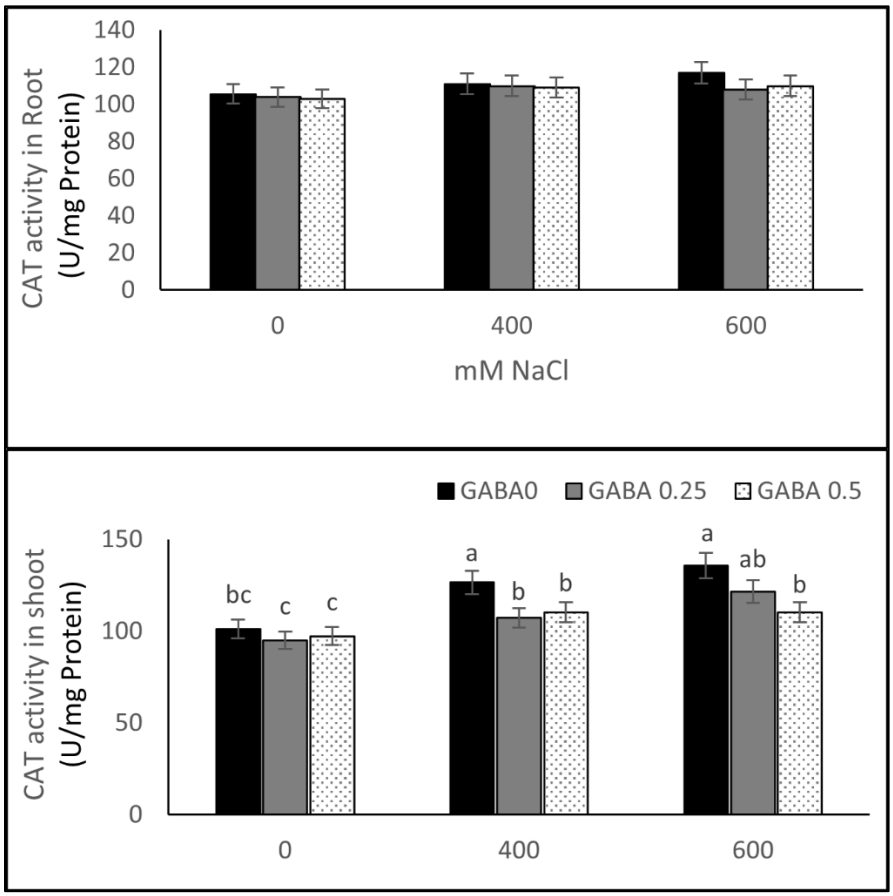

Figure 4. Effect of GABA pretreatment (0, 0.25, and 0.5 mM) on the catalase activity in the shoots and roots of *Prosopis koelziana* seedlings under salinity stress (0, 400, and 600 mM NaCl). Data are means ± SD (n= 3 independent pots). Different lowercase letters above bars indicate significant differences according to Duncan's multiple range test ($p < 0.05$).

Measurement of GPX enzyme activity also showed an increase in its activity under salt stress. As the salinity level increased, the activity of this enzyme, like other enzymes, increased. In the shoot of plants affected by 400 mM salinity, only the concentration of 0.25 mM GABA reduced enzyme activity, and the concentration of 0.5 mM had no significant effect on enzyme activity. However, in plants under 600 mM salt stress, both applied concentrations of GABA reduced enzyme activity, and the effect of the 0.5 mM concentration in reducing enzyme activity was greater than that of 0.25 mM. In the roots of *Prosopis koelziana* plants, both concentrations of GABA under 400 mM salinity and the concentration of 0.5 mM under 600 mM salinity had a significant effect in reducing the activity of this enzyme (Figure 5). The highest guaiacol peroxidase activity was observed in plant samples that were under 600 mM salinity stress and were not pretreated with GABA.

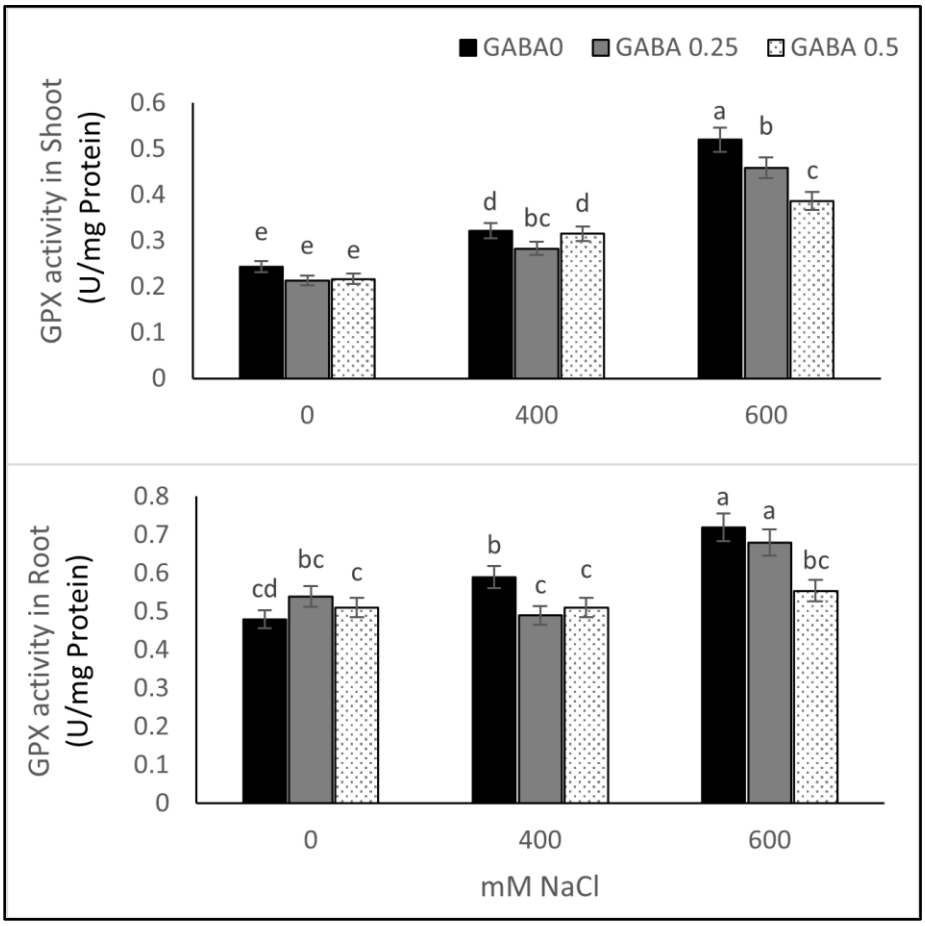

Figure 5. Effect of GABA pretreatment (0, 0.25, and 0.5 mM) on the guaiacol peroxidase activity in the shoots and roots of *Prosopis koelziana* seedlings under salinity stress (0, 400, and 600 mM NaCl). Data are means ± SD (n = 3 independent pots). Different lowercase letters above bars indicate significant differences according to Duncan's multiple range test ($p < 0.05$).

Data obtained from measuring sodium and potassium ions showed that in the roots of plants subjected to 400 and 600 mM salt stress, the sodium ion content increased by 55% and 62%, respectively, compared to control plants, while in the leaves, the sodium ion content in the 400 and 600 mM treatments showed a 73% and 100% increase, respectively. Application of GABA at concentrations of 0.25 and 0.5 mM reduced the sodium ion content in both roots and shoot.

Potassium ion assay showed that the content of this ion decreased under salt stress in both shoot and roots, and pretreatment with GABA increased this ion in root and shoot tissues (Table 1).

Table 1. Effect of GABA pretreatment on sodium and potassium content of shoot and root of *Prosopis koelziana* seedling under the control and stress conditions. Means were compared using Duncan's multiple range test. Differences were considered significant at $p < 0.05$. Means denoted by different letters represent significant difference.

Pretreatment and treatment	Root Na^+ (mg/gFW)	Shoot Na^+ (mg/gFW)	Root K^+ (mg/gFW)	Shoot K^+ (mg/gFW)
Control	43.22 cd	10.93 e	28.01 a	19.42 b
GABA 0.25 mM	44.81 c	11.26 de	25.57 ab	19.83 b
GABA 0.5 mM	45.09 c	13.12 d	32.39 a	17.72 c
Salinity 400 mM	66.94 ab	18.98 b	20.96 b	17.33 c
Salinity 400mM + GABA 0.25mM	58.04 b	15.36 c	24.85 ab	26.41 a
Salinity 400mM + GABA 0.5 mM	60.85 b	16.27 c	28.05 a	19.88 b
Sainity600mM	70.44 a	25.35 a	21.82 b	17.65 c
Salinity 600mM + GABA 0.25mM	59.97 b	23.82 ab	20.53 b	23.88 a
Salinity 600mM + GABA 0.5 mM	56.81 c	21.01 b	20.67 b	20.57 ab

Discussion

Seed germination and early seedling growth are critical stages of plant development that are particularly sensitive to abiotic stresses (Firoozkouhi et al., 2025). One significant issue caused by salinity is oxidative stress, which often results in increased lipid peroxidation. This process involves the oxidation of membrane lipids, ultimately compromising cell integrity and function. Elevated lipid peroxidation is a well-known indicator of increased oxidative stress under saline conditions. During salt stress, this heightened lipid peroxidation is a direct consequence of increased production of reactive oxygen species (ROS) (Golestani et al., 2025). This investigation emphasizes the benefits of GABA pretreatment in reducing lipid peroxidation in seedlings of *Prosopis koelziana,* suggesting that this approach enhances the plants' resilience to oxidative stress. The ameliorative effect of GABA under abiotic stress conditions has been reported in previous studies (Islam et al., 2024). Similar studies conducted on plants such as Prosopis (Soleimani et al., 2011), Haloxylon (Wang et al., 2014), and bean (Palma et al., 2009) under salt stress conditions have shown an increase in oxidative stress, alongside a rise in malondialdehyde levels, leading to a decrease in the membrane stability index. These findings are consistent with the results of this study on Prosopis seedlings. Additionally, the role of GABA in reducing membrane lipid peroxidation has been documented in tomato

(Malekzadeh et al., 2014) under cold stress, *Stellaria longipes*, lemon, Suger beet and mung bean (Kathiresan et al., 1998; Kinnersley and Lin, 2000; Ullah et al., 2023; Yu et al., 2024) under salt stress, as well as in black pepper (Shi et al., 2010) under osmotic stress. To manage oxidative stress, it is crucial to enhance the effectiveness of a plant's antioxidant defense system. The activity levels of antioxidant enzymes in plants serve as good indicators of the cell's redox state, which is vital for developing resistance to stress (Firoozkouhi et al., 2025). As these enzymes act as scavengers for reactive oxygen species (ROS), they play a significant role in protecting cells and the photosynthetic apparatus (Shi et al., 2010). Research data indicated that increased salinity heightened the activity of antioxidant enzymes, suggesting the onset of oxidative stress and the activation of the plant's antioxidant system. However, this study found that pretreating Prosopis seedlings with GABA reduced the activity of these antioxidant enzymes compared to non-pretreated plants. It appears that in seedlings pretreated with GABA, stress levels were lower, meaning the plants did not have to increase their antioxidant enzyme activity. Additionally, examining the levels of sodium and potassium ions showed that these ions were reduced in the pretreated plants, further supporting this hypothesis.

Salinity can lead to nutrient depletion or imbalance by competing with essential nutrients such as potassium (K^+) and calcium (Ca^{2+}) for chloride (Cl^-) and sodium (Na^+) ions (Hu et al., 2007). Research indicates that salt stress affects certain plants, including Guar (Firoozkouhi et al., 2025; Golestani et al., 2025), *Prosopis Koelziana* (Mousavi et al., 2025) and cotton (Dong et al., 2014), leading to alterations in the distribution of ions within their aerial parts. Potassium is crucial for various physiological processes and plant growth, including protein and starch synthesis, the activation of numerous photosynthetic and respiratory enzymes, the maintenance of photosynthetic system integrity, and osmotic regulation (Hu et al., 2005; Rahnama et al., 2004; Cardon et al., 2003). Research has shown that increased levels of sodium chloride (NaCl) can depolarize the cell membrane and create an antagonistic effect with sodium, which ultimately reduces potassium (K^+) uptake (Turan et al., 2010). Research has shown that one of the beneficial effects of GABA under salt stress conditions is its ability to enhance the absorption of essential mineral ions. For instance, treating seedlings with GABA resulted in increased absorption of minerals such as manganese, potassium, and iron (Kinnersley et al., 2010). Similarly, in wheat plants, the application of exogenous GABA led to a higher uptake of minerals crucial for plant metabolism, including manganese and calcium (Xing et al., 2007). One of the most significant effects of salinity is the increasing ratio of sodium to potassium, which has been reported in numerous studies (Juan et al., 2005; Abdel, 2010; Farsaraei et al., 2020). In the present experiment, the data indicated that GABA pretreatment decreased the absorption and transport of sodium into plant tissues while simultaneously increasing potassium content the Na+ absorption and increased the ratio in the leaves of plants subjected to salt stress.

Conclusions

The data from this study indicate that GABA can play an effective role in mitigating salt stress in *Prosopis koelziana* plants. In this research, it was observed that the mechanism of action of GABA was primarily through reducing the absorption and translocation of sodium ions from the roots to the shoots. It seems that, this function of GABA alleviated the intensity of the stress and resulted in decreased stress indicators and reduced antioxidant enzyme activity in plants pretreated with GABA.

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