



Life under salinity stress: Physiological insights into Soybean response to exogenous growth regulators under saline irrigation condition

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Abstract

Salinity stress is one of the most critical abiotic challenges affecting crop growth and productivity worldwide. High salt concentrations in soil or irrigation water disrupt osmotic balance, impair cellular metabolism, and cause significant yield losses in sensitive crops such as soybean (*Glycine max* L.). The present study investigated the physiological responses of soybean seedlings irrigated with saline water (6 dS m⁻¹) and treated with exogenous plant growth regulators—gibberellic acid (GA₃), salicylic acid (SA) and indole acetic acid (IAA) individually and in combinations. The physiological traits studied included relative water content (RWC), membrane stability index (MSI), leaf pH and stomatal morphology at 25 and 35 days after sowing (DAS). Results revealed that salinity stress significantly reduced RWC and MSI, increased leaf pH and altered stomatal morphology. Foliar application of growth regulators alleviated these negative effects, with the combined treatment of GA₃ @100 ppm + SA @100 ppm + IAA @500 ppm showing the highest improvement in physiological traits under saline irrigation. These findings highlight the potential of growth regulators in improving the resilience of soybean under salt stress, offering a promising strategy for sustainable crop management in saline-prone areas.

Keywords: Soybean, salinity stress, gibberellic acid, salicylic acid, indole acetic acid, relative water content, membrane stability index, stomatal morphology

Introduction

Salinity is a major abiotic stress that severely hampers crop productivity worldwide. Soybean (*Glycine max* L.) is one of the most important oilseed and protein-rich leguminous crops and is often referred to as a “miracle crop” owing to its high seed protein content (40–43%) and substantial edible oil fraction (18–20%). In addition to its nutritional value in human diets, soybean contributes to livestock feed, industrial applications, and soil fertility improvement through biological nitrogen fixation. Despite its agronomic importance, soybean is highly sensitive to abiotic stresses, particularly salinity and drought. Globally, soil salinity affects nearly 80 million hectares, representing about 20% of irrigated agricultural land (Zhu, 2001)^[26]. In India, salinity is a pressing issue in Gujarat, Rajasthan, and several coastal states, where low precipitation and high evaporation rates intensify salt accumulation in soils (ICAR-CSSRI, 2018)^[5]. Abiotic stresses such as salinity restrict water uptake, damage cellular membranes, disrupt stomatal function, and induce oxidative stress in plants (Parida and Das, 2005; Kapadiya *et al.*, 2017; Shaikh *et al.*, 2022)^[9, 13, 20]. Specifically, salinity impairs photosynthesis, disturbs ionic homeostasis, and promotes excessive generation of reactive oxygen species (ROS) in various crops (Anjum *et al.*, 2011; Joshi *et al.*, 2018)^[2, 8].

To mitigate salinity-induced damage, the exogenous application of plant growth regulators (PGRs) has emerged as a promising strategy. Gibberellic acid (GA₃) enhances cell elongation, photosynthesis, and osmolyte accumulation and ROS scavenging enzyme system (Lee, 1990; Patoliya *et al.*, 2024)^[11, 15]. Salicylic acid (SA), a phenolic phytohormone, regulates antioxidant defence mechanisms and osmotic adjustment under stress conditions (Vadhel *et al.*, 2025; Ram *et al.* 2025; Purohit *et al.* 2020)^[16, 17, 24]. Indole-3-acetic acid (IAA), the principal auxin, modulates root and shoot growth while improving nutrient uptake

efficiency under adverse environments (El-Tayeb, 2006)^[4]. Although several studies have examined the roles of individual growth regulators, the combined effects of GA₃, SA and IAA on soybean physiology under saline conditions remain insufficiently explored.

Therefore, the present study was undertaken to investigate the physiological responses of soybean seedlings to saline irrigation and to evaluate the effects of exogenous application of GA₃, SA and IAA, applied individually and in combination.

Materials and Methods

The present investigation was conducted during the Kharif season of 2024–25 at the Department of Biochemistry, College of Agriculture, Junagadh Agricultural University, Junagadh. Soybean [*Glycine max* L.] variety GS-4 was used as the experimental material. The experiment was laid out in a factorial completely randomized design (FCRD) in pots filled with calcareous, slightly alkaline soil collected from the Agronomy Farm of JAU. Two irrigation treatments were imposed: I₁ – tap water and I₂ – saline water (6 dS m⁻¹), the latter prepared by diluting natural saline water from the Mangrol coastal region with distilled water. Foliar sprays of plant growth regulators (PGRs) were applied at 15 days after sowing (DAS) as seven treatments: T₁ – Control (water spray), T₂ – GA₃ @ 100 ppm, T₃ – SA @ 100 ppm, T₄ – IAA @ 500 ppm, T₅ – GA₃ @ 100 ppm + SA @ 100 ppm, T₆ – SA @ 100 ppm + IAA @ 500 ppm, and T₇ – GA₃ @ 100 ppm + SA @ 100 ppm + IAA @ 500 ppm. Each treatment was replicated three times. Leaf tissue samples were collected at two growth stages, 25 DAS (G₁) and 35 DAS (G₂), corresponding to 10 and 20 days after foliar spray, respectively.

The fresh leaf samples of soybean weighed to 0.5g and transferred in petri dish and to this samples 25 ml of distilled water was added and kept for four hours. Then the

leaf samples were taken out, dried by blotting paper and weighed (Turgid weight). The samples kept in oven at 84 °C for 5 h and weighed until constant weight was obtained. After this, RWC was calculated as per formula and expressed as (%) Relative Water Content (Weatherley, 1962) [25].

$$\text{Relative Water Content (\%)} = \frac{\text{Fresh Weight(g)} - \text{Dry Weight(g)}}{\text{Turgid Weight(g)} - \text{Dry Weight(g)}} \times 100$$

The procedure for membrane stability index was followed as given by Sairam *et al.* (2005) [19]. Leaf samples of soybean seedling weighed 0.5g and placed in 50 ml distilled water. Simultaneously one set was kept at 40 °C in water bath for 30 min and its conductivity (C₁) for electrolytic leakage was recorded using conductivity meter. The second set was kept in boiling water bath (100° C) for 10 min and its conductivity (C₂) was recorded after cooling at room temperature. The MSI was calculated according to the formula:

$$\text{MSI} = 1 - \left(\frac{C_1}{C_2} \right) \times 100$$

Generally, the mature leaves of the plants give the most accurate leaf pH. Few lower leaves were taken to measure the leaf pH, roll them into a tight ball and squeeze out of a few drops of sap using a press. The leaf pH was measured by using the pH meter. (Johannes *et al.*, 2011) [7].

The lower surfaces of the leaves of were studied using SEM. The dried leaves were acetylated in 80 (%) ethanol for 2–3 min to remove all debris. All samples were prepared by s-cutting to produce two leaf tiny sections and its abaxial surfaces were mounted on the stub and coated with gold film. The samples were then observed under the SEM mode. (Kumar, 2000) [10].

Results and Discussion

The results pertaining to physiological parameters of soybean seedlings are presented to evaluate the impact of salinity stress and the mitigating influence of growth regulator treatments. Key observations were recorded on relative water content, membrane stability index, leaf pH and stomatal morphology, which serve as important indicators of plant water status, cellular integrity, ionic balance, and gas exchange efficiency. These parameters provide critical insights into how soybean plants respond to saline irrigation and how exogenous application of

gibberellic acid, salicylic acid, and indole acetic acid individually or in combination can enhance tolerance mechanisms.

Relative Water Content (RWC)

Relative water content (RWC) is a key physiological parameter that reflects the hydration status of plant tissues and is widely used as an indicator of cellular water balance under stress conditions. In the context of salinity, RWC is considered a reliable marker of a plant’s ability to regulate osmotic balance and retain water despite the presence of high salt concentrations.

The effect of irrigation regimes and growth regulator treatments on RWC of soybean leaves at 25 and 35 DAS is presented in Table 1. At 25 DAS, RWC ranged from 81.92% (T₄) to 87.90% (T₇), while at 35 DAS values varied between 79.18% (T₃) and 84.47% (T₇). The mean across irrigation levels showed relatively higher RWC under normal irrigation (I₁: 85.58% and 82.14%) compared to saline irrigation (I₂: 84.33% and 80.66%), confirming that salinity stress reduced tissue hydration and impaired water uptake. This reduction under saline irrigation is primarily due to osmotic stress, which diminishes the water potential gradient between soil and root tissues, thereby restricting water absorption (Chovatiya *et al.*, 2024) [3].

Among treatments, T₇ (combined GA₃ + SA + IAA) consistently maintained the highest RWC at both stages, while the lowest values were recorded in T₄ and T₃. The significant effects of irrigation, treatment, and their interaction suggest that both salinity and growth regulator application had a strong influence on plant water status. The ability of regulator-treated plants, particularly under T₇, to maintain higher RWC indicates that the combined application of GA₃, SA, and IAA enhanced osmotic adjustment, cellular hydration, and stress tolerance mechanisms. These improvements may be attributed to increased osmolyte accumulation, improved stomatal regulation, and antioxidant activity, which help maintain water balance under salinity (Patoliya *et al.*, 2024) [15].

Overall, the results clearly demonstrate that foliar application of growth regulators, especially in combination, effectively sustains leaf hydration and enhances salinity tolerance in soybean. These findings are consistent with earlier reports by Islam & Mohammad (2022) [6] in mustard and align with recent observations in soybean with other crops under saline conditions (Patel *et al.*, 2019; Shaikh *et al.*, 2022) [14, 20].

Table 1: Effect of plant growth regulators on Relative Water Content (%) in soybean leaves irrigated with tap water and saline water at different growth stages

Treatment	RWC (%) at 25 DAS (G ₁)			RWC (%) at 35 DAS (G ₂)		
	I ₁	I ₂	Mean T	I ₁	I ₂	Mean T
T ₁	90.23	78.48	84.35	84.16	74.74	79.45
T ₂	85.46	80.25	82.85	82.16	77.36	79.76
T ₃	80.18	86.58	83.38	76.00	82.36	79.18
T ₄	74.34	89.51	81.92	72.80	86.81	79.80
T ₅	87.57	86.70	87.13	84.67	82.52	83.59
T ₆	91.82	82.41	87.11	88.73	78.36	83.54
T ₇	89.42	86.38	87.90	86.46	82.49	84.47
Mean I	85.58	84.33		82.14	80.66	
	S.Em. ±	C.D. at 5%		S.Em. ±	C.D. at 5%	
I	0.37	1.06	C.V.% 1.98	0.43	1.23	C.V.% 2.39
T	0.69	1.99		0.80	2.31	
I×T	0.97	2.81		1.13	3.26	

Membrane Stability Index (MSI)

Membrane Stability Index (MSI) is a crucial physiological trait that reflects the integrity and functionality of cellular membranes under stress conditions. Stress-induced damage to membranes often leads to electrolyte leakage, lipid peroxidation, and loss of compartmentalization, which directly affect plant growth and productivity. A higher MSI value indicates stronger membrane stability and reduced oxidative injury, thereby serving as an important marker of tolerance to abiotic stresses such as salinity and drought.

The data on MSI (%) at 25 and 35 DAS revealed significant effects of irrigation, treatments, and their interaction (Table 2). At both stages, plants maintained under adequate irrigation (I₁) recorded higher MSI values (59.40% and 61.98%, respectively) compared to those under saline irrigation (I₂) (53.45% and 53.53%). This decline under stress reflects the destabilizing effects of salinity on lipid membranes due to osmotic imbalance, ionic toxicity, and oxidative stress (Chovatiya *et al.*, 2024) [3]. Among treatments, T₇ (GA₃ + SA + IAA) consistently registered the highest MSI

(60.40% at 25 DAS and 61.91% at 35 DAS), while T₁ (control) showed the lowest (53.64% and 53.57%). The progressive increase from T₁ to T₇ suggests that the application of growth regulators significantly contributed to maintaining cellular integrity under saline conditions, with the combined treatment being most effective. The higher MSI values observed at 35 DAS further highlight the adaptive response of plants with age, possibly due to improved antioxidant enzyme activity and osmolyte accumulation in regulator-treated plants (Patoliya *et al.*, 2024) [15].

These findings confirm that adequate irrigation helps preserve membrane stability, while saline stress reduces it, and that superior treatments such as T₇ enhance stress tolerance by stabilizing cellular membranes and reducing lipid peroxidation. Similar observations were reported by Sunitha *et al.* (2015) [22], who demonstrated that GA₃ and SA improved membrane stability under abiotic stress, and recent studies have further emphasized the synergistic effects of combined growth regulator application in mitigating oxidative damage.

Table 2: Effect of plant growth regulators on Membrane Stability Index (%) in soybean leaves irrigated with tap water and saline water at different growth stages

Treatment	MSI (%) at 25 DAS (G ₁)			MSI (%) at 35 DAS (G ₂)		
	I ₁	I ₂	Mean T	I ₁	I ₂	Mean T
T ₁	58.06	49.23	53.64	60.49	46.65	53.57
T ₂	58.30	50.42	54.36	60.79	48.15	54.47
T ₃	58.92	51.40	55.16	61.57	50.89	56.23
T ₄	59.05	52.56	55.80	61.94	54.61	58.27
T ₅	59.28	55.26	57.27	62.49	56.45	59.47
T ₆	60.17	56.46	58.31	62.80	57.87	60.33
T ₇	62.00	58.81	60.40	63.75	60.07	61.91
Mean I	59.40	53.45		61.98	53.53	
	S.Em. ±	C.D. at 5%	C.V.% 1.03	S.Em. ±	C.D. at 5%	C.V.% 3.76
I	0.13	0.37		0.10	0.28	
T	0.24	0.69		0.18	0.52	
I×T	0.34	0.98		0.25	0.73	

Leaf pH

Leaf pH is an important physiological indicator that reflects the ionic balance, metabolic activity and cellular homeostasis of plants under varying environmental conditions. Shifts in leaf pH are often associated with stress-induced changes in ion uptake, organic acid metabolism and osmotic regulation. A relatively stable leaf pH is critical for enzyme activity, nutrient assimilation and maintaining photosynthetic efficiency, making it a useful parameter to assess plant stress tolerance. The effect of irrigation regimes and growth regulator

treatments on leaf pH at 25 and 35 DAS is presented in Table 3. At 25 DAS, pH ranged from 6.42 (T₁) to 6.82 (T₇), while at 35 DAS it varied between 6.59 (T₁) and 6.89 (T₇). The mean across irrigation levels showed relatively higher values under saline irrigation (I₂: 6.84 and 6.81 at 25 and 35 DAS, respectively) compared to normal irrigation (I₁: 6.49 and 6.70). This increase in leaf pH under stress conditions indicates disruption in ionic balance, particularly due to excess Na⁺ accumulation and reduced uptake of essential cations like K⁺ and Ca²⁺, which alter cytoplasmic buffering capacity and raise cellular pH.

Table 3: Effect of plant growth regulators on pH in soybean leaves irrigated with tap water and saline water at different growth stages

Treatment	pH at 25 DAS (G ₁)			pH at 35 DAS (G ₂)		
	I ₁	I ₂	Mean T	I ₁	I ₂	Mean T
T ₁	6.19	6.65	6.42	6.57	6.62	6.59
T ₂	6.38	6.69	6.53	6.61	6.61	6.61
T ₃	6.40	6.87	6.63	6.66	6.78	6.72
T ₄	6.69	6.86	6.77	6.69	6.94	6.81
T ₅	6.43	6.88	6.65	6.73	6.86	6.79
T ₆	6.68	6.94	6.81	6.79	6.92	6.85
T ₇	6.68	6.96	6.82	6.83	6.95	6.89
Mean I	6.49	6.84		6.70	6.81	
	S.Em. ±	C.D. at 5%	C.V.% 1.06	S.Em. ±	C.D. at 5%	C.V.% 1.26
I	0.02	0.04		0.00	0.01	
T	0.03	0.08		0.01	0.02	
I×T	0.04	0.12		0.01	0.03	

Among treatments, T₇ (GA₃ + SA + IAA) consistently recorded the maximum leaf pH, followed by T₆ and T₄, while T₁ (control) exhibited the lowest values at both growth stages. The significance of irrigation, treatment, and their interaction highlights that both moisture regime and growth regulator application influenced pH regulation. The relatively moderated rise in pH in regulator-treated plants (T₇ and T₆) reflects better ionic balance, osmotic adjustment, and enhanced metabolic regulation under stress, consistent with the protective role of growth regulators in maintaining homeostasis.

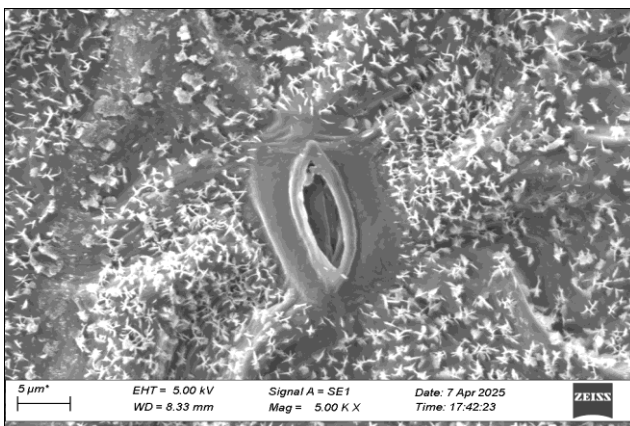
The slight increase in leaf pH under stress is therefore an adaptive physiological response linked to altered solute accumulation and osmotic adjustment. However, the ability of regulator-treated plants to stabilize pH within a narrower range demonstrates their effectiveness in minimizing ionic toxicity and sustaining metabolic activity. These results are in line with earlier findings in *Vigna mungo*, where exogenous SA helped mitigate salinity-induced changes in leaf pH (Solanki *et al.*, 2018) [21], and corroborate recent reports that combined application of PGRs improves stress resilience by maintaining ionic equilibrium and leaf tissue stability (Trivedi *et al.*, 2018) [23].

Stomatal Morphology

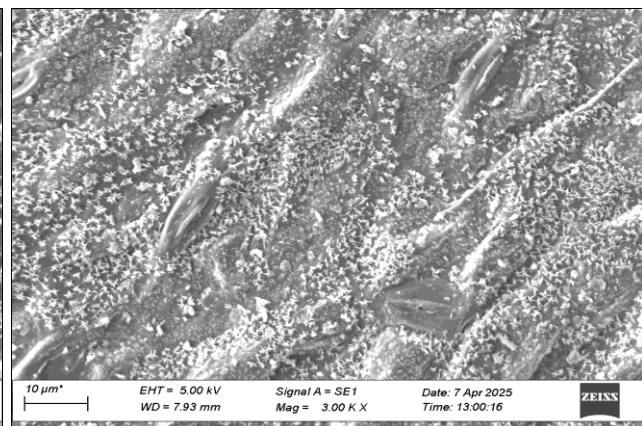
The scanning electron microscopy (SEM) observations revealed distinct modifications in stomatal morphology of soybean leaves under control, saline, and growth regulator treatments (Figure 1). Under control conditions (I₁T₁), stomata were open and well-structured at both 25 and 35

DAS, reflecting normal gas exchange and photosynthetic activity. In contrast, plants subjected to salinity stress without treatment (I₂T₁) displayed partially or completely closed stomata, indicating impaired guard cell function, reduced transpiration, and restricted CO₂ assimilation, which together contribute to growth inhibition under stress. Interestingly, foliar application of combined growth regulators (T₇: GA₃ @ 100 ppm + SA @ 100 ppm + IAA @ 500 ppm) maintained open and functional stomata under both normal and saline irrigation (I₁T₇ and I₂T₇). This suggests that exogenous regulators promoted guard cell stability, osmotic balance, and stomatal conductance, thereby counteracting salinity-induced closure. Such protective effects may be attributed to enhanced osmolyte accumulation and antioxidant activity, which prevent ion toxicity and maintain turgor in guard cells.

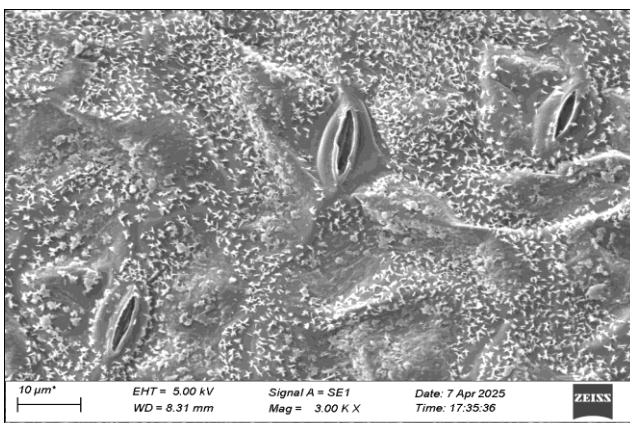
These findings are in line with Nimir *et al.* (2017) [12], who reported that salinity reduced stomatal conductance in sweet sorghum but foliar GA₃ and SA improved stomatal behavior, and with Rios *et al.* (2017) [18], who demonstrated that exogenous regulators, including silicon, help preserve aquaporin activity and stomatal dynamics under stress. Similarly, Álvarez-Méndez *et al.* (2022) [1] highlighted that improved stomatal regulation under PGR application supports higher photosynthetic efficiency and biomass production. Overall, the present results confirm that while salinity negatively affects stomatal morphology and function in soybean, combined application of GA₃, SA and IAA mitigate this damage, ensuring sustained gas exchange and improved stress tolerance.



1. I₁T₁ 25 DAS



2. I₂T₁ 25 DAS



3. I₁T₇ 25 DAS



4. I₂T₇ 25 DAS

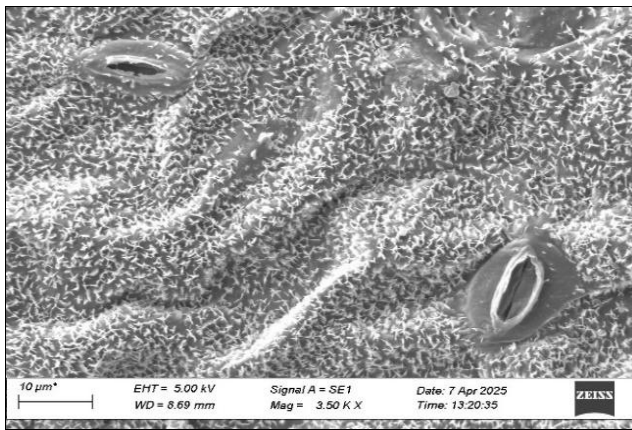
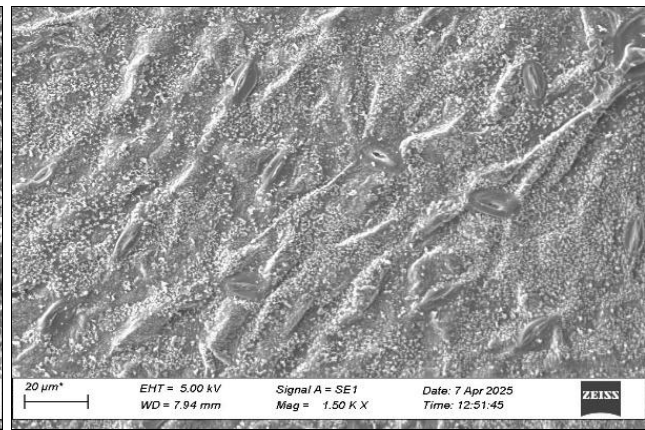
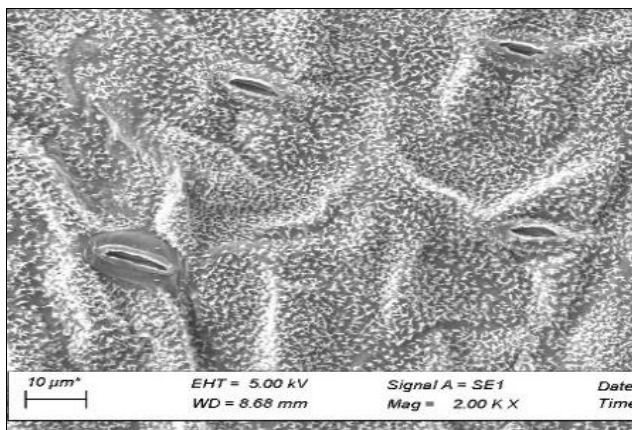
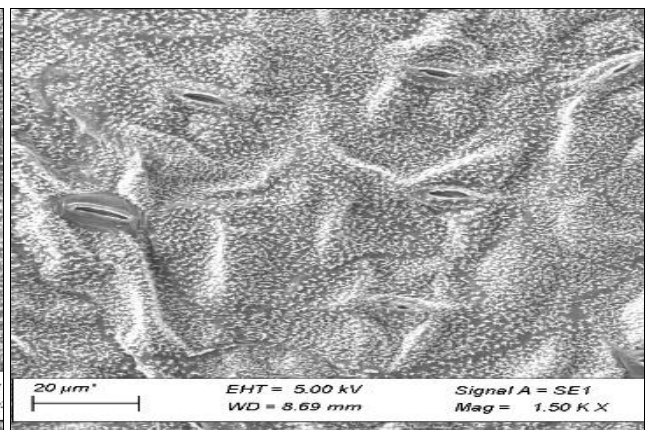
5. I₁T₁ 35 DAS6. I₂T₁ 35 DAS7. I₁T₇ 35 DAS8. I₂T₇ 35 DAS

Fig 1: Stomatal morphology in soybean leaves at control, salinity stress and growth regulators treatment

Conclusion

Salinity stress negatively impacted soybean by reducing relative water content, membrane stability, and stomatal functionality, while altering leaf pH. Foliar application of combined growth regulators (GA3 + SA + IAA) effectively mitigated these effects, maintaining higher RWC and MSI, stabilizing leaf pH, and preserving stomatal aperture under stress. These improvements are likely due to enhanced osmotic adjustment, antioxidant activity, and ion homeostasis. Overall, the combined PGR treatment enhanced physiological resilience and stress tolerance, demonstrating its potential as a practical strategy to improve soybean performance under saline conditions.

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