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MITIGATION OF SALT STRESS IN PROSO MILLET (*Panicum Miliaceum* L.) BY EXOGENOUS APPLICATION OF ASCORBIC ACID

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Abstract

Salinity is one of the most detrimental environmental factors that limits the growth and productivity of crops. Ascorbic acid (AsA) is a vital antioxidant of plants, which prevents the oxidative damage caused by salinity and improves plant growth performance. A semi-controlled experiment was conducted to evaluate the impact of salt stress (150 and 300 mM NaCl; S_1 and S_2, respectively) and AsA (250 and 500 µM; AsA_1 and AsA_2, respectively) on the seedling growth, physiological attributes, and yield of proso millet. The present study revealed that the salinity hampered the physiological processes and resulted in the reduction in yield attributes, while the application of AsA in salt-stressed plants improved the plant height, fresh and dry weight, leaf relative water content (RWC) and SPAD value, as well as yield contributing attributes. Foliar applications AsA at 10 days intervals for two times reported with enhanced plant parameters. Furthermore, the highest plant growth and yield attributes were observed while plants were sprayed with 500 µM AsA under salt stress. This study indicated that the exogenous addition of AsA can be a useful strategy to promote plant phenotypic characters and yield contributing characters of proso millet cultivated under saline regimes.

Introduction

Salt stress is one of the most common, prevalent, and serious forms of abiotic stress that is destructive and causes severe crop losses in arid and semi-arid parts of the world (Soliman *et al.,* 2020). It is assumed that worldwide around 6% of total cultivable area has been infected by salinity that causing retarded plant growth and development in different crops (Yang and Guo 2017; Zhang *et al.,* 2021). The salt effect and its injury mechanism is quite complex to understand in plants as it integrates several morphological and physiological alterations in plants at cellular levels. High soil salinity leads to ion imbalances, osmotic stress, oxidative damage, and disruption of various physiological processes in plants (Morton *et al.,* 2018; Mushtaq *et al*., 2025). Generally, the cumulation of sodium (Na^+) and chloride (Cl^-) ions are the main malefactors accountable for salt toxicity in crops. Plants exposed to salt may subsequently affect the major plant processes, including ion compartmentalization, nutrient assimilation, protein synthesis, photosynthesis, and hormonal balance (Farooq *et al.,* 2015). Salt stress also triggers oxidative stress in plants. The high salt concentration stimulates the production of reactive oxygen species (ROS), including superoxide radicals ($O_2^{\bullet-}$) and hydrogen peroxide (H_2O_2), which can cause oxidative damage to cellular components. ROS accumulation leads to lipid peroxidation, protein degradation, DNA/RNA damage, and overall disruption of cellular functions (Hasanuzzaman *et al.,* 2022).

Ascorbic acid, a low-molecular-weight antioxidant, has gained attention as a potential strategy to alleviate abiotic stress-induced damage in plants in recent years. This organic compound possessing antioxidant attributes plays a crucial role in scavenging ROS and protecting cells from oxidative stress (El-Hawary *et al.,* 2023; Kanwal *et al.,* 2024). Apart from

its antioxidant properties, AsA plays a pivotal role in various aspects of plant biology, including photosynthesis, hormone regulation, enzymatic activities, cell division, cell expansion, regulation of flowering, leaf aging, and apical meristem formation (El-Beltagi *et al.,* 2020). Additionally, it acts as a cofactor for enzyme activity. When exogenously applied, AsA stimulates the production of endogenous AsA within plant cells, thereby mitigating the detrimental effects of salt stress in numerous crop species (Akram *et al.,* 2017). In recent years, several studies have investigated the potential of exogenous AsA application in mitigating salt stress in various plant species (Xu *et al.,* 2015). These studies have reported positive effects on plant growth, photosynthesis, antioxidant defense systems, and ion homeostasis under salt stress conditions.

Proso millet (*Panicum miliaceum* L.) is an important cereal crop known for its adaptability to diverse environmental conditions, including marginal lands with limited access to water and poor soil quality (Saleem *et al.,* 2023; Samineni *et al.*, 2025). However, proso millet is also sensitive to salt stress, which limits its cultivation in saline-affected areas. The specific role of AsA in proso millet and its effectiveness in alleviating salt stress remain relatively unexplored. Understanding the effects of salt stress in proso millet is crucial for developing effective strategies to mitigate its impact. By gaining insights into the underlying morpho-physiological and yield responses, researchers and farmers can explore innovative approaches to enhance millet's tolerance to salt stress, improve crop productivity, and ensure food security in regions affected by salinity. Considering this, the experiment was conducted to know the effects of the application of AsA under varying salinity levels in proso millet cultivation.

Materials and Methods

Plant Material and Treatments

Healthy proso millet seeds (*Panicum miliaceum* L. var. BARI Cheena-1) were carefully selected and evenly planted in 16 L plastic pots. To nourish the plants, a combination of organic manure and chemical fertilizers, including urea, TSP, and muriate of potash, was applied as the initial dose. At the 20-days after sowing (DAS), salinity stress was induced in the plants, with treatments including a control group (0 mM NaCl), mild salinity stress (150 mM NaCl), and severe salinity stress (300 mM NaCl). Additionally, supplementation of AsA (250 and 500 µM) was carried out at 10 and 20 DAS, both under normal and saline conditions. The experiment was executed using a completely randomized design (CRD) with three replicates.

Estimation of plant phenotypical attributes

The height of the proso millet plants was assessed at three time points: 20 DAS, 30 DAS, and at the time of harvest. A measuring scale was employed to gauge the vertical distance from the ground level to the highest point of the leaf on each individual proso millet plant. The average height measurements were derived from five proso millet plants that were randomly chosen within each plastic pot. After termination of the stress period, three plants from each treatment were gently uprooted, thoroughly washed and water was removed by pressing with a dry towel. The plants were weighed using a balance, followed by averaging to determine the fresh weight (FW) plant^{-1}. The same samples after measuring the FW were subjected to oven drying at 80°C for 48 hours. Later on, the samples were weighed again to obtain the dry weight (DW). The average dry weight was then recorded and used as the DW plant^{-1}.

Measurement of SPAD Values and relative water content

Five leaves, chosen at random from each pot, were selected for the measurement of their top, middle, and base sections. An SPAD meter (Minolta Camera Co., Osaka, Japan) was employed for this purpose, and the readings from each section were subsequently averaged, following the approach outlined by Yuan *et al.,* (2016). To record the relative water content (RWC), five leaves from five plants from each treatment were randomly plucked and cleaned with a paper towel. The FW of the leaves was recorded immediately after plucking. Then the

leaves were submerged in distilled water within a Petri dish and kept for 24 hours. Excess water from the leaf surfaces was soaked by the towel, and the turgid weight (TW) was measured. Subsequently, the samples were dried in an oven for 72 hours to obtain the DW. The following formula by Barrs and Weatherley (1962) was employed to calculate the relative water content-

$$RWC\ (\%) = (FW - DW)/(TW - DW) \times 100$$

Measurement of yield contributing parameters

Number of tiller hill^{-1}, paniclae length, number of filled grains panicle^{-1}, number of unfilled grains panicle^{-1}, 1000-seed weight and gain yield were measured using standard procedures.

Statistical analysis

All data of three replications were statistically analyzed by using Staistix 10. Data were analyzed and the mean difference was compared by least significant difference (LSD) test with the 5% level of significance.

Results and Discussion

Salt stress has a detrimental effect on plant growth at different developmental stages. For the proso millet plant, while exposed to S_1 and S_2, plant height was reduced by 21 and 27% at 30 DAS, respectively. The highest reduction of plant height (29%) was observed at harvest while plants were exposed to 300 mM salt stress (S_2). However, the application of AsA gradually increased the plant height under salt stress at different intervals. Although AsA did not significantly increase plant height in the control condition, but its role under stress conditions was very prominent. The plant height gradually increased over time and the highest increase was observed at harvest while applied with AsA_1, which is 2 and 14% for S_2 and S_1, respectively (Table 1). More specifically, AsA_1 was found to be more effective in increasing plant height, thus mitigating the negative effect of both doses of salt stress in proso millet.

Table 1. Plant height at 30 DAS, 50 DAS and at harvest of proso millet under salt stress supplemented by ascorbic acid

Treatments	Plant height (cm)		
	30 DAS	50 DAS	At Harvest
C	27.74±2.20ab	51.38±0.44a	74.60±1.39a
AsA_1	29.15±0.42a	50.86±2.39a	76.15±0.69a
AsA_2	27.75±1.61ab	51.35±0.99a	75.22±0.72a
S_1	23.34±0.68e	43.71±0.05c	62.45±1.79d
S_1+AsA_1	26.91±1.84bc	49.55±1.63a	71.02±1.52b
S_1+AsA_2	26.85±0.69bc	46.56±1.58b	67.05±0.18c
S_2	21.43±1.00f	39.08±0.58d	53.22±2.08e
S_2+AsA_1	25.35±1.16cd	46.44±0.61b	66.21±1.00c
S_2+AsA_2	23.88±0.63de	42.92±0.78c	61.28±0.34d

Here, AsA_1 and AsA_2 denote 250 and 500 µM ascorbic acid, while the S_1 and S_2 represent 150 and 300 mM NaCl stress, respectively. Mean (±SD) was calculated from three replicates for each treatment. columns with different letters are significantly different at $p \leq 0.05$ applying Fisher's LSD test.

The imposition of osmotic stress resulting from salinity and ionic stress leads to an upsurge in the production of ROS within plants. This, in turn, results in detrimental effects on cell organelles and membrane components, ultimately leading to cell and plant demise, particularly in cases of severe salinity stress (Hasanuzzaman *et al.,* 2021). In this experimental

study, observed a significant reduction in plant height in response to salt stress. In severe stress conditions, the plant height decreased by 29% at the time of harvest (Table 1). This decline may be attributed to the heightened formation of ions in the soil solution during the plant's developmental stages. However, when applied AsA, commonly known as Vitamin C, observed an improvement in plant height, both during the vegetative and reproductive stages. This enhancement in plant height might be linked to AsA's role in facilitating early shoot formation during the seedling stage (Abdullah *et al.,* 2021).

Plant biomass has significantly reduced due to prolonged salt stress. However, plant DW was largely reduced under S_2 condition compared to plant FW. The highest reduction of FW and DW was 32 and 37%, respectively, under the S_2 condition. Exogenous foliar application of AsA significantly increased plant FW and DW under both levels of stress condition. The highest increase of FW and DW (24 and 27%, respectively) was observed while sprayed with AsA_1 under 300 mM salt stress (Fig. 1).

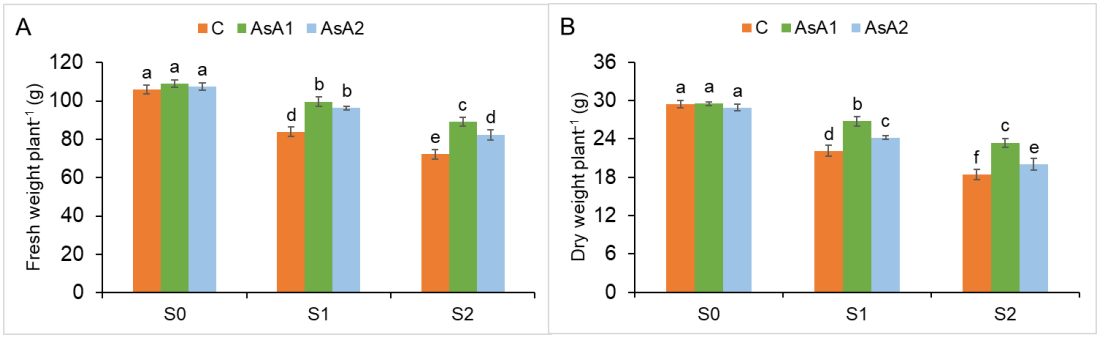

Fig. 1. Fresh weight (A) and dry weight (B) of proso millet under salt stress supplemented by ascorbic acid. Here, AsA1 and AsA2 denote 250 and 500 µM ascorbic acid, while the S1 and S2 represent 150 and 300 mM NaCl stress, respectively. Mean (±SD) was calculated from three replicates for each treatment. Columns with different letters are significantly different at $p \leq 0.05$ applying Fisher's LSD test.

The impact of salinity stress on plant biomass was notably detrimental, as indicated by the results. However, when AsA was applied to the foliage, it led to a substantial improvement in both plant fresh and dry weight. This enhancement can likely be attributed to the improved plant height and the increase in leaf RWC compared to the control treatment. Furthermore, AsA appears to mitigate the adverse effects of stress on the initial growth of seedlings, enabling them to better cope with unfavorable abiotic stress conditions as they progress into later growth phases (Gallardo *et al.,* 2001). Consequently, the increased count of tillers may contribute to the development of more robust seedlings at the outset of the proso millet's growth cycle.

Relative water content is one of the vital indicators in stress conditions that determines how much water is uptaken by plant cells. Results show that a significant reduction in leaf RWC was recorded while plants were exposed to both levels of salt stress. However, the maximum reduction (24%) of RWC was reporded in S_2 condition, followed by an 18% reduction in S_1 condition. In opposite, foliar application of AsA significantly increased leaf RWC under both levels of stress condition, whereas the highest increase was observed with AsA_1 application (19 and 18%) in both S_1 and S_2, respectively. In the case of SPAD value, salt stress has similar negative effect under both levels of salt stress. Salt stress reduced SPAD value by 15 and 22% under S_1 and S_2, respectively. Although no significant changes were observed due to AsA application under control condition, it had significantly increased SPAD value under stress condition. The highest increase of SPAD value (16%) was observed with AsA_1 applied under S_2 stress condition (Fig. 2).

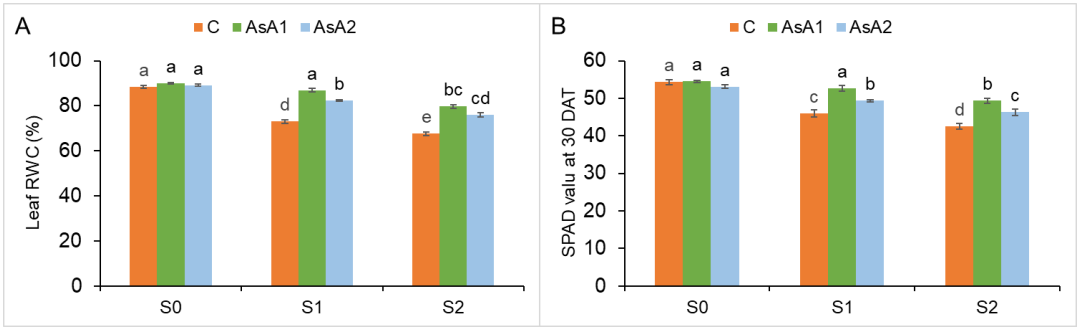

Fig. 2. RWC (A) and SPAD value (B) proso millet under salt stress supplemented by ascorbic acid. Here, AsA_1 and AsA_2 denote 250 and 500 µM ascorbic acid, while the S_1 and S_2 represent 150 and 300 mM NaCl stress, respectively. Mean (±SD) was calculated from three replicates for each treatment. Barrswith different letters are significantly different at $p \leq 0.05$ applying Fisher's LSD test.

In this study observed a reduction in leaf RWC and SPAD values, which serve as indicators of the content of photosynthetic pigments in leaves when plants were subjected to saline soil conditions. This decline in photosynthetic pigments can likely be attributed to a decreased rate of light absorption necessary for the photosynthesis process, and it is closely linked to the reduction in RWC. An increased rate of photosynthesis relies on adequate water uptake (EL-Hadidi *et al.,* 2018). The application of AsA proved effective in mitigating the detrimental impact of salinity. It did so by promoting an increase in the synthesis and upregulation of photosynthetic pigments. Notably, the content of photosynthetic pigments is a crucial parameter for assessing crop salt tolerance (Yildirim *et al.,* 2008). The exogenous application of AsA is anticipated to regulate stomatal opening under stress conditions, subsequently reducing transpiration rates, maintaining turgor, and ultimately enhancing plant growth and productivity in stress-inducing environments (El-Beltagi *et al.,* 2022).

When exposed to S_1 and S_2, plant tiller number was reduced by 27 and 43% at 30 DAS, 27 and 41% at 50 DAS, and 22 and 42% at harvest compared to the control. Application of AsA significantly increased the tiller number in plants where the highest increase was 34% followed by 23% with AsA_1 under S_2 condition at 50 DAS and at harvest, respectively. Interestingly, in the control condition, foliar application of AsA had no significant effect (Table 2).

Table 2. The number of tillers hill^{-1} at 30 DAS, 50 DAS, and at harvest of proso millet under salt stress supplemented by ascorbic acid

Treatments	Number of tiller hill^{-1}		
	30 DAS	50 DAS	At harvest
C	1.46±0.03b	3.98±0.08a	3.70±0.05a
AsA_1	1.60±0.06a	3.96±0.05a	3.69±0.10a
AsA_2	1.48±0.04b	3.88±0.07a	3.64±0.08a
S_1	1.06±0.04d	2.91±0.08e	2.91±0.08c
S_1+AsA_1	1.26±0.03c	3.56±0.09b	3.41±0.08b
S_1+AsA_2	1.21±0.02c	3.27±0.05c	3.01±0.04c
S_2	0.83±0.02f	2.34±0.04g	2.14±0.03e
S_2+AsA_1	0.98±0.01e	3.12±0.01d	2.64±0.07d
S_2+AsA_2	0.93±0.03e	2.61±0.05f	2.54±0.08d

Here, AsA_1 and AsA_2 denote 250 and 500 µM ascorbic acid, while the S_1 and S_2 represent 150 and 300 mM NaCl stress, respectively. Mean (±SD) was calculated from three replicates for each treatment. Columns with different letters are significantly different at $p \leq 0.05$ applying Fisher's LSD test.

The number of tillers in proso millet plays a pivotal role in determining crop yield, and this parameter is particularly vulnerable to the adverse effects of salt stress. In this experiment, the most significant reduction in tiller count was observed during both the early vegetative stage and the later growth stages. This decline is likely closely linked to the plant's access to water, as higher salt concentrations create oxidative stress and cellular damage, leading to diminished plant growth (Hasan *et al.,* 2020). The application of AsA had a positive impact on tiller numbers, which can be attributed to its supportive role in plant growth and development. It is conceivable that AsA helps alleviate the detrimental effects of salt stress on plants by enhancing mineral uptake and content.

Under stress conditions, the filled grain number was significantly reduced, whereas the unfilled grain number marked a slight increase. At S_1 and S_2 stress, the filled grain number drastically reduced by 30 and 43%, respectively. On the contrary, the unfilled grain number increased its highest by 49% at S_2 stress condition. However, AsA application notably reduced the unfilled grain number and increased the filled grain number panicle^{-1} (Fig. 3).

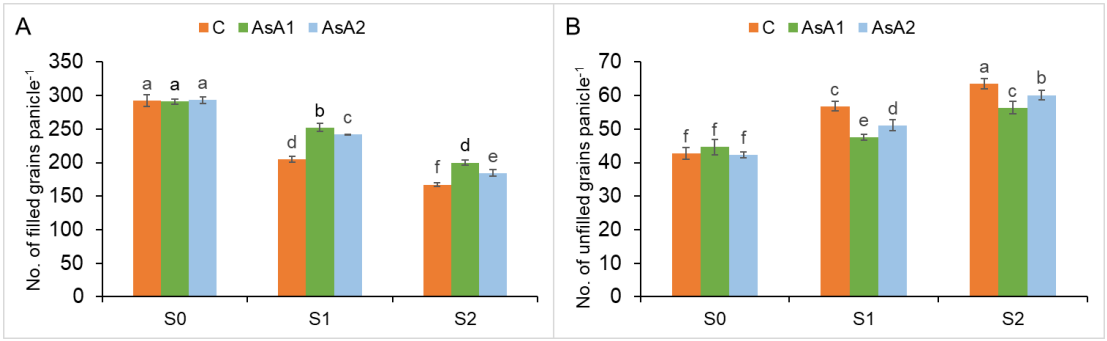

Fig. 3. The number of filled (A) and unfilled (B) grains panicle^{-1} of proso millet under salt stress supplemented by ascorbic acid. Here, AsA_1 and AsA_2 denote 250 and 500 µM ascorbic acid, while the S_1 and S_2 represent 50 and 300 mM NaCl stress, respectively. Mean (±SD) was calculated from three replicates for each treatment. Barrswith different letters are significantly different at $P \leq 0.05$ applying Fisher's LSD test.

In the presence of salt stress, plant water uptake reduces due to the toxic nature of ions in saline conditions. This decline in water uptake can be linked to the observed decrease in the number of filled grains. The reduced water availability hampers cell enlargement and disrupts the translocation of nutrients from leaves to grains due to insufficient water supply (Per *et al.,* 2017).

Table 3. Panicle length, 1000-grain weight and grain yield of proso millet under salt stress supplemented by ascorbic acid.

Treatments	Panicle length (cm)	1000 grain weight (g)	Grain yield pot^{-1}
C	19.00±0.22a	4.11±0.03ab	5.44±0.10a
AsA_1	19.11±0.49a	4.13±0.10a	5.51±0.05a
AsA_2	18.98±0.57a	4.03±0.07b	5.50±0.16a
S_1	14.62±0.44d	3.09±0.05f	4.26±0.10d
S_1+AsA_1	16.59±0.35b	3.71±0.07c	4.94±0.14b
S_1+AsA_2	15.30±0.46c	3.43±0.03d	4.67±0.13c
S_2	11.82±0.24g	2.37±0.01h	3.13±0.10g
S_2+AsA_1	13.92±0.12e	3.21±0.07e	3.97±0.10e
S_2+AsA_2	12.93±0.29f	2.86±0.06g	3.71±0.09f

Here, AsA_1 and AsA_2 denote 250 and 500 µM ascorbic acid, while the S_1 and S_2 represent 150 and 300 mM NaCl stress. Mean (±SD) was calculated from three replicates for each treatment. Bars with different letters are significantly different at $p \leq 0.05$ applying Fisher's LSD test.

In this experiment, salt stress led to a marked decrease in relative water content, which in turn resulted in a substantial reduction in the number of filled grains, especially under severe

stress conditions. However, the application of AsA has a multifaceted impact on various crucial physiological processes in plants, including enhanced nutrient uptake and the reduction of Na^+ levels in the presence of salinity stress. Furthermore, AsA applications shift the selectivity of ion uptake, favoring K^+ over Na^+ and consequently lowering the Na^+/K^+ ratio. This adjustment in ion balance safeguard the integrity of the cell membrane from damage (El-Nasharty *et al.*, 2019).

Salt stress significantly reduced the yield contributing parameters. At severe stress S_2, the reduction was highest, which is 38, 42, and 43% for panicle length, 1000-grain weight, and grain yield respectively. However, the application of AsA_1 significantly increased the panicle length by 18%, 1000-grain weight by 36%, and grain yield by 27% under 300 mM NaCl stress condition (Table 3). Interestingly, no significant change in the above-mentioned yield contributing parameters were observed under control condition with foliar application of AsA.

The decline in both crop yield and its constituent factors when cultivated in salt-stressed soil may primarily be attributed to the diminished assembly and motivation of photoassimilation processes. This reduction ultimately culminates in the lowest values observed in the harvest index (El-Nasharty *et al.*, 2019). Additionally, the reduction in yield can also be attributed to the adverse impact of salinity stress on various plant growth parameters and essential physiological processes. These include but are not limited to photosynthesis, water absorption capacity, and the filling of grains (Taha *et al.*, 2021).

Conclusion

Salt stress exerts significant adverse affects on plant growth and development, manifesting in reduced plant height and impeded water uptake. Furthermore, it leads to a decrease in leaf photosynthesis, resulting in diminished grain quality and yield in proso millet. However, the findings from this study provide clear evidence that foliar application of ascorbic acid effectively mitigates the detrimental effects of salt stress on proso millet. This intervention improves tiller numbers and reduces the occurrence of unfilled grains. Notably, a lower dose of ascorbic acid is more efficient in counteracting the effects of salt stress compared to higher concentrations. In summary, based on the preceding results and discussion, it can be concluded that foliar application of ascorbic acid at a concentration of 250 µM is highly effective in promoting the growth and enhancing yields of proso millet when confronted with salinity stress.

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