Received: 15 April 2023 | Revised: 17 December 2023 | Accepted: 12 February 2024

DOI: 10.1002/pld3.574

RESEARCH ARTICLE

Effects of melatonin, proline, and salicylic acid on seedling growth, photosynthetic activity, and leaf nutrients of sorghum under salt stress

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Abstract

Soil salinization poses a significant challenge to the sustainability and productivity of agriculture worldwide. This issue continues to hinder plant growth, requiring innovative solutions to alleviate salt stress. Moreover, climate change accelerates soil salinization, which may soon spread to previously unaffected agricultural areas. Therefore, the present study evaluated the potential role of different seed priming agents (hydro (H), salicylic acid (SA), proline (P), and melatonin (MEL)) on seedlings and leaf macro and micronutrients of sorghum grown under four (.27, 2.5, 5.0, and 8.0 dS m^{-1}) soil salinity conditions. Soil salinity drastically reduced all the growth parameters of sorghum seedlings, primarily the reduction in growth traits, which was remarkable after 2.5 dS m^{-1} soil salinity. In addition, plant height, shoot fresh weight, and stomata were reduced by 40.8%, 74.6%, and 36.5%, respectively, at 8.0 dS m^{-1} compared to .27 dS m^{-1}. SA- and MEL-primed seeds mitigated the harmful effects of soil salinity by reducing Na^+ accumulation in the leaves and increasing the K^+/Na^+ and Ca^{2+}/Na^+ ratios and photosynthetic activity under salt stress. However, the Zn^{2+}, Mn^{2+}, and Cu^{2+} contents of sorghum leaves increased with increasing soil salinity, and these nutrients also improved with seed priming by SA, MEL, and P. Considering all nutrients, MEL-primed sorghum seeds had better macro- and micro-nutrient uptake capacities than the H, SA, and P treatments under high soil salinity conditions. Finally, the present study showed that MEL-induced improvement in salt tolerance in sorghum seedlings was related to enhanced nutritional status, photosynthetic activity, and biomass production in salinized areas.

KEYWORDS
melatonin, proline, salicylic acid, soil salinity, sorghum

1 | INTRODUCTION

Soil salinization is a serious problem that is exacerbated by low and irregular precipitation, high evapotranspiration, irrigation with high-saline water, irrational fertilizer use, ineffective drainage, and poor irrigation management, especially in regions affected by water scarcity (Ali et al., 2021; Corwin & Scudiero, 2019; Kiremit & Arslan, 2016; Singh, 2022). Globally, soil salinization damages approximately 20% of irrigated areas and 3% of dry agricultural areas (Hopmans et al., 2021). Unfortunately, this phenomenon causes considerable adverse effects on the physiological and morphological changes in all plants, such as decreases in photosynthesis, transpiration, and gas exchange, by lowering chlorophyll and carotenoid concentrations, altering the ultrastructure of chloroplasts and PSII system, and reducing stomatal conductance (Arif et al., 2020; Dhokne et al., 2022; Hu et al., 2018). Furthermore, salinity causes excessive accumulation of Na^+ and Cl^- ions, which inhibit K^+ and Ca^{2+} uptake, resulting in an ionic imbalance in plant organs. (Farouk & Al-Huqail, 2022; Kiremit et al. 2022). In addition, salinity increases the levels of reactive oxygen species (ROS) in plant cells and leads to oxidative stress, causing membrane damage, lipid peroxidation, and DNA and protein damage (Hasanuzzaman et al., 2021). Thus, developing crops with high salt tolerance and adaptability to saline conditions is urgently required to ensure food security.

Sorghum is one of the five most important cereals in the world and has the potential to be grown in saline regions (Dehnavi et al., 2022). Farmers and scientists are concerned about growing sorghum with high yield and good quality in saline soils to obtain significant economic benefits. According to Huang (2018), sorghum is moderately salt tolerant. According to Roy et al. (2018), sorghum can tolerate soil salinity of up to 6.8 dS m^{-1} and produce a high biomass yield. However, Henderson et al. (2020) found significant differences in salt tolerance among sorghum genotypes. Crops are sensitive to salt stress during germination (Mansour, 1994). The ability of seeds to grow during the germination stage can boost the uptake and transport of minerals and water from the roots to the leaves, resulting in a higher yield.

Most plants have low stress tolerance to high salinity conditions (Raghuvanshi et al., 2021). Therefore, several cost-effective and time-efficient approaches, such as seed priming and foliar amelioration, are more suitable for mitigating the adverse effects of salt stress. Hydro priming is a cost-effective and eco-friendly method concerning plant growth regulators, which involves soaking seeds in pure water without any added chemicals (Johnson & Puthur, 2021). This method boosts water absorption and enhances seed hydration. Salicylic acid is an important plant hormone that regulates many metabolic and physiological responses in plants, including cell development, germination, seedling formation, and photosynthesis, under abiotic stress (Emamverdian et al., 2020). Melatonin is well known for its antioxidant capacity and, more recently, for its regulatory role in improving the tolerance of plants to salt and other abiotic stresses (Dawood, 2021). Proline is a growth-promoting amino acid that enhances mineral uptake and photosynthesis (Karalija & Selović, 2018). Earlier studies have shown that seed priming with exogenous plant growth regulators may be a practical way to mitigate salt stress (Ahmad et al., 2022; Quamruzzaman et al., 2021; Rhaman et al., 2021). Shihab and Hamza (2020) showed an improvement in the salinity stress tolerance of sorghum varieties up to 9 dS m^{-1} under pre-treatment with solutions containing gibberellic acid and salicylic acid (300 and 70 mg L^{-1}, respectively). Ambreen et al. (2021) found that seed priming with 15 mM proline increased fresh and dry weights of shoots and roots and enhanced plant height for all four wheat varieties compared to 0-, 5-, and 25-mM seed priming treatments. Chen et al. (2021) reported that sorghum seed priming $CaCl_2$ showed a better seedling growth ability than seed primed with polyethylene glycol, calcium chloride, potassium chloride, and sodium chloride under 150 mM NaCl stress conditions. Nimir et al. (2015) point out that sorghum seed priming with gibberellic acid and kinetin significantly improved seedling growth and the antioxidant enzyme system of sweet sorghum under high temperature and salinity stress. Pinheiro et al. (2018) showed that different sorghum genotypes primed with 100 ppm GA3 showed better germination and seedling vigor under water stress (−.6 MPa) and salinity stress (20 dS m^{-1}). The findings of Nie et al. (2023) indicated that sorghum seed priming with 100 µmol/l melatonin improved photosynthetic pigment biosynthesis, soluble sugar, soluble protein, proline content, and antioxidant enzyme activities of sorghum leaves under 120 mmol/l NaCl stress.

Previous studies have examined the protective effects of some chemical or hormonal priming treatments on sorghum seedlings under water or salt stress, as discussed above, although changes in macro- and micro-mineral accumulation in sorghum leaves under different soil salinity stresses have not been sufficiently discussed in the literature. To fill this gap in the scientific literature, the present study was designed to compare the effects of seed priming with hydro, salicylic acid, proline, and melatonin on plant height; shoot fresh weight; physiology; and Na^+, Ca^{2+}, K^+, Cu^{2+}, Mn^{2+}, and Zn^{2+} accumulation in sorghum leaves under soil salinity stress to understand the mechanisms by which different plant growth regulators alleviate salinity stress in sorghum seedlings. Our findings may contribute to efficiently enhancing sorghum seedlings in salt-affected soils.

2 | MATERIALS AND METHODS

2.1 | Growth conditions

The experiment was conducted under rain shelter conditions at the experimental site of the Faculty of Agriculture (41°21′47″ N, 36°11′23″ E), Ondokuz Mayıs University, Samsun, Türkiye, between June and September 2020. The meteorological data during the experimental period are illustrated in Figure 1. In addition, the daily mean temperature in the study area fluctuated between 16.3° and 34.1° C with 42–100% relative humidity.

2.2 | Seed material and seed priming treatments

The sorghum (*Sorghum bicolor* L.) cultivar Öğretmenoğlu 77 was used as the biological material in this study. Before sowing, 480 healthy and uniform sorghum seeds were surface-sterilized with 10% hydrogen peroxide (H_2O_2) solution for 10 min and then washed three times

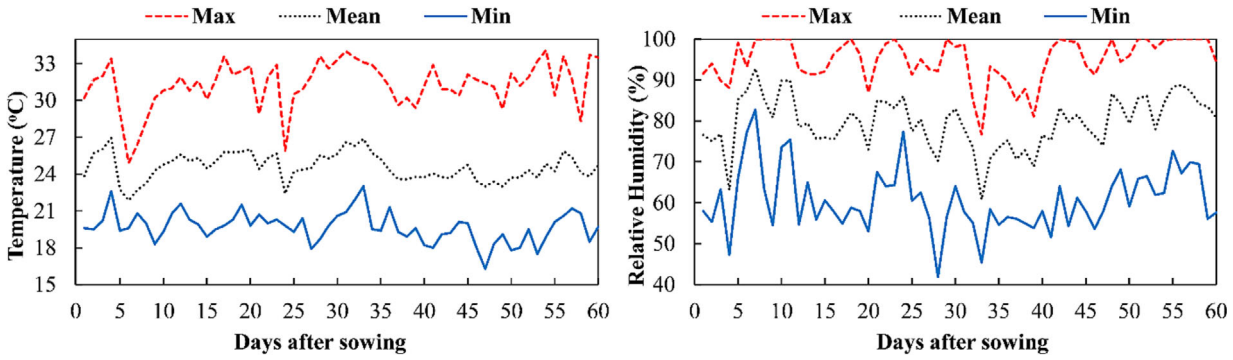
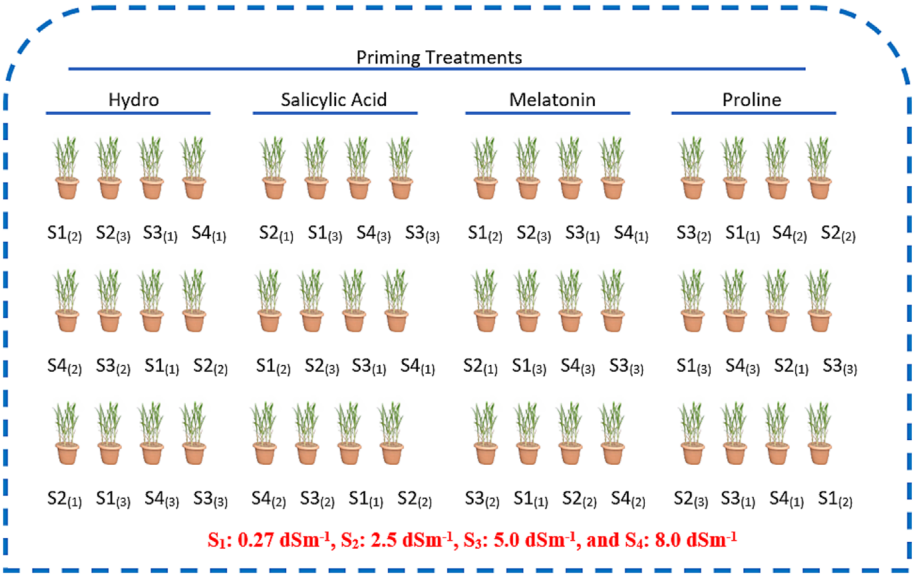


FIGURE 1 Daily mean temperature and relative humidity during the study.

FIGURE 2 Schematic design of the experiment.



with distilled water. The seeds were divided into four groups and treated with various priming agents. Seeds were soaked in a solution of 1 mM salicylic acid, 2 µM proline, 100 µM melatonin, and distilled water for 24 h at room temperature. These priming doses were chosen based on a preliminary laboratory experiment in which the greatest growth was achieved (data not shown). The primed seeds were then dried to their original weight for three days at room temperature.

2.3 | Experimental design

The study consisted of two experimental factors: four soil salinity levels, including S_1:.27 dS m^{-1}, S_2:2.5 dS m^{-1}, S_3:5.0 dS m^{-1}, and S_4:8.0 dS m^{-1} and four priming treatments, including hydropriming (H), salicylic acid (SA), proline (P), and melatonin (MEL). The study was conducted in 48 pots using a randomized complete block design, with three replicates for each treatment. The priming treatment was the main plot, and soil salinity was regarded as a subplot. A schematic of the experimental design is shown in Figure 2. According to the experimental design, pots were placed under a rain shelter until the end of the experiment.

2.4 | Soil salinity treatments

The soil used for the experiment was collected from a depth of 0–15 cm from the experimental farm, classified as a clay loam texture characterized by 36% clay, 17% silt, 47% sand, 1.4% organic matter, an EC of .27 dS m^{-1} and pH of 7.59. The soil for the experiment was air-dried, crushed, and sieved through a 2-mm sieve. Four saline soils (S_1, S_2, S_3, and S_4) were used in this study. S_1 was used as a low soil salinity treatment, while S_2, S_3, and S_4 were adjusted by mixing three salts (NaCl, $MgSO_4$, and $CaCl_2$) with irrigation water. Saline soil was prepared according to the method described by Sezer et al. (2021). After preparing the soil with different salinities, each pot [22 cm high and 18.4 cm inner diameter] was loaded with 2.6 kg of naturally dried soil.

2.5 | Irrigation and agricultural practices

Six pots were loaded with S_1 soil and irrigated with tap water to determine average field capacity (W_{FC}). The surfaces of the pots were covered with plastic film to avoid evaporation. Six pots were weighed

after drainage was stopped, and the average weight of the six pots was regarded as the W_{FC} for the pots. In addition, all pots were irrigated with .20 dSm^{-1} tap water during the growing season. The changes in pot weight were monitored daily using an electronic balance. When .40 of the available soil moisture was depleted, irrigation water was supplied to each pot during the growing period for all the treatments. Before each irrigation application, all pots were weighed, and the amount of water supplied to each pot was equal to the amount of water required by the existing soil moisture level to reach field capacity. Irrigation was performed slowly and carefully at 3–4 days intervals, and there was no water leakage from the bottom of each pot after irrigation application.

Prior to sowing, the sorghum fertilizer requirements were determined according to the recommendations of Wang et al. (2017). Phosphorus fertilizer (Triple Super Phosphate; 44% P_2O_5) was given to all pots at a rate of 1.5 g pot^{-1} and mixed with the topsoil. Then, each pot was weighed and watered with .20 dSm^{-1} tap water to field capacity. After a week, ten primed seeds were planted in soil at a depth of 1.5 cm. Ten days after sowing (stage 2–3 true leaves), all pots were thinned, and each pot contained six healthy and uniform seedlings. In addition, the seedlings were fertilized with potassium and nitrogen fertilizers (potassium nitrate, 46% K, and urea, 46% N). Potassium and nitrogen fertilizers were applied at the rate of 1.2 g pot^{-1} and 1.9 g pot^{-1}, respectively, with irrigation water. Potassium was applied after sowing, whereas nitrogen fertilizer was applied twice. The first dose (50% N) was applied after sowing, and the other half was applied after the 6–7 leaf stage.

2.6 | Data collection

2.6.1 | Growth and physiological parameters

After sowing for sixty days, six seedlings were collected from each pot to evaluate growth characteristics and the nutrient content of leaves. A total of 288 seedlings were analyzed in the experiment. The plant height of each seedling was measured with a tape scale from the soil surface to the plant tip and then averaged for each pot. Stem and leaf biomass samples from each pot were weighed immediately after harvest using an electronic balance and expressed as shoot fresh weight (g pot^{-1}). To determine the dry weights of the stem and leaf samples, they were dried at 70 °C to a constant weight, expressed as g pot^{-1}. To determine the ash content of the leaves, 1 g of oven-dried leaf samples from each pot was burned in a muffle furnace at 550 °C for 7 h and then weighed using a digital scale with a sensitivity of .0001 g. The chlorophyll content and stomatal conductance of sorghum seedlings were measured 59 d after sowing using a portable SPAD-502 Plus [Minolta Co. Ltd., Japan] and an AP4 Leaf Porometer [Delta-T Devices AP4, United Kingdom]. Measurements were taken in each pot between 10:00 a.m. and 12:00 p.m. from the non-destructively fully expanded middle leaves of three seedlings (three readings per seedling).

2.6.2 | Nutrient analysis

Dry leaves (1 g) were used to determination of sodium (Na^+), potassium (K^+), Ca^{2+}), zinc (Zn^{2+}), manganese (Mn^{2+}), and copper (Cu^{2+}) contents. Dry leaf samples were burned at 550 °C for 7 hours and then digested in 4 ml of 3 N hydrochloric acid (HCl); the extract was then filtrated in a Florence flask and filled up to 50 ml with distilled water. The micronutrient (Na^+, K^+, and Ca^{2+}) and macronutrient (Cu^{2+}, Mn^{2+}, and Zn^{2+}) contents of the leaf samples were determined using a flame photometer and inductively coupled plasma spectrophotometer (Optima 2,100 DV; Perkin-Elmer, Shelton, CT), respectively.

2.7 | Statistical analysis

Before the analysis of variance, the data were subjected to a normality test. Next, Analysis of variance (two-way ANOVA) was performed to evaluate the effects of priming treatments, soil salinity, and their interaction on seedling growth characteristics, stomata, chlorophyll content, and leaf nutrients of sorghum using JMP 13.2 statistical software. Differences between means were separated using the Least Significant Difference (LSD) test at $P < .05$. According to the statistical analysis results, leaf Zn^{2+}, Cu^{2+}, and Mn^{2+} bar graphs were prepared in Microsoft Excel 2021, indicating the mean ± standard error (S.E.). A correlation plot and principal component analysis (PCA) of the data were generated using RStudio software [version 4.1.1, R Core Team]. The metan package in R Studio was used to visualize the correlation plots, whereas the FactoMiner and factoextra packages were used to visualize the PCA plots.

3 | RESULTS

3.1 | Growth traits

The main effects of soil salinity (SS), priming treatment (PT), and their interaction (SS × PT) on plant height shoot fresh and dry weights, stomatal conductance, and chlorophyll content were highly significant ($P < .01$) (Table 1). However, a highly significant main effect of soil salinity ($P < .01$) and priming treatment ($P < .01$) on ash content was observed, while the interaction between soil salinity and priming treatment did not affect ash content ($P > .05$) (Table 1).

Plant height decreased significantly with increasing soil salinity (Table 1), decreasing by 5.9%, 18.7%, and 40.8% for S_2, S_3, and S_4, respectively, compared with the S_1 treatment (Table 1). In terms of priming treatments, the highest plant height (83.7 cm) was observed in MEL-primed seeds, while the lowest (67.3 cm) was found in H-primed seeds (Table 1). Furthermore, the plant height of sorghum seedlings increased by 23.3%, 7.8%, and 24.3% for the P, SA, and MEL priming treatments, respectively, compared to the H priming treatment (Table 1). Comparing the results of plant height between the SS × PT interactions, plant height was strongly influenced by

TABLE 1 Effects of different seed priming treatments and soil salinities on growth traits, ash content, stomata, and chlorophyll content of sorghum.

Soil salinity (SS)	Plant height (cm)	Shoot fresh weight (g pot^{-1})	Shoot dry weight (g pot^{-1})	Ash Content (%)	Stomata conductivity (mmol m^{-2} s^{-1})	Chlorophyll content (SPAD)
S_1 (.27 dSm^{-1})	91.6 ± 1.3a	72.8 ± 5.0a	17.8 ± 1.1a	6.3 ± 1.1d	18.8 ± 5.5a	53.2 ± .8a
S_2 (2.50 dSm^{-1})	86.2 ± 2.8b	66.0 ± 8.1b	14.3 ± 1.9b	7.0 ± 1.9c	148.0 ± 2.4b	4.0 ± .9b
S_3 (5.00 dSm^{-1})	74.5 ± 3.1c	4.6 ± 6.8c	10.1 ± 1.5c	7.6 ± 1.5b	139.1 ± 1.7c	37.6 ± .7c
S_4 (8.00 dSm^{-1})	54.2 ± 2.2d	18.5 ± 6.4d	3.5 ± 2.2d	9.5 ± 2.2a	114.9 ± 3.6d	31.6 ± 0.3d
Priming treatments (PT)						
Hydro (H)	67.3 ± 3.8c	38.3 ± 3.7d	9.9 ± 1.3c	7.4 ± 0.4b	129.3 ± 5.8c	38.9 ± 2.2b
Proline (P)	82.9 ± 4.5a	53.8 ± 2.9b	11.3 ± .7b	8.0 ± 0.4a	148.0 ± 8.5b	42.4 ± 2.3a
Salicylic acid (SA)	72.5 ± 3.4b	5.2 ± 1.3c	12.3 ± 0.4a	7.4 ± 0.4b	150.7 ± 7.8b	39.5 ± 2.6b
Melatonin (MEL)	83.7 ± 3.7a	55.6 ± 1.2a	12.3 ± 0.1a	7.6 ± 0.3ab	154.9 ± 7.4a	41.7 ± 2.7a
SS×PT interaction						
S_1 × H	84.3 ± 1.3 cd	53.2 ± 1.7e	12.0 ± 0.5 fg	6.1 ± 0.1	149.4 ± .0 cd	49.6 ± .9c
S_1 × P	94.1 ± 0.4a	76.3 ± .7b	16.3 ± .7 cd	6.4 ± .0	189.3 ± 2.2a	53.6 ± 0.4b
S_1 × SA	94.5 ± 0.1a	75.0 ± 1.2bc	23.2 ± 0.3a	6.1 ± .2	191.1 ± 1.5a	53.8 ± .7ab
S_1 × MEL	93.3 ± 0.4a	86.5 ± 1.1a	2.0 ± 0.5b	6.7 ± 0.1	193.4 ± 1.4a	55.7 ± 1.1a
S_2 × H	71.3 ± .2e	51.9 ± .8e	12.1 ± .2 fg	6.9 ± 0.1	135.4 ± .2 gh	40.3 ± .9e
S_2 × P	93.2 ± 0.5a	72.9 ± 0.3c	14.6 ± .9de	7.4 ± 0.1	148.3 ± .9cde	42.8 ± 0.3d
S_2 × SA	85.3 ± .7bc	62.4 ± .8d	13.6 ± .6ef	6.5 ± .2	152.0 ± 2.0bc	35.5 ± 0.4gh
S_2 × MEL	95.0 ± .8a	76.9 ± 0.5b	16.7 ± 1.7c	6.9 ± 0.3	156.5 ± 1.7b	41.6 ± .6de
S_3 × H	63.4 ± 1.2f	36.1 ± .8 g	12.0 ± 0.4 fg	7.4 ± .2	134.1 ± 2.6hı	34.9 ± 1.0 h
S_3 × P	87.1 ± .6b	44.9 ± .8f	1.7 ± .2 g	8.2 ± 0.3	143.0 ± 3.4def	40.9 ± .2de
S_3 × SA	65.2 ± .9f	44.9 ± .7f	8.9 ± .2 h	7.1 ± 0.3	137.8 ± 0.1 fgh	37.2 ± .8 fg
S_3 × MEL	82.1 ± 0.5d	36.6 ± .6 g	8.6 ± 0.3 h	7.2 ± 0.3	141.7 ± 4.5efg	37.6 ± .7f
S_4 × H	5.2 ± 1.3 h	12.1 ± 1.6j	3.3 ± .2j	9.3 ± .7	98.3 ± 3.2 L	30.7 ± 1.1ı
S_4 × P	57.4 ± 0.5 g	21.1 ± 1.1 hı	5.9 ± .2ı	9.8 ± 0.1	111.4 ± 1.1 k	32.5 ± 0.3ı
S_4 × SA	45.2 ± .2ı	18.5 ± 0.5ı	3.8 ± 0.3j	9.3 ± .2	121.9 ± 2.3j	31.5 ± 0.3ı
S_4 × MEL	64.2 ± 1.1f	22.6 ± 0.5 h	3.5 ± .2j	9.5 ± 0.3	128.2 ± 2.9ij	31.8 ± .0ı
Two-way ANOVA						
LSD$_{.05}$ SS	1.08**	1.31**	.85**	.27**	3.33**	1.03**
LSD$_{.05}$ PT	1.08**	1.31**	.85**	.27**	3.33**	1.03**
LSD$_{.05}$ SS × PT	2.16**	2.63**	1.70**	.54^{NS}	6.65**	2.06**

#: Mean (± SE) values marked with a different letter in each column differed significantly by LSD test ($P < .05$). * and ** significant at $P < .01$ and $P < .05$, respectively. NS indicates not significant at $P < .05$.

increasing soil salinity, while seed priming with P, SA, and MEL increased plant height in treatments S_2, S_3, and S_4 compared to H-primed seeds. (Table 1). Moreover, no significant differences in plant height were observed between the S_1 × P, S_1 × SA, and S_1 × MEL treatments (Table 1). However, P- and MEL-primed seeds showed greater plant height than H- and SA-primed seeds in S_2, S_3, and S_4 treatments (Table 1).

Significant variations for shoot fresh weight (SFW) were observed with increasing soil salinity (Table 1). The greatest SFW (72.8 g pot^{-1}) was observed at the S_1 treatment, which was 9.3%, 44.2%, and 74.6% higher than S_2, S_3, and S_4, respectively (Table 1). In addition, the SFW of the sorghum seedlings varied significantly according to the priming treatments (Table 1). The maximum SFW value (55.6 g pot^{-1}) was observed in the MEL priming treatment, which was 31.1%, 3.3%, and 9.8% higher than in the H, P, and SA priming treatments, respectively (Table 1). According to the interaction of SS × PT, the S_1 × MEL treatment exhibited the highest SFW (86.5 g pot^{-1}), while the S_4 × H treatment showed the lowest SFW (12.1 g pot^{-1}) (Table 1). Moreover, sorghum seeds primed with MEL had 6.6%, 18.2%, and 46.2% higher SFW than P-, SA, and H-primed seeds at 8.0 dS m^{-1} (S_4), respectively (Table 1).

As shown in Table 1, shoot dry weight (SDW) was significantly reduced with increasing soil salinity, and it was reduced by 19.7%, 43.3%, and 80.3% in S_2, S_3, and S_4, respectively, compared with S_1 (Table 1). Furthermore, the priming treatment significantly affected SDW, whereas no significant differences in SDW values were found

between MEL and SA pre-sowing treatments (Table 1). The maximum SDW value was 23.2 g pot^{-1} at $S_1 \times$ SA treatment, while the minimum was 3.3 g pot^{-1} at $S_4 \times$ H treatment (Table 1). Seeds primed with P, SA, and MEL had 36.3%, 93.9%, and 67.1% higher SDW under S_1 conditions; 20.6%, 12.5%, and 38.2% higher SDW under S_2 conditions; and 10.5%, 25.2%, and 27.9% higher SDW under S_3 conditions, respectively, compared to H-primed seeds (Table 1).

The effects of the SS, PT, and SS × PT interactions on the ash content of sorghum seedlings are presented in Table 1. Soil salinity led to a significant increase in the ash content of the sorghum seedlings (Table 1). The highest ash content was observed in the S_4 treatment (9.5%). The reduction in the ash content of sorghum seedlings was 33.7%, 26.4%, and 20.0% for S_1, S_2, and S_3, respectively, compared to the S_4 treatment (Table 1). Regarding priming treatments, P-primed seeds had a greater effect on ash content than H, SA, and MEL-primed seeds (Table 1).

Significant variation and decreasing trends in stomatal conductance and chlorophyll content were observed with increasing soil salinity (Table 1). The seeds exposed to 8.0 dS m^{-1} (S_4) had the lowest value (114.9 mmol m^{-2} s^{-1}) stomatal conductance, 21.1%, 28.8%, and 57.4 lower than S_3, S_2, and S_1 treatments. However, sorghum seeds treated with P, SA, and MEL priming under soil salinity stress had higher stomatal conductance values than hydro-primed seeds. The highest stomatal conductance value was observed in the MEL treatment (154.9 mmol m^{-2} s^{-1}), while the lowest was in the H pretreated seeds (129.3 mmol m^{-2} s^{-1}). In addition, there were no statistically significant differences in stomatal conductance between seeds pretreated with salicylic acid and proline. Regarding the SS × PT interaction, the highest value of stomatal conductance was found for the S1 × MEL treatment (193.4 mmol m^{-2} s^{-1}), and the value of stomatal conductance of the $S_1 \times$ H, $S_1 \times$ P, and $S_1 \times$ SA treatments was 22.7%, 2.1%, and 1.2% lower than this, respectively (Table 1). Moreover, under 8.0 dS m^{-1} (S_4) soil salinity levels, MEL-pretreated seeds showed better stomatal conductance values than the H-, SA-, and P-pretreated seedlings, which were 23.3%, 13.1%, and 4.9% higher than the $S_4 \times$ H, $S_4 \times$ P, and $S_4 \times$ SA treatments, respectively (Table 1).

The chlorophyll content of sorghum seedlings decreased significantly with increasing soil salinity; accordingly, the highest and lowest values (53.2 and 31.6 SPAD) were found in treatments S_1 and S_4, respectively (Table 1). In addition, seeds pretreated with proline and melatonin had higher SPAD values than those pretreated with hydro and salicylic acid (Table 1). Accordingly, seeds treated with proline exhibited the highest SPAD value at 42.4, which did not show a significant difference compared to those treated with MEL. (Table 1). For the SS × PT treatments, seedlings pretreated with P, SA, and MEL generally had higher SPAD values than those under S_1, S_2, and S_3 conditions, whereas SPAD values (30.7, 32.5, 31.5, and 31.8 SPAD) of seeds pretreated with H, P, SA, and MEL did not differ remarkably under S_4 conditions (Table 1).

The macronutrient contents (Na^+, K^+, and Ca^{2+}) of sorghum leaves and the ratios of K^+/Na^+ and Ca^{2+}/Na^+ shown in Table 2 were considerably affected by SS, PT, and the SS × PT interaction. The highest Na^+ content (.86%) was recorded in S_4, whereas the lowest (.51%) was observed in S_1 (Table 2). However, pre-treatment with SA, H, and MEL considerably lowered the Na^+ content in sorghum seedlings compared to that in the proline-primed seeds. Generally, Na^+ accumulation in sorghum leaves increased with increasing soil salinity under all priming treatments. However, MEL had greater ameliorative effects on reducing Na^+ accumulation in sorghum seedlings than the H, SA, and P priming treatments. For instance, the highest Na^+ content (.91%) in sorghum leaves was observed in $S_4 \times$ P, which was 4.8%, .7%, and 13.4% higher than that in the $S_4 \times$ H, $S_4 \times$ SA, and $S_4 \times$ MEL treatments, respectively (Table 2).

The results in Table 2 show that the K^+ and Ca^{2+} contents of sorghum significantly decreased with increasing soil salinity. Concerning soil salinity levels, the highest K^+ and Ca^{2+} contents (5.05% and 1.59%) of sorghum were observed in the S_1 treatment, which was 24.3% and 18.4% higher for K^+ and Ca^{2+}, respectively, than the S_4 treatment. Regarding priming treatments, leaf K^+ and Ca^{2+} concentrations in sorghum leaves differed significantly among the priming treatments (Table 2). The highest leaf K^+ and Ca^{2+} concentrations (4.61% and 1.61%, respectively) were recorded in the MEL priming treatment, whereas the lowest values (4.10% and 1.28%, respectively) were measured in the hydropriming treatment. Regarding the SS × PT interaction, K^+ and Ca^{2+} concentrations in sorghum leaves ranged from 5.26% to-3.53% for K^+ concentration and 1.79% to-1.12% for Ca^{2+} concentration, respectively (Table 2). Accordingly, the maximum K^+ and Ca^{2+} concentrations (5.26% and 1.79%, respectively) in the sorghum leaves were observed in the $S_1 \times$ MEL treatment. At the highest soil salinity conditions (8.0 dS m^{-1}), pre-treated with MEL and SA had higher K^+ and Ca^{2+} accumulation in sorghum leaves than H and P pre-treated treatments (Table 2). Compared to $S_4 \times$ MEL, leaf K^+ content was reduced by 2.7%, 14.5%, and 13.2% for $S_4 \times$ SA, $S_4 \times$ P, and $S_4 \times$ H, respectively, and leaf Ca^{2+} content was decreased by 1.4%, 19.0%, and 22.8% for $S_4 \times$ SA, $S_4 \times$ P, and $S_4 \times$ H, respectively (Table 2).

As clearly shown in Table 2, soil salinity had a noticeable deleterious effect on leaf K^+/Na^+ and Ca^{2+}/Na^+ ratios, the highest of which (10.39% and 3.29%, respectively) was recorded in the S_1 treatment, which was reduced by 57.2% and 53.8%, respectively, in the S_4 treatment relative to the S_1 treatment (Table 2). However, pre-treatment with MEL, SA, and P considerably boosted the K^+/Na^+ and Ca^{2+}/Na^+ ratios of sorghum seedlings compared to the hydro-priming treatment (Table 2). Hence, seeds pretreated with MEL and SA under soil salinity stress had higher K^+/Na^+ and Ca^{2+}/Na^+ ratios in the hydro and proline-primed seeds. However, the K^+/Na^+ and Ca^{2+}/Na^+ ratios did not differ significantly between MEL-SA and H-P priming treatments. Comparing the effects of the SS × PT interaction on K^+/Na^+ and Ca^{2+}/Na^+ ratios, SA and MEL priming treatments greatly improved the K^+/Na^+ and Ca^{2+}/Na^+ ratios in sorghum seedlings under all soil salinity conditions (Table 2). However, the MEL priming treatment resulted in higher K^+/Na^+ and Ca^{2+}/Na^+ ratios in sorghum seedlings at S_2, S_3, and S_4 soil salinity levels than the H, P, and SA priming treatments (Table 2). The K^+/Na^+ ratio in the $S_1 \times$ P, $S_1 \times$ SA, and $S_1 \times$ MEL treatments increased by 3.2%, 66.1%, and 60.2%,

TABLE 2 Influence of different seed priming treatments on Na^+, K^+ and Ca^{2+} content of sorghum leaves and K^+/Na^+ and Ca^{2+}/Na^+ ratio at different soil salinity.

Soil salinity (SS)	Na^+ (%)	K^+ (%)	Ca^{2+} (%)	K^+/Na^+ ratio	Ca^{2+}/Na^+ ratio
S_1 (.27 dSm^{-1})	.51 ± .0d	5.05 ± 0.1a	1.59 ± 0.1a	10.39 ± .8a	3.29 ± 0.3a
S_2 (2.50 dSm^{-1})	.62 ± .0c	4.63 ± 0.1b	1.48 ± .0b	7.64 ± 0.3b	2.49 ± .2b
S_3 (5.00 dSm^{-1})	.78 ± .0b	4.20 ± 0.1c	1.41 ± .0c	5.42 ± .2c	1.86 ± 0.1c
S_4 (8.00 dSm^{-1})	.86 ± .0a	3.82 ± 0.1d	1.29 ± 0.1d	4.45 ± .2d	1.51 ± 0.1d
Priming treatments (PT)					
Hydro (H)	.73 ± .0a	4.10 ± 0.1c	1.28 ± .0d	5.86 ± 0.5b	1.77 ± 0.1b
Proline (P)	.75 ± .0a	4.42 ± .2b	1.31 ± .0c	6.14 ± 0.5b	1.84 ± 0.1b
Salicylic acid (SA)	.66 ± 0.1b	4.55 ± 0.1ab	1.56 ± .0b	7.81 ± 1.0a	2.70 ± 0.3a
Melatonin (MEL)	.64 ± 0.1b	4.61 ± 0.1a	1.61 ± .0a	8.03 ± .9a	2.80 ± 0.3a
SS×PT interaction					
S_1 × H	.61 ± 0.1 fgh	4.64 ± 0.1 cd	1.35 ± .0de	7.85 ± .8bc	2.08 ± .2 cd
S_1 × P	.64 ± .0 fgh	5.14 ± 0.1ab	1.48 ± .0c	8.10 ± 0.5bc	2.33 ± 0.1c
S_1 × SA	0.40 ± .0ı	5.14 ± 0.1ab	1.72 ± .0a	13.03 ± 0.5a	4.37 ± 0.3a
S_1 × MEL	0.42 ± .0ı	5.26 ± 0.1a	1.79 ± .0a	12.57 ± 0.3a	4.28 ± 0.1b
S_2 × H	.67 ± 0.1efg	4.36 ± 0.2de	1.34 ± 0.1e	6.59 ± 0.3de	2.03 ± 0.1c-f
S_2 × P	.70 ± .0def	4.90 ± .0bc	1.34 ± .0e	7.03 ± 0.2 cd	1.92 ± 0.1d-g
S_2 × SA	.54 ± .0 h	4.64 ± 0.1 cd	1.62 ± .0b	8.39 ± .6b	2.98 ± 0.2b
S_2 × MEL	.58 ± .0gh	4.61 ± .0 cd	1.62 ± 0.1b	8.54 ± .0bc	3.02 ± 0.1b
S_3 × H	.79 ± .0bcd	3.81 ± 0.2 gh	1.33 ± .0ef	4.84 ± 0.3fgh	1.68 ± .0 fg
S_3 × P	.76 ± .0 cde	4.13 ± 0.1ef	1.25 ± .0 fg	5.55 ± 0.2ef	1.82 ± 0.1 fg
S_3 × SA	.80 ± .0bc	4.41 ± .0de	1.49 ± .0c	5.55 ± 0.1ef	1.87 ± .0efg
S_3 × MEL	.78 ± 0.1bcd	4.44 ± 0.1d	1.59 ± .0b	5.74 ± 0.5ef	2.05 ± 0.2 cde
S_4 × H	.86 ± .0ab	3.59 ± 0.2 h	1.12 ± .0 h	4.16 ± 0.3 h	1.30 ± .0 h
S_4 × P	.91 ± .0a	3.53 ± 0.1 h	1.18 ± .0gh	3.90 ± 0.2 h	1.30 ± .0 h
S_4 × SA	.90 ± .0a	4.02 ± 0.1 fg	1.43 ± .0 cd	4.47 ± 0.1gh	1.59 ± .0gh
S_4 × MEL	.79 ± .0bcd	4.13 ± 0.1ef	1.45 ± .0c	5.27 ± .0 fg	1.85 ± .0efg
Two-way ANOVA					
$LSD_{.05}$ SS	.05**	0.15**	.04**	.54**	.18**
$LSD_{.05}$ PT	.05**	0.15**	.04**	.54**	.18**
$LSD_{.05}$ SS × PT	0.10**	.30**	.09*	1.07**	.36**

#: Mean (± SE) values marked with a different letter in each column differed significantly by LSD test ($P < .05$). * and ** significant at $P < .01$ and $P < .05$, respectively. NS indicates not significant at $P < .05$.

respectively, compared to the S_1 × H treatment (Table 2). The ratio of K^+/Na^+ was drastically reduced under S_4 conditions, and the ratios of K^+/Na^+ in S_4 × H, S_4 × P, S_4 × SA, and S_4 × MEL were reduced by 46.9%, 50.3%, 43.1%, and 32.8%, respectively, compared to the S_1 × H treatment (Table 2). In terms of the Ca^{2+}/Na^+ ratio, the S_1 × H treatment had the lowest ratio (2.08%), which was 12.4%, 110.4%, and 106.1% lower than those of the S_1 × P, S_1 × SA, and S_1 × MEL treatments, respectively (Table 2). Moreover, the lowest Ca^{2+}/Na^+ ratio in sorghum seedlings was observed at the hydro priming treatment under all soil salinity conditions compared to the other treatments (Table 2).

The Cu^{2+}, Mn^{2+}, and Zn^{2+} contents of sorghum seedlings were significantly affected by soil salinity (Figure 3a, b, c), priming treatment (Figure 3d, e, f), and two-way interaction between soil salinity and priming treatment (Figure 4a, b, and c). As shown in Figure 3a, the Cu^{2+} content of the sorghum leaves increased with increasing soil salinity. The highest and lowest values (19.66 and 14.38 ppm) were observed in the S_4 and S_1 treatments, respectively. However, priming the seeds with different plant growth regulators significantly affected the leaf Cu^{2+} uptake (Figure 3d). In this respect, the lowest levels of Cu^{2+} in sorghum leaves were observed in the hydro and proline treatments, and statistically insignificant differences were found between the two treatments (Figure 3d). However, the leaf Cu^{2+} content in the proline and melatonin seed treatments was 19.17 ppm and 19.54 ppm, respectively, which are classified in the same group (Figure 3d). Concerning the interaction between soil salinity and priming treatment, the priming treatment of the seeds with P, SA, and MEL increased the Cu^{2+} content of the leaves under all soil salinity

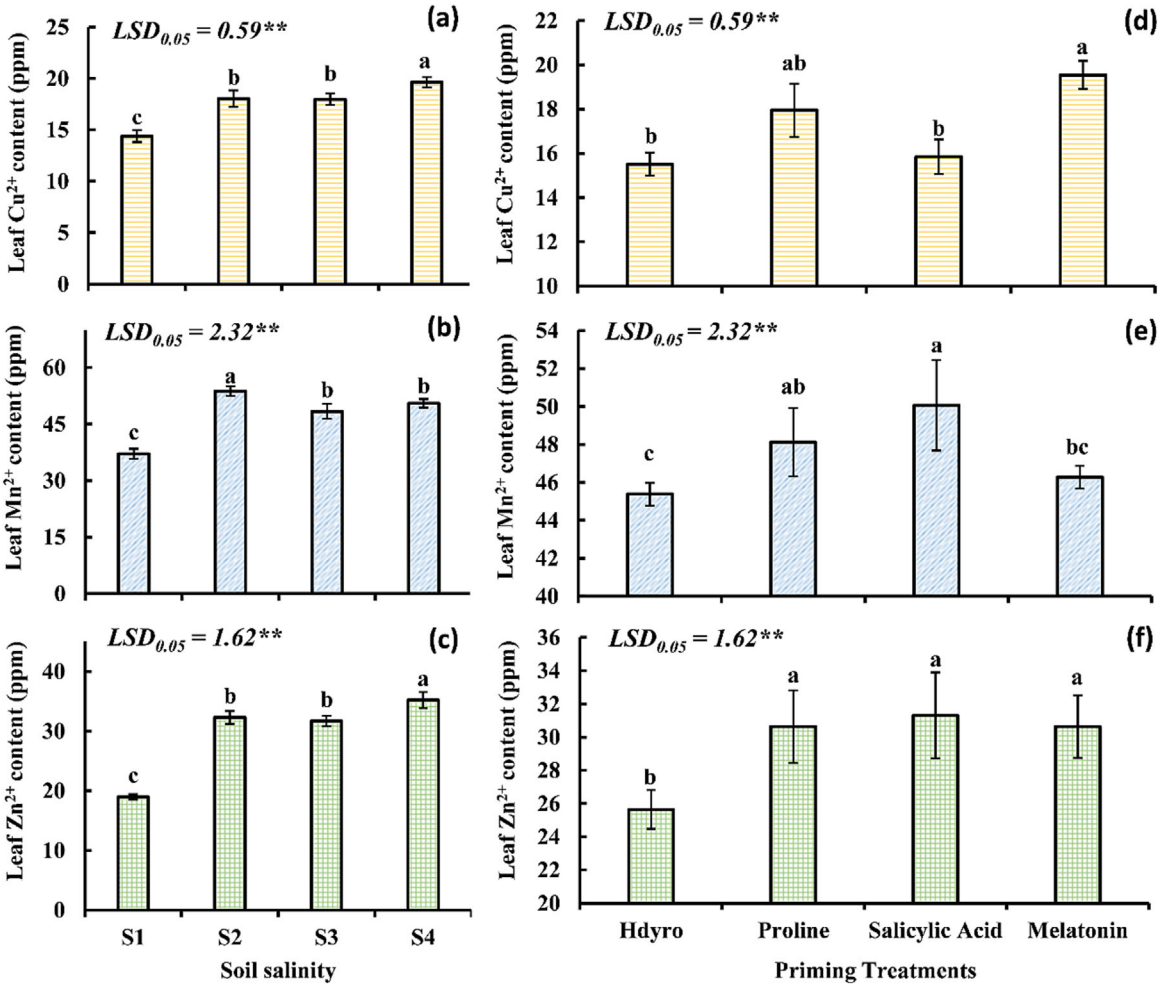


FIGURE 3 The main effects of soil salinity and seed priming with different PGRs on leaf Cu^{2+}, Mn^{2+}, and Zn^{+2} contents of sorghum seedlings. Mean values within each column followed by different letter cases significantly differed by LSD test ($P < 0.05$). **: $P < .01$.

conditions compared with the hydro-priming treatment (Figure 4a). For instance, under 8.0 dSm^{-1} soil salinity conditions (S_4), leaf Cu^{2+} content decreased by 17.6%, 8.5%, and 14.8% for the H, P, and SA treatments, respectively, compared to the MEL treatment (Figure 4a).

Mn^{2+} content in sorghum seedling leaves increased up to S_2 but decreased by 10.0% and 6.1% in S_3 and S_4, respectively, compared with the S_1 treatment (Figure 3b). However, no statistically significant differences in leaf Mn^{2+} concentrations were observed between S_3 and S_4 treatments (Figure 3b). The Mn^{2+} content in sorghum leaves responded differently to soil salinity in different priming treatments (Figure 3e). On average, across all priming treatments, the P, SA, and MEL treatments increased leaf Mn^{2+} content by 6.0%, 10.3%, and 2.0%, respectively, compared with the hydropriming (Figure 3e). Regarding the soil salinity×priming treatment interaction, the lowest leaf Mn^{2+} content in sorghum seedlings was observed under the S_1 condition (Figure 4b), whereas it increased with increasing soil salinity (Figure 4b). At the S_2 and S_3 conditions, the highest Mn^{2+} levels (60.0 and 54.5 ppm, respectively) were found in seeds primed with salicylic acid compared to the other treatments (Figure 4b), while in the S_4 condition, the lowest level (45.6 ppm) was found in seeds primed with salicylic acid (Figure 4b).

The Zn^{2+} content of the sorghum leaves increased significantly with increasing soil salinity (Figure 3c). The Zn^{2+} content in sorghum leaves increased by 70.3%, 67.0%, and 85.6% in treatments S_2, S_3, and S_4, respectively, compared with S_1 (Figure 3c). Considering the priming treatments, leaf Zn^{2+} content was considerably increased by 88.1%, 122.2%, and 61.4% at pre-sowing with P, SA, and MEL treatments, respectively, compared to the H priming treatment, whereas the P, MEL, and SA treatments were categorized in the same group (Figure 3f). Interestingly, leaf Zn^{2+} content did not differ excessively between priming treatments at soil salinity of .27 dS m^{-1}, whereas the effects of the priming treatments were increased with increasing soil salinity (Figure 4c). The P, SA, and MEL treatments considerably enhanced Zn^{2+} accumulation in sorghum leaves compared to hydropriming under soil salinity conditions higher than .27 dS m^{-1} (Figure 4c). The highest value (39.9 ppm) was found in the $S_4 \times$ SA treatment, which was 27.9%, 10.6%, and 7.9% higher than that in the $S_4 \times$ H, $S_4 \times$ P, and $S_4 \times$ MEL treatments, respectively (Figure 4c).

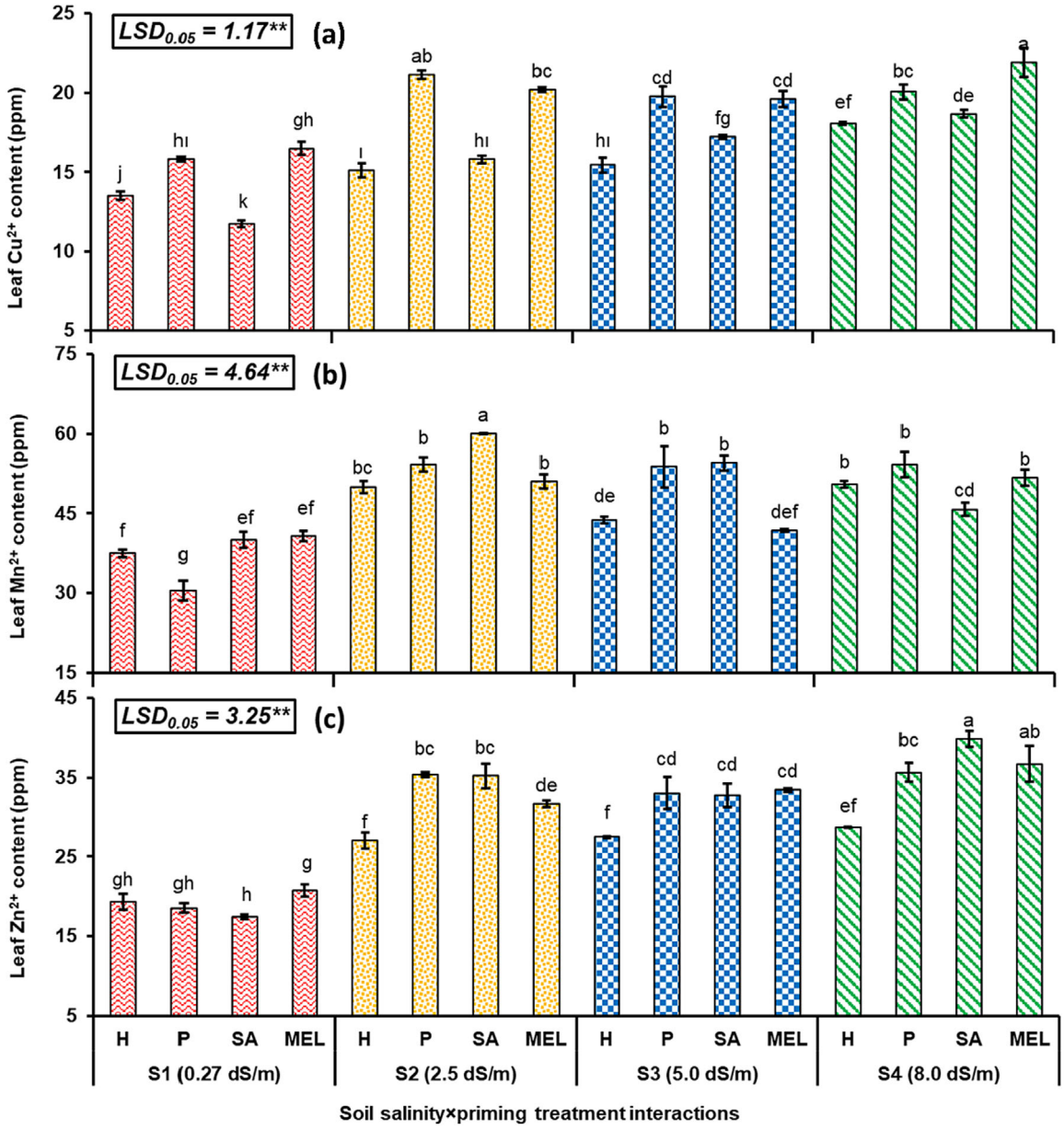


FIGURE 4 Effects of the different priming treatments on leaf Cu^{2+}, Mn^{2+}, and Zn^{2+} contents of sorghum seedlings under soil salinities conditions. Mean values within each column followed by different letter cases significantly differed by LSD test ($P < .05$). **: $P < .01$.

3.2 | Correlation analysis

The correlation coefficients between the investigated parameters are depicted in Figure 5. Plant height was positively correlated with leaf K^+ and Ca^{2+} contents (r = .77***; r = .52***), whereas it was highly and positively related to SFW (r = .90***) and SDW (r = .83***) (Figure 5). SDW was highly and positively correlated with stomatal conductance (r = .89***), chlorophyll content (r = .84***), and leaf Ca^{2+} and K^+ contents (r = .63***; r = .79***), whereas it was negatively associated with ash content (r = −.78***). Leaf Na^+ content was substantially and positively linked with ash content (r = .73***) and leaf Zn^{2+} content (r = .62***) but negatively related with all growth characteristics and leaf K^+ and Ca^{2+} content (r = −.76***; r = −.68***). Correlation analysis also showed that leaf Ca^{2+}/Na^+ was strongly correlated with leaf K^+/Na^+ content (r = .96***), stomatal conductance (r = .84***), and chlorophyll content (r = .72***), whereas the correlation with leaf Zn^{2+} and Cu^{2+} content was negative (r = −.53***; r = −.46***), indicating that leaf micronutrient content decreased with increasing leaf Ca^{2+}/Na^+. Moreover, leaf Zn^{2+} content showed a high and positive correlation with leaf Mn^{2+} and Cu^{2+} content (r = .74***; r = .76***), while the correlation with stomatal conductance (r = −.65***) and chlorophyll content (r = −.81***) was negative. These results indicate that the Zn^{2+} content of sorghum seedlings increased significantly with decreasing photosynthetic parameters. In addition, only leaf Mn^{2+} content was positively and highly related to leaf Cu^{2+} content (r = .47***), whereas it was

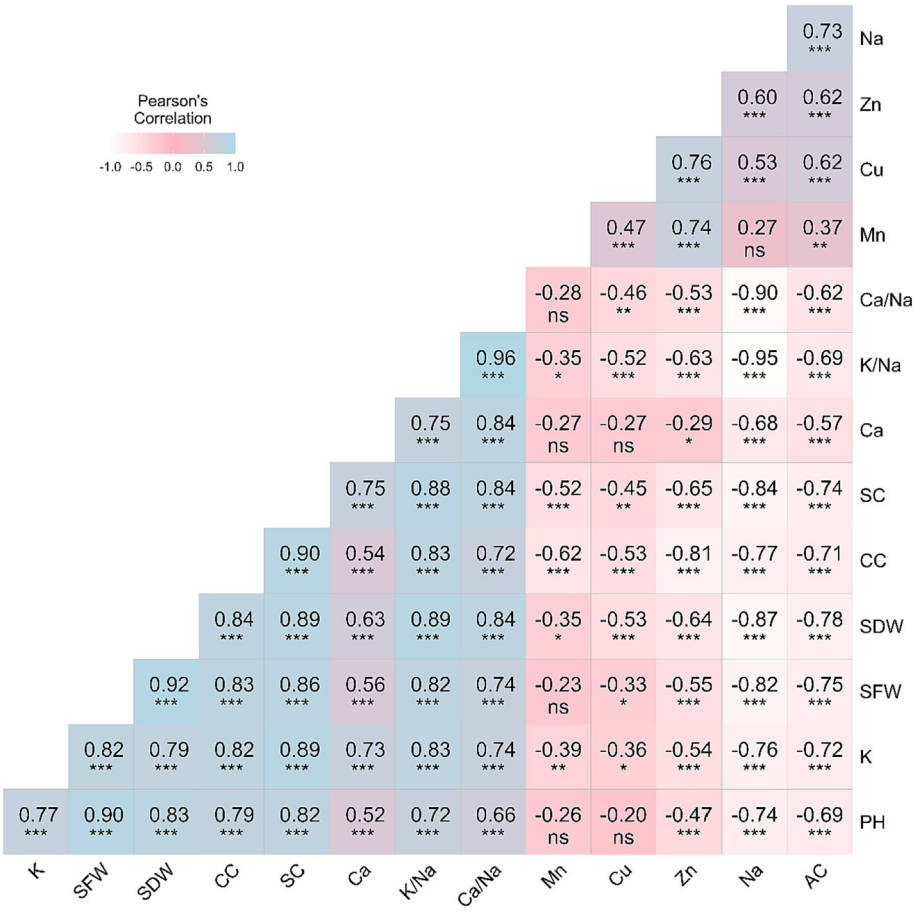


FIGURE 5 Correlation matrix between leaf nutrients and morpho-physiological traits. *Abbreviations:* PH: plant height, SDW: shoot dry weight, SFW: shoot fresh weight; Na^+: sodium; K^+: potassium, Ca^{2+}: calcium, K^+/Na^+: potassium per sodium; Ca^{2+}/Na^+: calcium per sodium; Cu^{2+}: copper; Mn^{2+}: manganese; Zn^{2+}: zinc; AC: ash content; CC: chlorophyll content; SC: stomatal conductance. ***: $P < .001$; **: $P < .01$; *: $P < .05$; ns: non-significant.

negatively correlated with SDW ($r = -.35^*$) and the K^+/Na^+ ratio ($r = -.35^*$) (Figure 5).

3.3 | Principal component analysis (PCA)

PCA was performed to evaluate the role of seed priming with SA, MEL, P, and H in alleviating salt stress in sorghum seedlings. In addition, PC scores helped categorize the best priming treatment across all plant growth regulators and revealed the interaction of priming treatment with the soil salinity response. The means of treatment for the 14 dependent variables were used for PCA (Table 3). These variables were categorized into two major principal components (PC1 and PC2), which explained 83.054% of the total variance (Figure 3). Regarding the eigenvalue rule, the first two PCs (PC1 and PC2) had eigenvalues greater than one (Table 3). PC1 discriminated most of the research variables, explaining a larger proportion of the variance (72.33%), whereas PC2 explained a lower proportion of the variance (1.22%). (Figure 6a). PC1 was highly and negatively correlated with AC and Na^+, while positively and highly correlated with K^+, PH, SFW, SDW, K^+/Na^+, Ca^{2+}/Na^+, AC, CC, and SC. Moreover, PC2 received the main positive contributions from Cu^{2+}, Mn^{2+}, and Zn^{2+} (Table 3).

At .27 dS m^{-1}, sorghum seed priming with melatonin and proline treatments showed high values of growth parameters and photosynthetic and leaf micronutrient traits located on the positive side of PC1 (Figure 6b). These traits were positively correlated with PC1, implying that growth and leaf micronutrient traits increased with increasing PC1 (Table 3). As depicted in Table 3, leaf Cu^{2+} content had the highest effect (.718) on PC2, which was placed on the positive side of PC2. At 5.0 dS m^{-1} soil salinity, seed priming with SA and P was strongly related to AC and Na^+ traits (Figure 6a-6b).

4 | DISCUSSION

High-quality seeds are essential in agriculture to improve seedling morphogenesis under high-stress conditions (Kiremit et al., 2022). Improving seed quality is critical here because it can help seeds germinate under suboptimal environmental conditions, and plants develop earlier and more uniformly, resulting in higher crop yields. Priming seeds with growth regulators is a common technique to increase plant tolerance to stress factors. Determining the optimal plant growth regulator for seed priming is critical to minimizing salt stress, increasing nutrient uptake, and improving plant growth. This will be of great interest to future researchers in the coming years. In the present study, priming seeds with P, MEL, and SA significantly reduced the deleterious effects of salt stress and improved nutrient uptake and biomass-related traits in sorghum seedlings compared to hydro priming treatment.

TABLE 3 Factor loadings and variables contributions for parameters of the two principal components analysis.

Traits	PC1	Contribution of variables	PC2	Contribution of variables
PH	.822	6.666	.181	2.193
SFW	.890	7.823	0.108	.785
SDW	.947	8.864	.070	0.332
Na	−.945	8.819	−.160	1.720
K	.919	8.343	.180	2.166
Ca	.738	5.385	.393	10.328
K/Na	.950	8.918	.152	1.543
Ca/Na	.885	7.736	.269	4.836
Cu	−.617	3.755	.553	20.423
Mn	−.525	2.725	.668	29.770
Zn	−.768	5.823	.588	23.066
AC	−.866	7.402	.075	.383
CC	.935	8.631	−0.177	2.086
SC	.960	9.110	.074	.369
Eigenvalue	10.127		1.500	
Variability (%)	72.334		10.720	
Cumulative (%)	72.334		83.054	

Abbreviations: PH: plant height, SFW: shoot fresh weight, SDW: shoot dry biomass; Na: sodium; K: potassium, Ca: calcium, K/Na: potassium per sodium; Ca/Na: calcium per sodium; Cu: copper; Mn: manganese; Zn: zinc; AC: ash content; CC: chlorophyll content; SC: stomata conductivity.

Salt stress adversely affected the plant height, SFW, SDW, and ash content of sorghum seedlings. Soil salinity of 2.5 dS m^{-1} had little effect on sorghum plant height and shoot fresh and dry weights, indicating that sorghum seeds were tolerant to soil salinity up to 2.5 dS m^{-1}. The reduction in growth characteristics was more pronounced at a soil salinity of 8 dS m^{-1}. Previous studies, such as those by Guo et al. (2022) and Dehnavi et al. (2022), have shown that soil salinity negatively affects sorghum's fresh and dry weights. Plant growth regulators positively affect salinity tolerance by maintaining cell turgor and protecting plants from oxidative stress, thus increasing plant growth (Ibrahim, 2016; Mansour et al., 2021). Our results showed that seeds primed with MEL, SA, and P showed better growth performance than those primed with hydro. Moreover, seeds primed with melatonin exhibited better plant height, shoot fresh weight, and stomatal conductance than the rest priming treatments. This improvement in stomatal conductance and shoot fresh weight of melatonin-primed seeds could be due to maintaining membrane integrity and promoting cell expansion and elongation.

Stomatal conductance and chlorophyll content play significant roles in plant energy assimilation, and stress conditions strongly influence these levels (Xu et al., 2015). Stomata and chlorophyll content significantly decreased with increasing soil salinity levels. In addition, sorghum seedlings growing at soil salinity levels of 2.50, 5.0, and 8.0 dS m^{-1} had shorter leaves and darker green color than seedlings growing at soil salinity levels of .27 dS m^{-1}. As observed in the current study, decreased stomatal and chlorophyll concentrations may lead to lower radiation usage efficiency and carbohydrate synthesis, resulting in lower plant growth and biomass in salt-stressed plants. Guimarães et al. (2020) reported that the transpiration of salt-sensitive sorghum plants decreased by up to 70% under salt stress compared with that in control plants. Ibrahim et al. (2020) found that the stomatal conductance of sorghum decreases considerably with increasing soil salinity. Previous studies have depicted that salt stress inhibits intercellular CO_2 concentration and thus decreases the photosynthetic rate by closing stomata (Nigam et al., 2022; Rajabi Dehnavi et al., 2019; Sezer et al., 2021). Plant growth regulators protect plants by reducing the harmful effects of salt stress on stomatal conductance, chlorophyll concentration, and photosynthetic pigments, thereby increasing their photosynthetic potential (Johnson & Puthur, 2021). In the present study, seeds primed with MEL, P, or SA showed increased stomatal conductance and chlorophyll content under salt stress. In contrast, seeds primed with MEL, P, and SA showed no statistical difference in stomatal conductance of sorghum seedlings at 2.5 dS m^{-1} soil salinity. However, seed priming with MEL further increased the stomatal conductance of sorghum seedlings with increasing soil salinity compared to the rest of the priming treatments. These findings indicate that melatonin can enhance the regulation of photosynthesis in sorghum seedlings and plays a role in forming chloroplasts by shielding them from reactive oxygen species and enhancing chlorophyll stability. This could help to maintain photosynthetic pigment levels when plants are exposed to high levels of salt stress. Thus, improving stomatal regulation induced by melatonin may have contributed to better nutrient and water uptake, thereby increasing plant salt tolerance.

Mineral uptake is one of the most important adaptations for stress tolerance (Kiremit et al. 2023). Na^+ and K^+ have the same

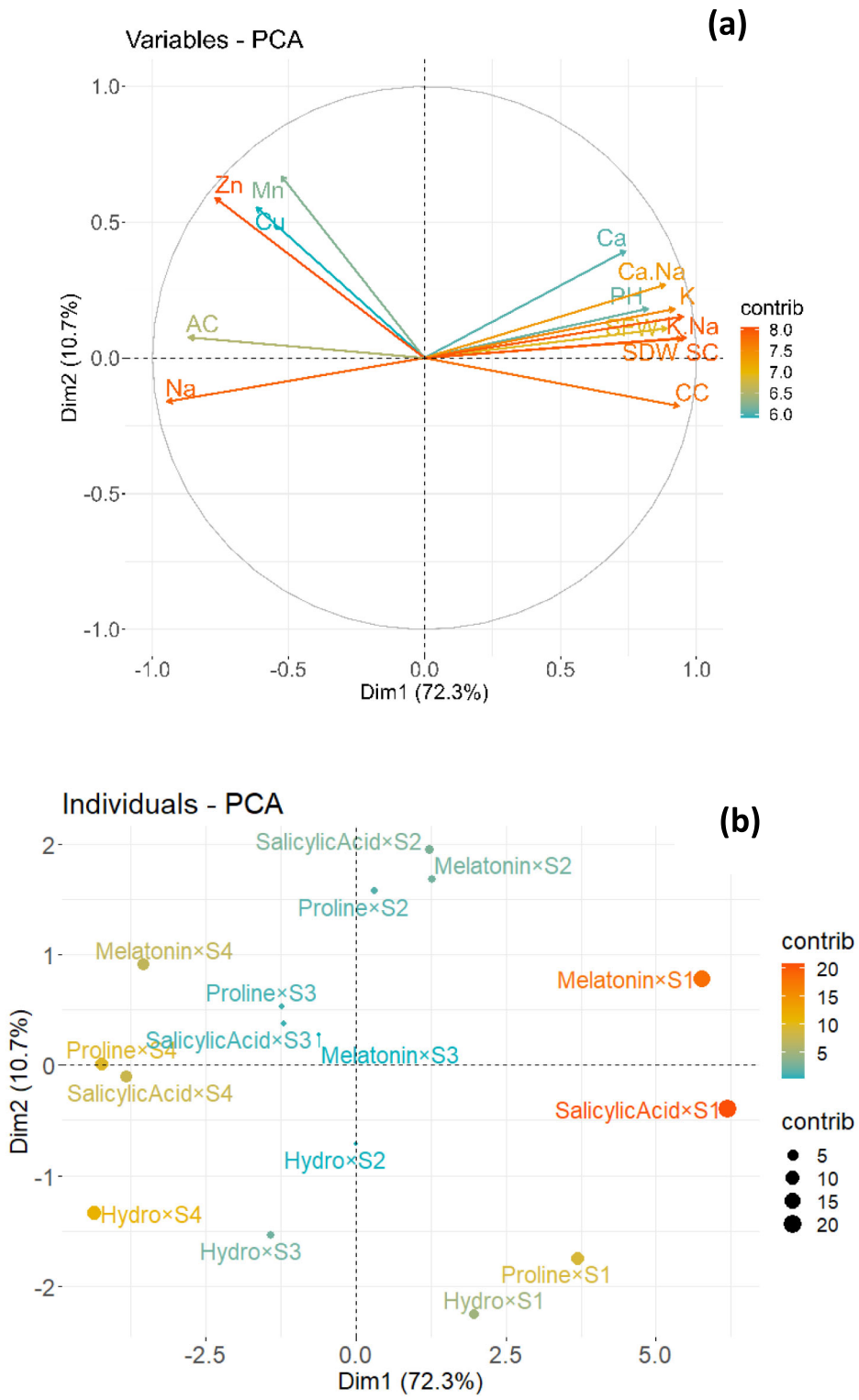


FIGURE 6 PCA-loading plot (a) and scores plot (b) of the effects of seed priming and soil salinity interactions on evaluated traits of sorghum seedlings. *Abbreviations:* PH: plant height, SFW: shoot fresh weight, SDW: shoot dry weight; Na: sodium; K: potassium, Ca: calcium, K/Na: potassium per sodium; Ca/Na: calcium per sodium; Cu: copper; Mn: manganese; Zn: zinc; AC: ash content; CC: chlorophyll content; SC: stomatal conductance.

physicochemical structure; therefore, the two ions compete for uptake (Ahanger & Agarwal, 2017). Due to the similarity of Na^+ and K^+ ions, K^+ is the most affected ion. In this study, K^+ and Ca^{2+} contents in sorghum leaves decreased with increasing soil salinity, whereas Na^+ accumulation in sorghum leaves increased. Similar results were found in sorghum plants by Zhang et al. (2020), who observed a significant decrease in K^+ and Ca^{2+} ions in the leaves of sorghum plants exposed to 240 mM soil salinity. Our results are consistent with those of Sezer et al. (2021) for sweet corn plants, who found that Na^+ uptake increased with increasing soil salinity, significantly reducing Ca^{+2} and K^+ uptake. Under salt stress, high K^+/Na^+ and Ca^{2+}/Na^+ ratios are critical for the long-term regulation of plant

metabolic functions, which play active roles in intracellular enzyme processes. The sensitivity of sorghum seedlings to salt stress is manifested by the inhibition of photosynthetic pigments and metabolic imbalance, which reduces plant growth. This situation could be related to the excessive translocation of Na^+ ions through the cell membranes, decreasing the osmotic potential of the leaves, and reducing the translocation of assimilates (de Bang et al., 2021). The results of the current study showed that seed priming with P, SA, and MEL inevitably enhanced the salt tolerance of sorghum seedlings by lowering Na^+ accumulation and improving K^+ and Ca^{2+} uptake, which increased the K^+/Na^+ and Ca^{2+}/Na^+ ratios in the leaves under salt stress. Similarly, copious studies have shown that priming seeds with MEL, SA, and P increases the nutrient uptake ability of different plants under different environmental constraints (Ambreen et al., 2021; Ashraf et al., 2022; Gupta & Seth, 2021; Wakchaure et al., 2020). Likewise, Dehnavi et al. (2022) found that SA-primed sorghum seeds under salt stress had a higher K^+/Na^+ uptake than unprimed seeds. In our study, K^+ and Ca^{2+} uptake was higher in seeds treated with MEL, and Na^+ uptake was lower than in seeds treated with SA. These results indicate that the higher accumulation of K^+/Na^+ and Ca^{2+}/Na^+ ratios in the MEL-pretreated seeds indicates better regulation of nutrient and water uptake through cell membranes during salinity stress, which may have assisted the plant in maintaining growth and function.

Zn^{2+}, Cu^{2+}, and Mn^{2+} are essential for plant growth and participate in metabolic and enzymatic activities (Horuz et al., 2017). Rajabi Dehnavi et al. (2019) expressed that micronutrient availability in saline soils depends on soil pH and the solubility of these elements. Furthermore, Grattan and Grieve (1998) identified a complicated relationship between salt stress and micronutrient absorption, suggesting that salt stress may either increase or decrease micronutrient uptake in plant tissues or have no effect on micronutrients. Statistically, the Zn^{2+}, Cu^{2+}, and Mn^{2+} levels in the sorghum seedling leaves did not show significant differences among the S_2, S_3, and S_4 treatments. The increase in Zn^{2+}, Cu^{2+}, and Mn^{2+} ions in sorghum leaves might be due to the availability of micronutrients in the soil and the uptake of minerals from the soil by the plant. Accumulation of micronutrient elements may vary from plant to plant (Broadley et al., 2012). In contrast to our results, Rajabi Dehnavi et al. (2019) found a significant decrease in Zn^{2+}, Cu^{2+}, and Mn^{2+} content in sorghum shoots when sorghum plants were exposed to 100 mM compared to 0 mM NaCl. However, similar to our results, Sezer et al. (2021) found that the accumulation of Zn^{2+}, Cu^{2+}, and Mn^{2+} in sweet corn increases with increasing soil salinity. Also, Rashad and Hussien (2014) reported that irrigating maize crops with saline water caused a decrease in Mn content while increasing Zn content in plant tissue. In summary, increasing the amount of Zn^{2+}, Cu^{2+}, and Mn^{2+} ions in sorghum leaves could be associated with the functions of these elements in plant adaptation processes to improve resilience under soil salinity.

The accumulation of Zn^{2+}, Cu^{2+}, and Mn^{2+} minerals in sorghum leaves varied with the seed priming treatments. (Figure 6d-f). Seed priming with P, MEL, and SA resulted in higher Zn^{2+}, Cu^{2+}, and Mn^{2+} accumulation in sorghum leaves than in hydro-primed seeds. Accordingly, sorghum seeds primed with MEL showed better Zn^{2+}, Cu^{2+}, and Mn^{2+} accumulation than other treatments. In other words, the content of these ions in the seeds primed with MEL increased with increasing soil salinity. However, priming the seed with P increased the accumulation of Zn^{2+}, Cu^{2+}, and Mn^{2+} ions in sorghum up to a soil salinity of 2.5 dS m^{-1}, while it did not show large differences between 2.5, 5.0, and 8.0 dS m^{-1} soil salinities. Differences in micronutrient accumulation among seed priming treatments may be caused by the ability to prime agents for osmotic adjustment of the plant and enhance plant photosynthetic activity under salt stress. Chen et al. (2021) mentioned that the priming agents' effects varied with solution concentration because their various osmotic potentials resulted in differing imbibition rates in salinity stress. Sezer et al. (2021) found that priming sweet corn seeds with 50 μM MEL increased the ability of seeds to absorb micronutrients compared with 100 and 200 μM MEL priming. Also, Hussein et al. (2015) reported that foliar spraying with 100 and 200 ppm SA increased canola plants' Zn^{2+} and Mn^{2+} content compared to 0 ppm SA under saline conditions.

According to PCA analysis, SFW, SDW, SC, CC, Ca^{2+}, Ca^{2+}/Na^+, K^+, K^+/Na^+, and PH vectors were significantly correlated with Salicylic Acid×S_1 and Melatonin×S_1 treatments, indicating that sorghum seeds primed with salicylic acid and melatonin showed better photosynthetic activity and enhanced nutrient uptake ability compared to the other treatments. In other words, the present results showed that at a soil salinity of .27 dS m^{-1}, seed priming with MEL or SA improved photosynthetic activity and translocation of photosynthates compared to other seed priming treatments. AC and Na^+ were significantly and negatively correlated with P × S_4 and SA × S_4 treatments. Also, Zn^{2+}, Cu^{2+}, and Mn^{2+} ions were negatively and significantly related to Melatonin×S_4, suggesting that at a soil salinity of 8.0 dS m^{-1}, seed priming with MEL enhanced the micronutrient uptake ability of sorghum seedlings. Considering all the results, priming sorghum seeds with melatonin could be recommended to improve salt tolerance at the seedling stage of sorghum seedlings.

5 | CONCLUSION

The current study shows fundamental changes in the growth characteristics, photosynthetic activity, and nutrient uptake of seeds treated with hydro, melatonin, salicylic acid, and proline in response to salt stress. Seedling growth characteristics, leaf K^+ and Ca^{2+} contents, and K^+/Na^+ and Ca^{2+}/Na^+ ratios significantly decreased under salinity stress, especially at 5 and 8 dSm^{-1} soil salinities. However, the seeds primed with SA, MEL, and P showed better growth and nutrient status (higher K^+ and Ca^{2+} content, higher K^+/Na^+ and Ca^{2+}/Na^+ ratios, higher Zn^{2+}, Cu^{2+}, and Mn^{2+} content) and better seedling performance than the hydro primed seeds. Taken together, seed priming with MEL significantly improved the salt tolerance of sorghum by reducing Na^+ accumulation and enhancing photosynthetic and nutrient uptake activities under soil salinity conditions. Finally, MEL priming at a concentration of 100 μM could be used as an effective growth regulator against salt stress in the sorghum seedling stage.

AUTHOR CONTRIBUTIONS

Mehmet Sait Kiremit contributed to the investigation, methodology, writing of the original draft, statistical analysis, and software. Elif Öztürk contributed to the investigation and resources, Hakan Arslan helped in the writing-original draft, supervision, and statistical analysis, Bhaskara Anggarda Gathot Subrata, Hasan Akay, and Aigerim Bakirova provided help in investigation and resources. All authors have reviewed the results and approved the final version of the manuscript.

ACKNOWLEDGMENTS

This study did not receive financial support from any institution.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

PEER REVIEW

The peer review history for this article is available in the Supporting Information for this article.

DATA AVAILABILITY STATEMENT

Not applicable.

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How to cite this article: Kiremit, M. S., Öztürk, E., Arslan, H., Subrata, B. A. G., Akay, H., & Bakirova, A. (2024). Effects of melatonin, proline, and salicylic acid on seedling growth, photosynthetic activity, and leaf nutrients of sorghum under salt stress. *Plant Direct*, *8*(3), e574. https://doi.org/10.1002/pld3.574