

EXOGENOUS APPLICATION OF POTASSIUM MITIGATES SALT STRESS AND ENHANCES SOYBEAN GROWTH THROUGH IMPROVED PHOTOSYNTHETIC EFFICIENCY, ANTIOXIDANT ACTIVITIES, AND IONIC HOMEOSTASIS

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(Received 24th Oct 2024; accepted 4th Feb 2025)

Abstract. Salinity is a major abiotic stress that significantly reduces crop yields worldwide. Potassium possesses an excellent potential to induce abiotic stress tolerance in plants. This study aimed to evaluate the effects of potassium on salt tolerance in salt-sensitive and salt-tolerant soybean cultivars. The study was included salinity stress along with potassium levels (control, 60 mM NaCl, 120 mM NaCl, 60 mM NaCl + 6 mM K, 60 mM NaCl + 9 mM K, 120 mM NaCl + 6 mM K, and 120 mM NaCl + 9 mM K) and soybean cultivars: William 82, Ajmeri, AARI 62, and AARI 13. Salinity caused a profound decrease in growth and biomass production by decreasing relative water contents (RWC), chlorophyll contents, membrane stability index, leaf area, photosynthetic rate, transpiration rate, stomata conductance, inter-cellular carbon dioxide (CO₂) concentration, potassium (K) accumulation and increasing accumulation of sodium (Na) and Na/K. The exogenous application of K mitigated the adversities of salinity which was linked with improved relative water contents (RWC), chlorophyll contents, membrane stability index, leaf area, photosynthetic rate, transpiration rate, stomata conductance, inter-cellular CO₂ concentration, potassium (K) accumulation and decreasing accumulation of sodium (Na) and Na/K. Cultivar AARI 62 was identified as salt-tolerant, whereas cultivar Ajmeri was salt-sensitive. In conclusion, potassium application mitigates the adverse effects of salinity on soybeans by enhancing photosynthetic efficiency, antioxidant activity, and ionic homeostasis.

Keywords: *electrolyte leakage, growth, membrane stability, potassium, salinity, soybean*

Introduction

Soil salinization is increasing globally due to both human activities and natural processes (Gkotzamani et al., 2024). Intensive agricultural practices have exacerbated salinity stress (Rasool et al., 2013), and globally more than 30% of soils are salt-affected (Hopmans et al., 2021). Soil salinization is expanding at an annual rate of 10%, and projections indicate that 50% of cultivated lands may be affected by salt stress by 2050 (Machado et al., 2017; Zhao et al., 2021). Thus, salinity stress is a serious challenge in agriculture development, crop production, and food security. Salinity stress also threatens biodiversity, disrupts ecosystems, and diminishes soil biological activity (Mukhopadhyay et al., 2021). Salinity stress negatively affects leaf growth, leaf expansion, root growth, and surface area resulting in decreased nutrients by plants, leading to poor biomass, and grain productivity (Robin et al., 2016; Seleiman et al., 2021; Atta et al., 2023). Salinity stress also increases the production and accumulation of reactive oxygen species (ROS) which interact with vital cell components cause oxidative damage to proteins, deoxyribonucleic acid (DNA), and lipids, and disrupt nutrient and hormonal levels in plants (Seleiman et al., 2021). Salinity stress also interrupts water and nutrient uptake and negatively affects photosynthesis by damaging photosynthetic apparatus thereby, causing a reduction in growth (Giordano et al., 2021).

Salinity stress also imposes osmotic stress owing to a reduction in water potential which is accompanied by ionic stress owing to the entry of toxic ions (Na and Cl) (Rozentsvet et al., 2017). Besides this, soil salinity often reduces plant biomass production by decreasing CO₂ assimilation in photosynthesis due to stomata closure (Pompeiano et al., 2017; Asrar et al., 2017). The prolonged salinity stress also negatively affects the activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCo) and all these changes inhibit the use of adenosine triphosphate (ATP) and nicotinamide adenine dinucleotide phosphate (NADPH: Asrar et al., 2017). The excessive excitation energy due to salinity also damages the photosynthetic apparatus and proteins (D1 and D2) of photosystem-II (PS-II) (Takahashi and Badger, 2011; Percey et al., 2016). Globally different strategies are being used to mitigate the adversities of salinity stress. The application of nutrients has shown promising results in countering the toxicity of salinity.

Potassium is an essential nutrient for plants and its deficiency reduces plant's resistance to stress conditions. Plants facing K deficiency under saline conditions face a reduction in photosynthesis, plant growth, and even death (Cakmak et al., 2005). A sufficiency supply of K promotes the accumulation of osmolytes, enzyme activity, and photosynthetic efficiency, protects photosynthetic apparatus, and maintains a better K⁺/Na⁺ ratio which ensures better plant growth under salinity conditions (Munir et al., 2019; Huang et al., 2022). The plant growth and K uptake and absorption can be enhanced by the exogenous application of K fertilizers (Huai et al., 2022). The optimum supply of K improves root growth which in turn increases nutrient and water uptake under saline conditions, thereby leading to significant improvement in plant growth (Yaldiz et al., 2018; Ihtisham et al., 2020). The study findings on cabbage showed that an exogenous supply of K (10 mM) significantly improved the synthesis of proteins, amino activities, and antioxidant activities maintained K⁺/Na⁺ and improved salt tolerance (Ahmad et al., 2019). The application of K also improves water use efficiency, and carbohydrate accumulation and reduces the toxicity of salinity by decreasing ROS production (Turcios et al., 2021). In the literature, there is limited information available about the effect of K on growth and the biochemical functioning of soybean growing in

a hydroponic system. Thus, it was hypothesized that K application can mitigate the toxic impacts of salinity on soybeans by improving antioxidant activities, and photosynthetic efficiency and decreasing the uptake of Na^+ . Thus, this study was executed to assess the impact of K on growth, photosynthetic characteristics, water relations, antioxidant activities, and nutrient homeostasis of hydroponically grown soybeans.

Materials and method

Experimental details

The present hydroponic study was conducted at the University of Agriculture in Faisalabad Pakistan. The study was comprised of different treatments and details are given in *Table 1*.

Table 1. Details of experimental treatments

Soybean cultivars (Factor A)
William 82
Ajmeri
AARI 62
AARI 13
Salinity stress levels (Factor B)
0 mM
60 mM
120 mM
Potassium levels (Factor C)
6 mM
9 mM

The doses of salinity stress and potassium were selected based on preliminary experiment. The application of 6 and 9 mM showed appreciable results in mitigating salinity stress on soybean. The study was conducted in a completely randomized designed and each treatment has four tubs where plants were grown. The genotypes of soybeans were planted in trays supplemented with prewashed sand. When seedlings reached to second leaf stage, they moved into a 200-L iron tub containing the Hoagland's solution. The aeration in the tubs was maintained through an air pump. After one week of transplanting the stress treatments (60, 120 mM) were applied by using NaCl, while in control distilled water was applied. The Hoagland's solution was applied to fulfill crop nutrient needs and after 30 days seedlings were to determine different physiological and biochemical parameters.

Growth traits

The plants were harvested after 120 days of transplanting to determine different growth traits. The plants from each treatment were harvested and separated into roots and shoots. Then roots and shoots were weighed to determine fresh weight, and later

they were dried (65°C) until constant weight to determine their dry weights. Further, a leaf area meter was used to measure the leaf area of soybean plants.

Determination of relative water contents, membrane stability index, and leaf water relations

Fresh green leaves (5 g) were plucked from each treatment and immediately weighed to determine their fresh weight (FW). Then these leaves were submerged in distilled water for a half-day and weighed again (TW). Then these leaves were removed from the water and dried for 20 h at 75°C and finally, RWC was determined as:

$$\text{RWC (\%)} = \frac{\text{FW} - \text{DR}}{\text{TW} - \text{DR}} \times 100 \quad (\text{Eq.1})$$

The fresh leaves were collected and separated into two portion. The first portion of leaves were placed in water-bath (40°C) for 30 min and its EC (C1) taken. The other group of leaves was placed in water-bath (100°C) for 15 min and its EC was taken (C2) and finally membrane stability index (MSI) was calculated with following equation:

$$\text{MSI} = [1 - (\text{C1} / \text{C2})] \times 100 \quad (\text{Eq2})$$

The flag leaves from plants were collected to determine their water potential (Ψ_w). The Scho-lander natural pressure chamber (ARIMAD-2, ELE-International) was used to collect the readings in the morning between 6:00 am and 7:00 am. To determine the osmotic potential (Ψ_s), the leaves were coated in ice and kept at a temperature of -20°C. Next, the frozen portion of the leaf was thawed, and a glass rod was used to crush the leaves in order to remove the cell sap. An osmometer was directly utilized to determine Ψ_s from the extracted sap (Wescor 5520). To estimate the leaf turgor potential (Ψ_p), the difference between the values of Ψ_w and Ψ_s was calculated.

Determination of leaf gas exchange characteristics

The fully extended newest leaf was collected after 30 days of transplanting and different leaf gas exchange characteristics were measured using an open system portable infrared gas analyzer (6400–40 LCF, Li-Cor, USA)

Determination of photosynthetic pigments

The leaves were randomly collected from different plants, thereafter, 0.5 g of fresh soybean leaves were collected and extracted by using 80% acetone. Then, the extract was centrifuged at 10000 rpm for 10 min and a spectrophotometer was used to measure absorbance at 645 and 663 nm to determine chlorophyll a and chlorophyll b concentration (Arnon, 1949).

Determination of ion concentration

Soybean plant leaves were collected, dried and ground to make powder. Then, 0.5 g ground samples were collected and digested by using 7 ml HNO_3 and 3 ml HClO_3 . Then, the volume was increased to 50 ml, and the concentration of sodium and chloride in samples was determined by using a flame photometer (Jenway PFP-7, Burlington, NJ, USA).

Determination of antioxidant activities

To determine superoxide dismutase (SOD) activity the reaction mixture was prepared which contain 100 µl enzyme extract, 2 mM riboflavin, 75 µM NBT, 10 µM ethylenediaminetetraacetic acid (EDTA), 13 mM methionine, and 50 mM sodium phosphate buffer. The reaction was initiated by placing the samples under fluorescent lamps for 10 min, there absorbance was measured at 560 nm to determine SOD activity. For determination of POD activity the reaction mixture containing 100 µl of each enzyme extract, guaiacol, H₂O₂, and 2.7 ml 25 mM potassium phosphate buffer with 2 mM EDTA was prepared. Then the absorbance was measured by using a spectrophotometer (Hitachi U-2001, Tokyo, Japan) at 470 nm to determine POD activity. For determination of catalase, the mixture containing 2.8 ml 50 mM phosphate buffer with 2 mM EDTA and 100 µl enzyme extract and H₂O₂ was prepared. Finally, CAT activity was measured by monitoring the absorbance at 240 nm.

Data analysis

The data reported in this study is the average of four replications. The collected data on different traits was analyzed by analysis of variance by using Statistics 8.1® software. Further, means were separated by LSD test ($\leq 0.05P$) and principal component analysis (PCA) was performed by R-Studio.

Results

Growth traits

The results indicate that growth and biomass were significantly decreased under salinity stress (*Figs. 1* and *2*). The results indicated a varied response of different cultivars to salinity stress and potassium application. Overall, salinity significantly reduced the root and shoot biomass of all the cultivars. The cultivars AARI 62 and AARI 13 showed less reduction in growth traits than Ajmeri and William-82. This indicates that AARI 62 and AARI 13 were salt-tolerant cultivars, whereas Ajmeri and William-82 were sensitive against salinity stress. Overall maximum root and shoot fresh and dry weights were observed in cultivar AARI-62 and lowest root and shoot fresh and dry biomass were observed in Ajmeri (*Fig. 1*). In case of salinity stress the greatest reduction in root and shoots biomass was noted with 120 mM as compared to 60 mM salinity stress. The results also indicated that application of 9 mM KNO₃ significantly enhanced the root and shoot biomass of all the cultivars under both levels of salinity stress as compared to 6 mM KNO₃ application (*Fig. 1*). The results also depicted that salinity stress also caused a serious decrease in root and shoot length of soybean cultivars. The maximum decrease in root and shoot length was observed under 120 mM in cultivar Ajmer and lowest decrease was observed in AARI-62. The presented results also depicted that applying 9 mM KNO₃ remarkably increased the root and shoot length of all the cultivar under salinity stress than the 6 mM KNO₃ (*Fig. 1*).

Photosynthetic pigments, membrane stability index, and plant water relations

Salinity stress significantly decreased chlorophyll contents maximum reduction in chlorophyll a and chlorophyll b was observed with 120 mM. However, an exogenous supply of KNO₃ improved the synthesis of both chlorophyll a and chlorophyll b, in this

regard application of 9 mM KNO₃ remained the top performed in increasing in chlorophyll a and chlorophyll b (Fig. 2). All genotypes of soybeans displayed a decrease in the MSI and RWD in response to salinity stress (60 and 120 mM NaCl) levels (Fig. 2).

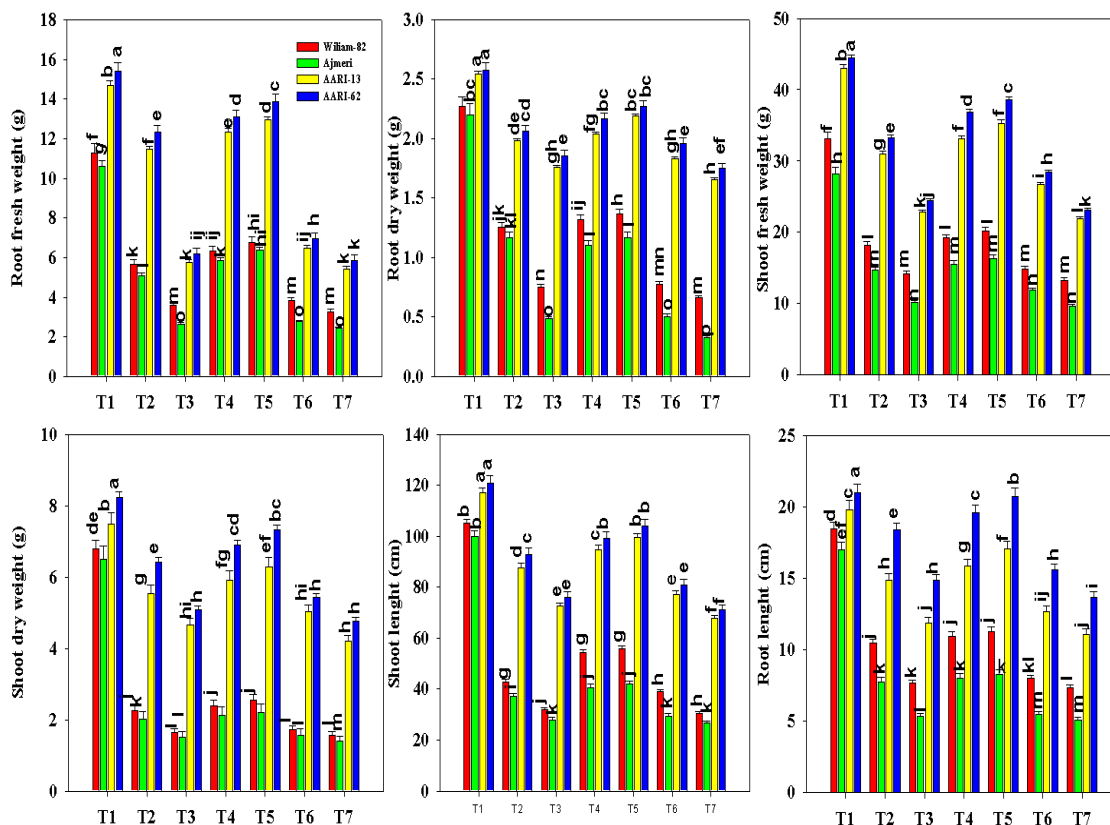


Figure 1. Effect of different potassium application on growth traits of soybean cultivars growing under salinity stress. T1: Control, T2: 60 mM NaCl, T3: 120 mM NaCl, T4: 60 mM NaCl + 6 mM K, T5: 60 mM NaCl + 9 mM K, T6: 120 mM NaCl + 6 mM K, T7: 120 mM NaCl + 9 mM K. The data in indicating the mean with $\pm$ SE

The plants facing higher concentrations NaCl (120 mM NaCl) experienced the most reduction in RWC and MSI. Salinity-tolerant genotypes (AARI-62 and AARI-13) demonstrated a smaller decline than salinity-sensitive genotypes (Ajmeri and William-82). The exogenous application of KNO₃ improved the RWC and MSI however, the degree of improvement was higher in salt-tolerant genotypes than salt-sensitive genotypes. Potassium application significantly raised Ψ_p while decreasing Ψ_s . The application of potassium (9 mM) greatly reduced Ψ_s , which helped to maintain turgor and produced the highest Ψ_p in plants under salinity stress (Fig. 2).

Leaf gas exchange characteristics

Salinity stress significantly decreased leaf gas exchange characteristics. The maximum decrease in all four genotypes of soybeans was seen with 120 mM salinity stress. The exogenous supply of KNO₃, showed an observable enhancement in the leaf gas exchange. However, maximum improvement in leaf gas exchange characteristics was seen with the application of 9 mM KNO₃ in all the studied soybean genotypes (Fig. 3).

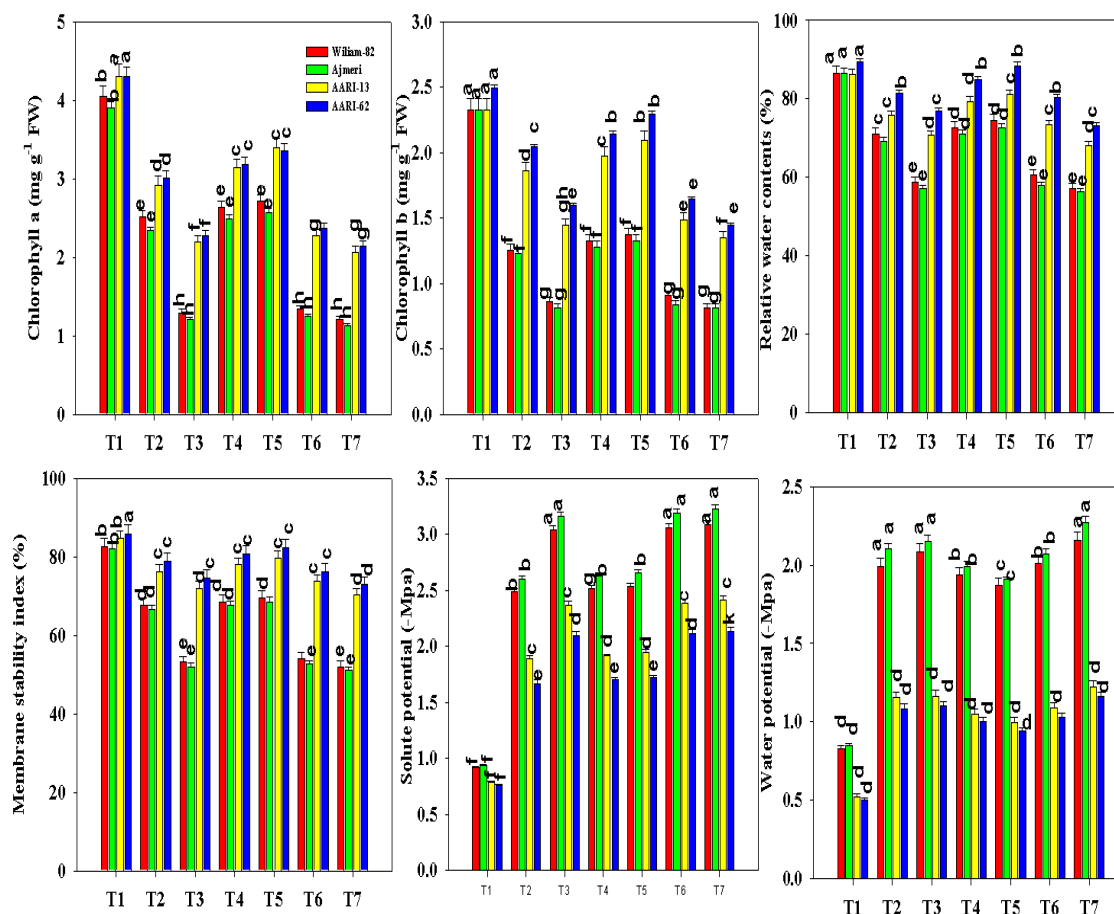


Figure 2. Effect of different potassium application on photosynthetic pigments, relative water contents, membrane stability index, solute and water potential of soybean cultivars growing under salinity stress. T1 indicates control, T2 and T3 60 and 120 mM NaCl, T4 and T5 indicate 60 mM NaCl + 6 mM K and 60 mM NaCl + 9 mM K and T6 and T7 indicates 120 mM NaCl + 6 mM K, and 120 mM NaCl + 9 mM K respectively. The data in indicating the mean with $\pm$ SE

Ionic concentration

The concentration of Na⁺ in the leaves and roots in roots and leaves of all soybean genotypes was increased with increasing salinity stress levels. However, the concentration of K was decreased in roots and leaves with increasing salinity stress. The cultivar AARI 62 demonstrated superior performance in saline circumstances by maintaining a lower Na⁺/K⁺ ratio in response to K application. Moreover, potassium addition to the solution greatly reduced the Na⁺/K⁺ ratio in soybean genotypes (Fig. 4).

Antioxidants activities

There was a discernible rise in antioxidant enzyme activity under salinity stress. The activity of SOD at 60 mM NaCl was considerably higher in AARI-62 and AARI-63 compared to salt-sensitive soybean genotypes (William 82 and Ajmeri). Further, all four soybean genotypes exhibited significantly lower POD and CAT activity at low salt stress levels and significantly higher with increasing salt stress. Improvements in CAT and POD activities were greater under low salinity stress, but reductions under high salinity stress were smaller in genotypes of salt-tolerant soybeans than in genotypes of

salt-sensitive soybeans. The application of potassium showed a non-significant impact on the activities of CAT, POD, and SOD in salt-sensitive soybean genotypes (*Fig. 5*).

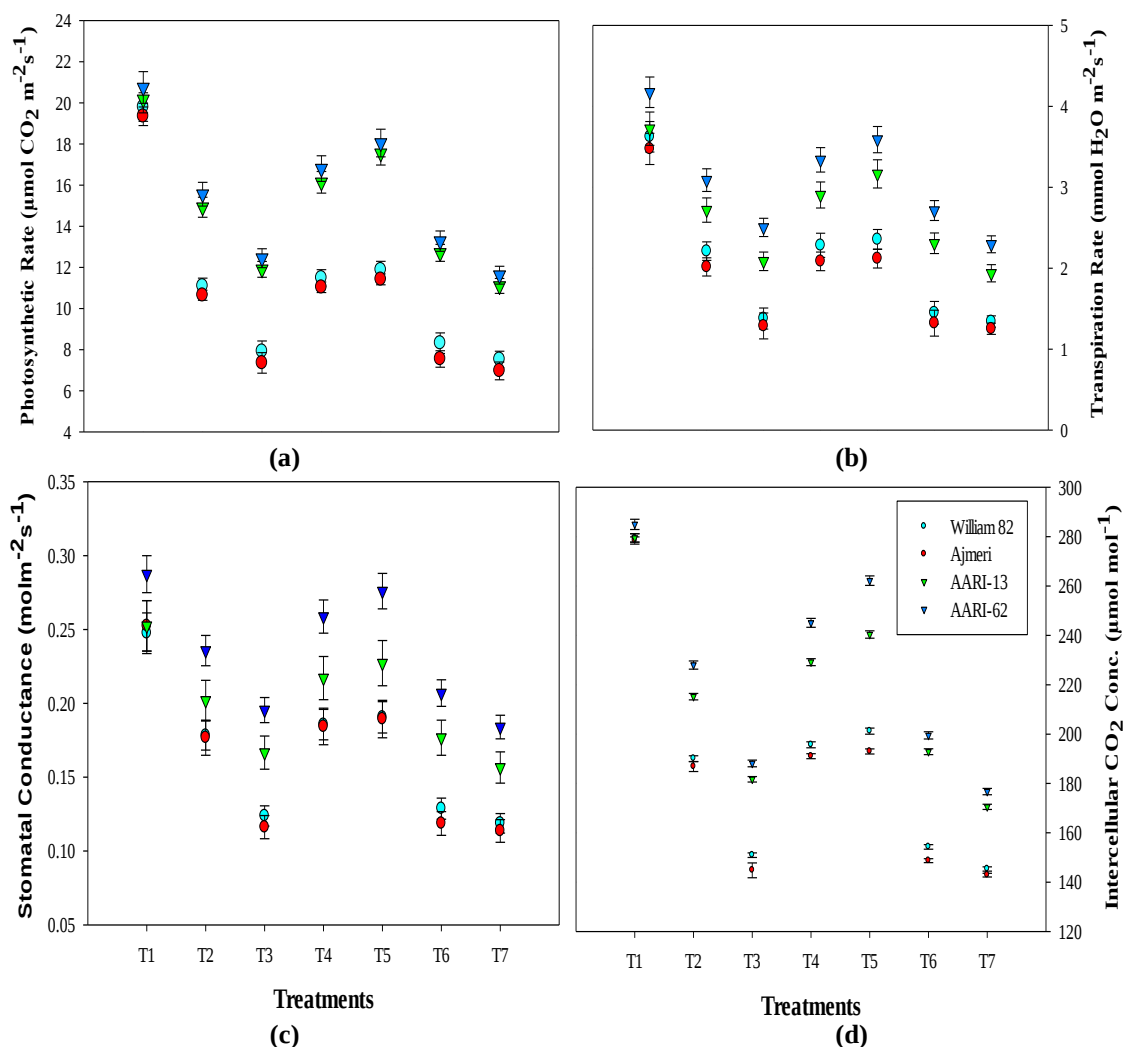


Figure 3. Effect of different potassium application on leaf gas exchange characteristics of soybean cultivars growing under salinity stress. T1 indicates control, T2 and T3 60 and 120 mM NaCl, T4 and T5 indicate 60 mM NaCl + 6 mM K and 60 mM NaCl + 9 mM K and T6 and T7 indicates 120 mM NaCl + 6 mM K, and 120 mM NaCl + 9 mM K respectively. The data in indicating the mean with $\pm$ SE

Discussion

Salinity stress induces negative impacts on plant functioning, resulting in a substantial reduction in biomass and yield (Alam et al., 2019). Salt stress decreased the growth and biomass production by affecting nutrient homeostasis, and damage membranes and starch metabolism thereby leading to abnormal growth (Saqib et al., 2020; Jiang et al., 2023). Besides this, salinity stress also damages the chlorophyll synthesis and photosynthetic efficiency which resulted in a substantial reduction in plant growth (Taher et al., 2023). Potassium is an important nutrient that improves plant growth, and physiological and biochemical function under salinity stress (Abbas et al., 2022). The application K maintains osmotic potential, and turgor pressure, drives xylem

transport, and maintains water balance thus reducing the toxic impacts of salinity (Ahmad et al., 2019). In addition, K application also improves antioxidant activities, and photosynthetic performance and mitigates salinity induce oxidative damages that leads to improved plant growth under saline conditions (Ahmad et al., 2019).

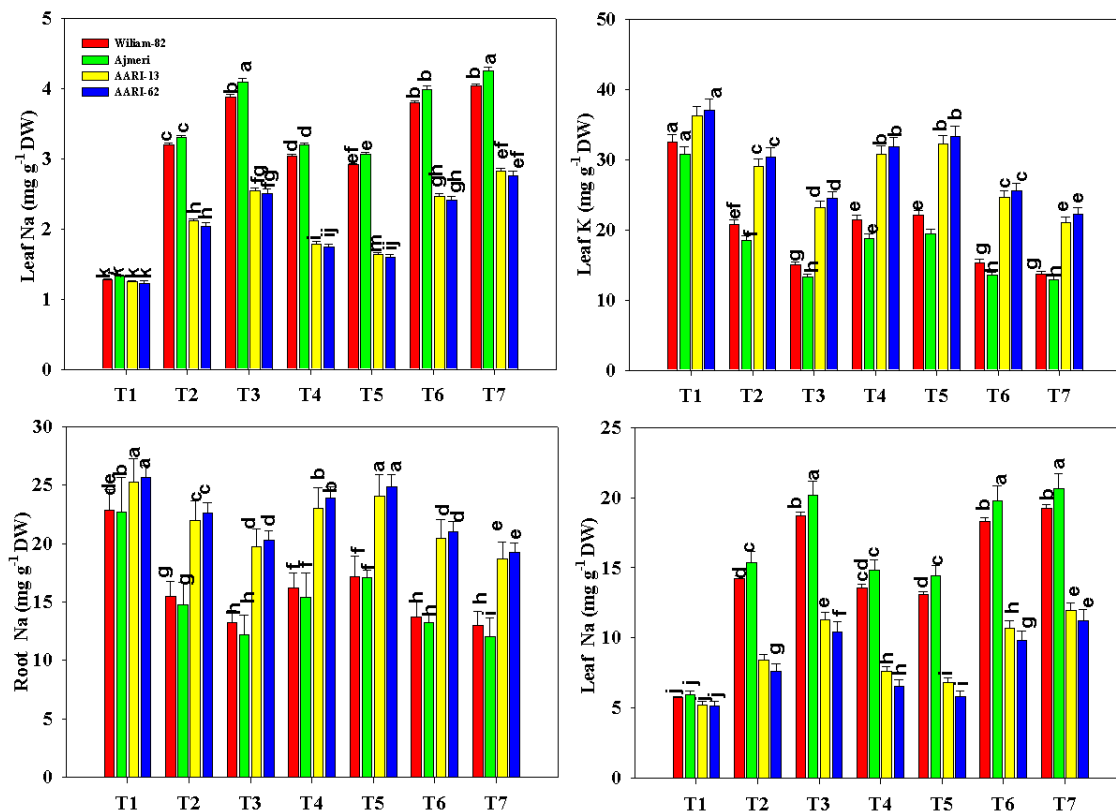


Figure 4. Effect of different potassium application on leaf and root Na and K concentrations of soybean cultivars growing under salinity stress. T1 indicates control, T2 and T3 60 and 120 mM NaCl, T4 and T5 indicate 60 mM NaCl + 6 mM K and 60 mM NaCl + 9 mM K and T6 and T7 indicates 120 mM NaCl + 6 mM K, and 120 mM NaCl + 9 mM K respectively. The data in indicating the mean with $\pm$ SE

The results indicate that salinity stress decreased the RWC and increased the electrolyte leakage. This aligns with Abdelaal et al. (2020) they also found that salinity decreased the RWC and increased electrolyte leakage. The decrease in RWC in the present study was linked with salinity-induced reduction in water potential which lowered the ability of plants to extract water (Ashraf et al., 2017). However, K supply maintained a better RWC which could be attributed to better water potential which allowed plants to extract maximum water from soil, thereby resulting in better RWC. Salinity reduced the chlorophyll contents which is attributed to the disintegration of chlorophyll enzymes by salinity, deficiency of magnesium, and structural damage to chloroplast (Uddin et al., 2012; Li, 2017). However, the application of K significantly increased the chlorophyll contents in soybean cultivars. Potassium protects the photosynthetic apparatus by increasing antioxidant activities and it also increases the uptake and absorption of nutrients, leading to an increase in chlorophyll synthesis (Fayez and Bazaid, 2014). K also maintains and improves the efficiency of the

photosynthetic apparatus by increasing leaf area, accelerating the photosynthetic rate and ATPase synthesis which facilitate the photosynthetic processes under stress conditions (Shingles and McCarty, 1994; Zörb et al., 2014).

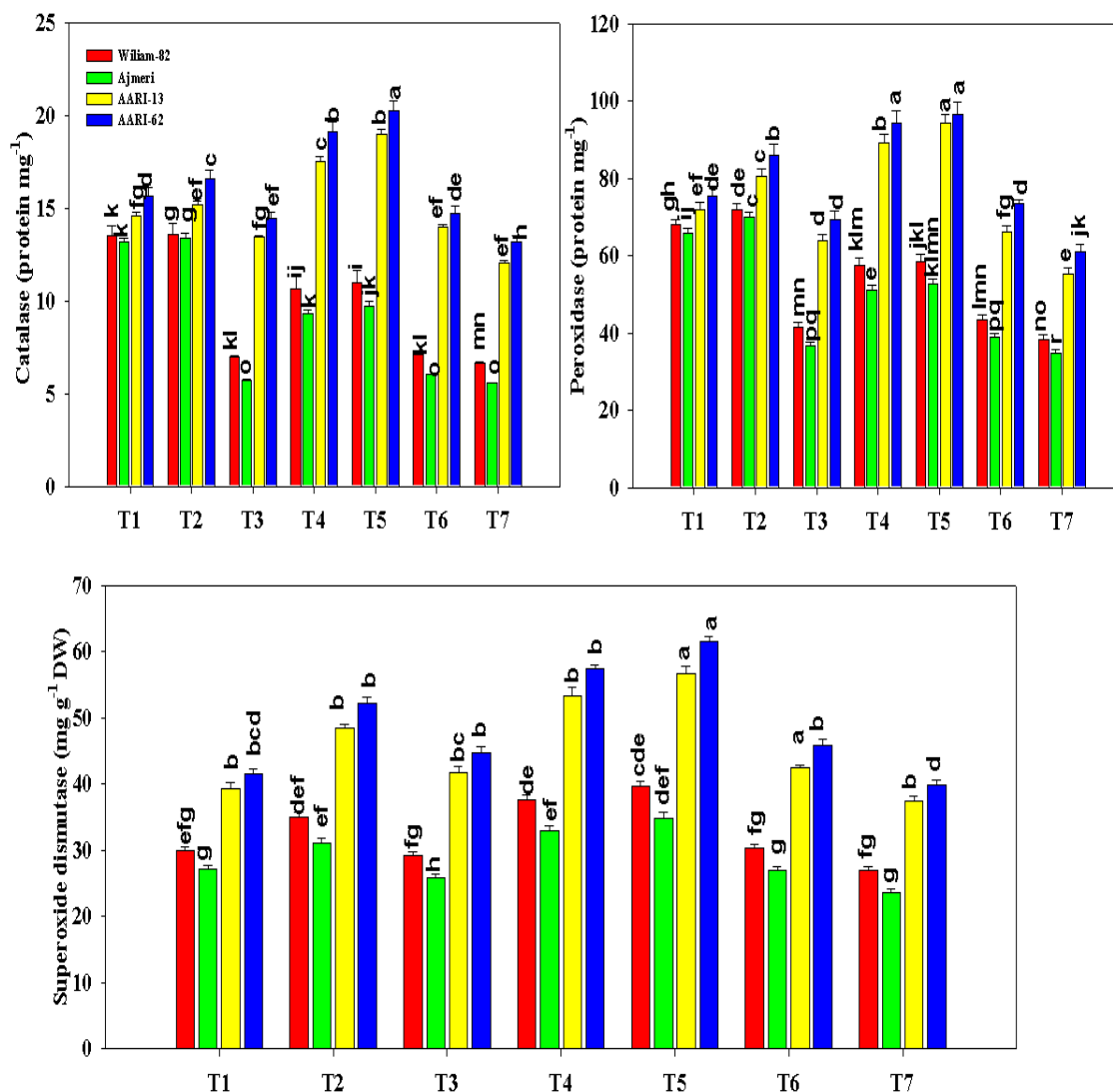


Figure 5. Effect of different potassium application on antioxidant of soybean cultivars growing under salinity stress. T1 indicates control, T2 and T3 60 and 120 mM NaCl, T4 and T5 indicate 60 mM NaCl + 6 mM K and 60 mM NaCl + 9 mM K and T6 and T7 indicates 120 mM NaCl + 6 mM K, and 120 mM NaCl + 9 mM K respectively. The data in indicating the mean with $\pm$ SE

The maintenance of water potential is considered as an effective way to withstand the toxic effects of stress conditions. The soybean plants exposed to salinity stress showed a lower Ψ_w which aligns with earlier studies of Sajedi et al. (2011). The application of K improved the Ψ_w which increased the root activity to uptake more water leading to reduction in Ψ_s (Yao et al., 2009). The results indicate that Pn, Gs, and Tr were significantly decreased under saline conditions which aligns with previous findings of Degl'Innocenti et al. (2009) and Cheeseman (2015). Though, foliar spray of K significantly increased the Pn, Gs, and Tr under salinity stress. This is consistent with

earlier studies where authors noted that K application reduces the toxic impacts of salinity and improves plant photosynthetic efficiency (Zrig et al., 2021). Potassium drives stomata movements and protects against changes in cell expansion, and maintains stomata movement, thus improves plant photosynthetic efficiency (Jákli et al., 2017).

The balance of Na and K is considered as an important factor in maintaining salt tolerance in plants. Potassium absorption is very crucial to resist the Na and absorption of K in plants is mediated by K channels and transporters (Shen et al., 2015). The exogenous supply of K reduced the Na uptake and maintained better K uptake. The application of K improves ionic homeostasis relieves salinity-induced oxidative damage and improves plant growth (Kaddour et al., 2009; Rady et al., 2023). The excessive production of ROS damages the cellular membranes by increasing membrane damage and electrolyte leakage (Anjum et al., 2014; Iqbal et al., 2015). In this study, K application reduced the membrane damage and electrolyte leakage which could be attributed to increased antioxidant activities. This aligns with findings of Qureshi et al. (2013) they also reported that K decreased the membrane damage and leakage of electrolyte by increasing antioxidant activities. Plants possess an excellent antioxidant system that protects them against oxidative damage. In the present study K application significantly increased the activity of all the antioxidants. Previously, Liang et al. (2007) documented a significant increase in CAT and SOD activity and reduction in ROS production with K application. Further, Zheng et al. (2008) noted that the application of K KNO₃ at appropriate amounts detoxifies ROS by increasing CAT, SOD, and POD activity in wheat under saline conditions. Moreover, Jan et al. (2017) also witnessed a marked increase in APX, CAT, and SOD activity with K application which lowered the salinity-induced inhibitory impacts and improved growth and yield.

Conclusion

Salinity toxicity caused a reduction in plant growth by decreasing chlorophyll content, relative water contents, membrane stability, photosynthetic activities, and photosynthetic pigments, and increasing Na accumulation. Potassium application improved the chlorophyll synthesis, membrane stability, plant water relations, antioxidants activities, and K uptake and reduced the Na uptake which accelerated the growth of soybean plants.

Acknowledgements. The authors extend their appreciation for the support of the Deanship of Scientific Research, Vice Presidency for Graduate Studies and Scientific Research, King Faisal University, Saudi Arabia [Grant No. KFU251214].

Funding. This work was supported by the Deanship of Scientific Research, Vice Presidency for Graduate Studies and Scientific Research, King Faisal University, Saudi Arabia [Grant No. KFU251214].

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