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Beyond osmotic stress: salinity and drought shape early seedling performance of sweet corn cultivar 'Bonanza' across germination, growth, and physiological responses

Nur Izzatul Maulidah[a], Andi Kurniawan[b], Ikhwan Adhirakha Mullatif[b], Akhmad Rizal Oktafian[a], Agung Nur Muhammad[a], Mohd Fauzihan Karim[c] and Ridho Victory Nazara[d]

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ABSTRACT

Salinity and drought impair maize seedling growth through osmotic and physiological stress. This study evaluated the effects of NaCl and PEG 6000 on early growth of sweet corn (*Zea mays* L.) cv. 'Bonanza'. Two independent completely randomized experiments were conducted using NaCl (0–150 mM) and PEG (0–15%) treatments with five replications. Increasing stress intensity significantly reduced seedling performance. Germination decreased by 44% under salinity and 36% under drought. Plant height declined by up to 30% and 25%, respectively, while chlorophyll content and relative water content also decreased. Root growth traits were reduced by 20–30% under severe stress. However, DPPH scavenging activity increased by 142% under salinity and 121% under drought. Proline accumulation increased by 37.63% and 35.92%, catalase activity by 25.24% and 19.64%, while malondialdehyde increased by 54.67% and 71.05% under salinity and drought stress, respectively. Multivariate analysis showed coordinated reductions in growth and biomass traits alongside enhanced antioxidant responses, suggesting a trade-off between growth maintenance and stress defense. These findings provide physiological insights for early stress screening and support the development of climate-resilient maize management strategies (SDG 2 and 13). Further studies using biostimulants or plant growth regulators are needed to clarify tolerance mechanisms under salinity and drought stress.

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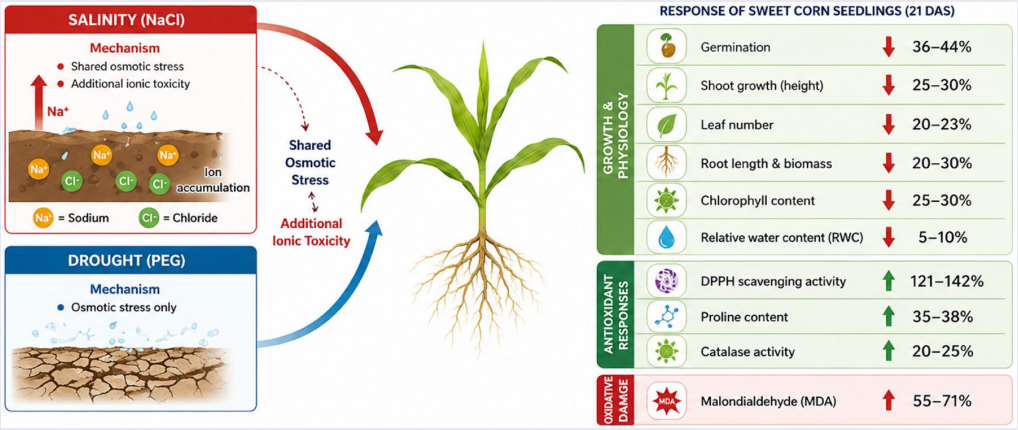
GRAPHICAL ABSTRACT



Introduction

Maize (*Zea mays* L.) is one of the most widely grown cereals worldwide. It is a major component of food, animal feed, and industrial supply chains, especially in developing countries where it serves as a significant source of energy. In terms of harvested area, maize is the third most widely grown crop globally after wheat and rice (Salama, 2019). However, maize productivity is threatened by an increasingly adverse environment, with the growing prevalence of drought stress (Argentel-Martínez et al., 2024) and soil salinity (Fatima et al., 2025), driven by climate change. This problem is especially pronounced during the early stages of crop establishment, when stress-associated disruptions in ionic balance reduce yields (Hu et al., 2022).

The osmotic effects of salinity and drought are often difficult to distinguish because both impose similar constraints on plant water relations. Nevertheless, they differ markedly in their other physiological effects on plants. Water stress affects plants by reducing soil water potential, thereby limiting root water uptake, relative water content (RWC), cell expansion, stomatal conductance, and photosynthesis (Seleiman et al., 2021). Osmotic stress due to salinity, by contrast, initially operates through the excess ionic content of the soil solution (Na^+ and Cl^-), followed by inhibition of Ca^{2+} uptake, disruption of K^+ transport, impairment of enzymatic protein function, disruption of membrane integrity, or the resultant overproduction of reactive oxygen species (ROS) (Hosseini et al., 2025; Ikram et al., 2025; Kumar et al., 2024). The osmotic-ionic nature of salinity stress complicates the analysis of plant physiological responses, as growth inhibition may stem from either osmotic or ionic stress.

To separate the osmotic stress component from the ionic component, the non-penetrating osmotic agent polyethylene glycol (PEG) has been widely used in controlled experiments to simulate osmotic stress. Its application reduces the water potential of the growth medium without inducing ionic toxicity (Sajid et al., 2025). As a case of maize seedlings, the application of PEG to generate osmotic stress in maize seedlings was indicated to reduce germination, seedling growth, relative water content (RWC), while concurrently promoting osmolyte accumulation and activating antioxidant systems. In maize, salinity has been reported to reduce stomatal conductance, transpiration, leaf area, biomass, chlorophyll content, and inhibit nutrient uptake (K, Mg, P), in addition to increasing near-infrared (NIR) leaf reflectance due to mineral nutritional imbalances, and disturbing ion homeostasis and effects that severely impair performance at salinity levels above 3 dS m^{-1}. Nonetheless, increasing antioxidant activity, enhancing membrane stability, and optimizing K^+/Na^+ regulation have been shown to help plants mitigate salinity-induced toxicity (Alamer et al., 2022; Vennam et al., 2024). Recent studies have further highlighted critical components mediating maize salt tolerance, including stress signaling, antioxidant regulation, hormone regulation, and ion transport (Fatima et al., 2025; He et al., 2025; Pienaar et al., 2025).

Early seedling growth is a critical phase that determines maize performance under abiotic stress, yet the effects of drought and salinity are rarely evaluated side-by-side using comparable measurements under controlled conditions. This limits the identification of physiological traits that reliably distinguish osmotic from salt-specific stress responses. In this study, drought and salinity were imposed independently under controlled conditions in parallel to evaluate their effects on germination, growth, and physiological traits of sweet corn cultivar 'Bonanza'; therefore, any cross-stress comparisons are descriptive rather than statistically tested contrasts, providing a quantitative basis for early stress characterization and tolerance screening. This study provides critical insights into stress-specific and shared physiological responses in maize, enabling the development of precise, level-specific agronomic strategies to mitigate the impacts of drought and salinity under changing environmental conditions.

Materials and methods

Experimental design

This study was conducted in May 2025 in the greenhouse of the Faculty of Agriculture and Animal Science, University of Muhammadiyah Malang, East Java, Indonesia (667 m elevation; 17–27 °C; 74–82% relative humidity). Two independent one-factor experiments were conducted under a completely randomized design (CRD): (i) salinity (NaCl) and (ii) PEG-induced osmotic stress. Salt stress consisted of four levels: S0 = 0 mM, S1 = 50 mM, S2 = 100 mM, and S3 = 150 mM NaCl, whereas drought stress was induced using PEG 6000 at D0 = 0%, D1 = 5%, D2 = 10%, and D3 = 15%. Within each experiment (NaCl or PEG), each treatment level was replicated five times, with 20 seeds per replicate, and each replicate was considered as one experimental unit. Seeds were sown individually in seedling trays filled with organic soil medium consisting of topsoil:compost (2:1) v/v, and germination was assessed at 2, 4, and 6 days after sowing (DAS), followed by measurements of morphological and physiological parameters. Because the NaCl and PEG experiments were conducted separately with different stress scales, no inferential statistical comparisons were performed between stress types.

Plant material

Sweet corn (*Zea mays* L.) cultivar 'Bonanza' seeds (PT East West Seed Indonesia/Panah Merah; Indonesian Ministry of Agriculture Decree No. 2071/Kpts/SR.120/5/2009) were used in this study.

Plant growth conditions and stress treatments

Before sowing, sweet corn seeds were surface-sterilized with 1% (v/v) sodium hypochlorite for 5 min, rinsed thoroughly with distilled water, and pre-soaked for 4 h. Stress treatments were applied at the time of sowing by saturating the soil medium to field capacity with NaCl or PEG 6000 solutions corresponding to the respective treatment levels (S0-S3 and D0-D3), where field capacity was defined as the point at which the medium was fully saturated without free drainage. Approximately 10 mL of solution per tray was applied to reach field capacity. In contrast, control media were saturated with distilled water. Plants were grown in a controlled-environment greenhouse maintained at 25 ± 2 °C, with a 16/8 h light/dark photoperiod, a photosynthetic photon flux density (PPFD) of 300–400 µmol m^{-2} s^{-1}, and relative humidity of 60–70%. Throughout the experiment, irrigation was performed every 2–3 days using the same NaCl or PEG solutions at the corresponding treatment concentrations and equal volumes to maintain consistent stress conditions, whereas control plants received distilled water. A half-strength Hoagland nutrient solution was applied weekly to avoid nutrient deficiencies. NaCl (analytical grade, Merck, Germany) and PEG 6000 (Sigma-Aldrich, USA) were used. Seedlings were grown in plastic trays (cell size: 5 × 5 × 10 cm). The experiment was conducted for 21 days after sowing. This setup ensured stable and uniform exposure of sweet corn cultivar 'Bonanza' seedlings to salinity and drought conditions throughout germination and early growth.

Chlorophyll content

Total chlorophyll content was determined following the spectrophotometric method of Lichtenthaler (1987) with minor modifications. Approximately 0.10 g of fresh, fully expanded leaf tissue was weighed and homogenized in 95% (v/v) ethanol. The homogenate was transferred into capped tubes, shaken for 30 min to ensure complete pigment extraction, then centrifuged at 10,000 × g for 10 min to obtain a clear supernatant. The absorbance of the resulting extract was measured at 664 nm and 648 nm using 95% ethanol as the blank. These wavelengths correspond to absorption maxima of chlorophyll a and b in ethanol, respectively. Total chlorophyll concentration (mg L^{-1}) was calculated using Lichtenthaler's linear equation:

$$\text{Total chlorophyll} = (5.24 \text{ x OD664}) + (22.24 \text{ x D648})$$

Antioxidant activity (DPPH radical scavenging assay)

Antioxidant capacity was measured using the DPPH free radical scavenging assay. Approximately 0.20 g of fresh leaf tissue was extracted in 80% methanol (1:20, w/v) for 1 h at 4 °C and centrifuged at 10,000 × g for 10 min. An aliquot of the extract (0.10 mL) was mixed with 3.90 mL of freshly prepared 0.1 mM DPPH solution, vortexed, and incubated in the dark at room temperature for 30 min. Absorbance was measured at 517 nm, and the following formula was used to compute the percentage of antioxidant radical scavenging activity (Valko et al., 2007):

$$\%\text{antioxidant activity} = \frac{\text{Ac} \quad \text{As}}{\text{Ac}} \text{x} 100$$

where Ac = absorbance of the control reaction; As = absorbance of the sample

Proline content

Proline accumulation was quantified following the colorimetric method described by Bates et al. (1973). Fresh leaf samples (0.5 g) were immediately frozen in liquid nitrogen and pulverized to a fine powder using a mortar and pestle. The powder was subsequently homogenized in 10 mL of 3% sulfosalicylic acid, and the resulting suspension was passed through Whatman No. 1 filter paper to obtain a clear filtrate. An aliquot of 2 mL from the filtrate was combined with equal volumes (2 mL each) of ninhydrin reagent prepared by dissolving 1.25 g of ninhydrin in a mixture of 30 mL glacial acetic acid and 20 mL of 6 M phosphoric acid and glacial acetic acid in a reaction tube. The mixture was incubated in a boiling water bath at 100 °C for 60 min and subsequently quenched by immersion in an ice bath. Following cooling, 4 mL of toluene was added, and the mixture was vigorously vortexed for 30 seconds to facilitate phase separation. The chromophore partitioned into the upper toluene phase, forming a distinct red-colored layer, whose absorbance was recorded spectrophotometrically at 520 nm to determine proline concentration.

Catalase activity

Catalase activity was determined spectrophotometrically according to the method of Aebi (1984), based on the rate of hydrogen peroxide (H_2O_2) decomposition. Fresh leaf tissue (0.5 g) was homogenized under liquid nitrogen and extracted in 5 mL of ice-cold 50 mM potassium phosphate buffer (pH 7.0) containing 1 mM ethylenediaminetetraacetic acid (EDTA) and 1% (w/v) polyvinylpyrrolidone (PVP). The homogenate was centrifuged at 12,000 × g for 20 min at 4 °C, and the resulting supernatant was collected as the crude enzyme extract for subsequent analysis. The reaction mixture consisted of 2.9 mL of 50 mM potassium phosphate buffer (pH 7.0) supplemented with 30 mM H_2O_2, to which 0.1 mL of the enzyme extract was added to initiate the reaction. The decomposition of H_2O_2 was monitored continuously by recording the decline in absorbance at 240 nm over a 3 min interval using a UV spectrophotometer. Catalase activity

was calculated using the molar extinction coefficient of H_2O_2 ($\varepsilon = 39.4\,mM^{-1}cm^{-1}$) and expressed as micromoles of H_2O_2 decomposed per minute per milligram of protein (μmol H_2O_2 $min^{-1}mg^{-1}$ protein).

Lipid peroxidation (malondialdehyde (MDA))

The lipid peroxidation product MDA was quantified by following the method of Gechev et al. (2013). Briefly, 50 mg of leaf tissue was homogenized in 1 mL 0.25% thiobarbituric acid (TBA) dissolved in 10% trichloroacetic acid (TCA). The extract was heated to 95 °C for 15 min and then quickly chilled on ice. The extracted sample was then centrifuged for 10 min at 13,800x g, and the supernatant was collected. The absorbance at 532 and 600 nm was measured, and the equation described by Taulavuori et al. (2001) was used to quantify MDA.

Relative water content (RWC)

Relative water content (RWC) was determined following the classical method of Barrs and Weatherley (1962), with adjustments for leaf sampling under stress conditions. Fully expanded leaves from randomly selected seedlings were excised and immediately weighed to obtain the fresh weight (FW), ensuring minimal water loss during handling. The leaf samples were then floated on sterilized deionized water in the dark for 8 hours, allowing tissues to rehydrate to full turgidity without photosynthetic water loss. After rehydration, samples were gently blotted to remove surface moisture and weighed to record the turgid weight (TW). The tissues were subsequently oven-dried at 80 °C for 48 hours until constant mass was achieved, after which the dry weight (DW) was recorded. Relative water content was calculated using the standard formula:

$$RWC(\%) = \left(\frac{FW\ \ DW}{TW\ \ DW} \right) \times 100$$

Data analysis

Data were analyzed using RStudio version 2024.09.1 + 394 (Posit Software, Boston, MA, USA). Salinity (NaCl) and PEG-induced osmotic stress experiments were analyzed separately; therefore, all statistical tests were conducted independently for each stress type without fitting a combined model including 'stress type' as a factor. Within each experiment, treatment effects were evaluated using one-way analysis of variance (ANOVA), followed by Tukey's honestly significant difference (HSD) test at a significance level of $p < 0.05$. These analyses were performed using the *stats* and *agricolae* packages. Principal component analysis (PCA) was conducted using the *prcomp()* function and visualized with the *factoextra* package. Pearson correlation coefficients were calculated using the *cor()* function and visualized with the *corrplot* package. Heatmaps with hierarchical clustering were generated using the *pheatmap* package. All graphical outputs were produced using *ggplot2*.

Results and discussion

Germination sensitivity to osmotic and ionic stressors

Results for NaCl and PEG are presented in parallel; however, because the experiments were independent, cross-stress comparisons were descriptive and were not statistically tested. Germination increased steadily from 2 to 6 days after sowing, but both salinity and drought treatments delayed this process relative to the control (Figure 1). Germination at 2 DAS did not differ significantly between 50 mM NaCl and the control (0 mM NaCl), indicating that moderate salinity had a negligible effect on germination. The highest salinity, 150 mM NaCl, reduced germination to 14%, significantly lower than all other treatment levels, indicating strong inhibitory effects at this early stage. Similarly, at 4 and 6 DAS, the control reached 75%, whereas 150 mM NaCl reached 42%, representing a 44% decrease relative to the control. A similar dose-dependent response was observed under drought stress. The control (0%

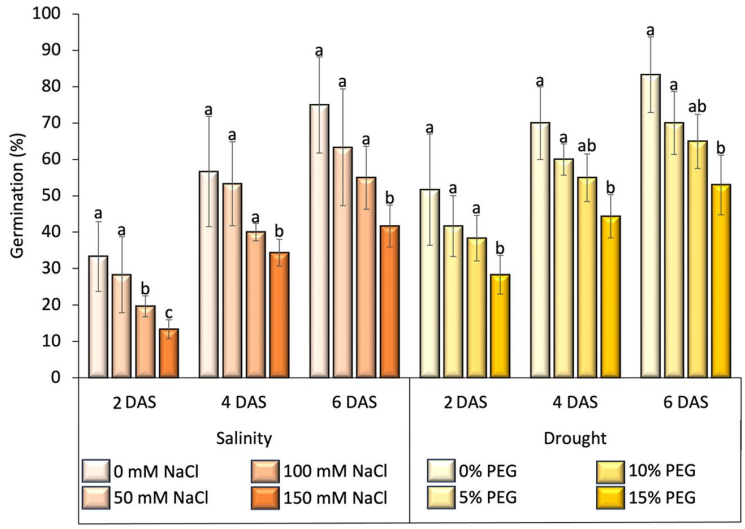


Figure 1. Germination percentage of sweet corn under salinity and drought stress. (A) Salinity stress and (B) drought stress. Values are means ± SD (n = 5). Different letters within each observation day indicate significant differences among treatments according to Tukey's HSD test ($p < 0.05$). DAS, days after sowing.

PEG) reached 83% germination at 6 DAS, whereas the most severe drought treatment (15% PEG) reached 53%, representing a 36% reduction relative to the control. Overall, these results indicated that increasing NaCl (50–150 mM) and PEG (5–15%) levels significantly limited germination at this early stage.

Our observations of reduced germination are consistent with previous studies demonstrating that both salinity and drought stress inhibit seed water uptake, delay radicle emergence, and reduce seed vigor due to osmotic and oxidative stress (Kurniawan et al., 2025). Increasing NaCl concentration progressively inhibited germination, likely due to combined osmotic stress and ion toxicity associated with Na^+ and Cl^-, which can disrupt membrane integrity and enzymatic processes essential for germination (Fatima et al., 2025). Similarly, drought stress lowered external water potential, thereby reducing imbibition rates, slowed metabolic and enzymatic activities, and ultimately reduced germination performance (Seleiman et al., 2021). These findings are consistent with reports in wheat, where drought stress has been shown to inhibit radicle emergence and leads to variability in germination (Mahpara et al., 2022).

Growth suppression patterns under salt and drought conditions

Our results demonstrated that both plant height and leaf number increased from 7 to 21 DAS across all treatments, whereas salinity and drought significantly restricted vegetative growth relative to the control. Under salinity, at 7 DAS, plant height at 50 mM NaCl was similar to the control (0 mM NaCl), with only an 8–10% reduction. In contrast, 150 mM NaCl significantly reduced shoot elongation at all growth stages, and by 21 DAS shoot length reached 16 cm, compared to 22 cm for the control, representing a 27–30% reduction. Shoot elongation at 100 mM NaCl was intermediate, with a 12–18% reduction, indicating a clear dose-dependent inhibition. A similar trend was observed under drought stress. Plants grown without PEG (0%) reached 24 cm by 21 DAS, while those subjected to 15% PEG reached 18 cm, representing a 25% reduction. Shoot elongation decreased by 12–15% under moderate drought (10% PEG) and by 5–7% under mild drought (5% PEG), confirming a graded osmotic effect on shoot development. Leaf number followed a similar pattern. At 21 DAS, control plants had 4.8 leaves, whereas plants grown under 150 mM NaCl had 3.7 leaves, representing a 23% reduction. At 100 mM NaCl, leaf number decreased by 12–15%, while 50 mM NaCl reduced it by 6–8%. A similar reduction was observed under drought stress. Plants under 15% PEG developed 4 leaves compared to 5 in the control, representing a 20% reduction, while 5–10% PEG resulted in a 5–15% reduction.

The reduced growth of the seedlings, as reflected in decreases in height and leaf number, indicated impaired post-emergence development. Exposure to high salinity (150 mM NaCl) impaired shoot growth, likely due to ion-related disturbances commonly reported under salinity, including altered K^+/Na^+ homeostasis, disruption of chloroplast membranes, and reduced carbon assimilation, as reported in previous studies (Vennam et al., 2024). Likewise, increasing PEG (5–15%) reduced turgor pressure and slowed leaf and meristem growth. This resulted in limited leaf expansion and shorter internodes, consistent with findings from research on drought stress, which demonstrating that reduced water availability inhibits leaf growth by limiting cell wall (Seleiman et al., 2021). Our results indicated that vegetative growth is highly susceptible to osmotic limitation under both stress treatments and may additionally be affected by ion-related processes under salinity, both of which reduce structural and metabolic activities essential for shoot development. As shown in Figure 2, plant height and leaf number differed significantly among treatments at 7, 14, and 21 DAS under both salinity and drought stress.

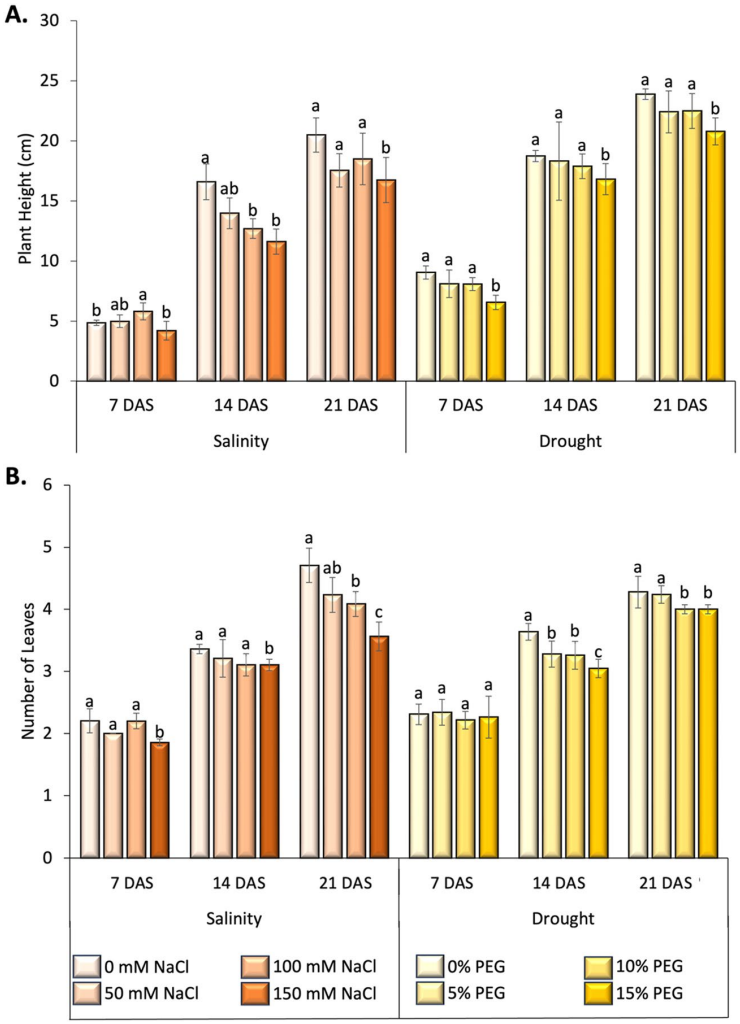


Figure 2. Plant height and leaf number of sweet corn under salinity and drought stress. (A) Plant height at 7, 14, and 21 DAS and (B) leaf number at 7, 14, and 21 DAS. Values are means ± SD (n = 5). Different letters within each observation day indicate significant differences among treatments according to Tukey's HSD test ($p < 0.05$). DAS, days after sowing.

Physiological impairment driven by salinity and drought

Our results indicated that as salinity and drought stress increase, all measured physiological parameters decreased (Figure 3). Total chlorophyll content gradually declined from mild to severe conditions. At 50 mM NaCl and 5% PEG, the reduction in total chlorophyll content was relatively small, approximately 3–5% compared to the control. However, at 100 mM NaCl and 10% PEG, the decrease was more pronounced, reaching 10–15%. Under the most stressful conditions (150 mM NaCl and 15% PEG), the largest reduction of approximately 25–30% was observed (Figure 3(A)). Relative water content showed a similar pattern. Mild concentrations of 50 mM NaCl or 5% PEG resulted in small decreased of approximately 1–2%. At intermediate concentrations of 100 mM NaCl and 10% PEG, RWC decreased by 2–3%. In the most stressful conditions of 150 mM NaCl or 15% PEG, RWC decreased by 5–10%, indicating substantial tissue dehydration (Figure 3(B)). A similar trend was observed for antioxidant activity, with reductions of 5–8% under mild stress (50 mM NaCl; 5% PEG), 10–15% under moderate stress (100 mM NaCl; 10% PEG), and the greatest decline under severe stress (150 mM NaCl; 15% PEG).

Decreases in chlorophyll content, relative water content, and antioxidant activity are consistent with known physiological disturbances in plants under salt stress and drought. Under salinity, the stronger decline in chlorophyll may reflect an additional ion-related component beyond osmotic stress, as ionic imbalance has been reported to disrupt chloroplast structure and pigment stability. High salinity reduced chlorophyll content, thereby impairing photosynthetic capacity (Wang et al., 2024a). Drought reduced leaf water potential and induced stomatal closure, limiting gas exchange and reducing transpiration. This reduced relative water content and restricted carbon assimilation (Burlett et al., 2025). The consistent decline across all measured parameters indicated a coordinated physiological stress response. These findings are consistent with a recent study demonstrating that both drought and salinity can elicit similar stress syndromes, including declines in chlorophyll content and water status (Qiao et al., 2024).

Antioxidant responses of plants to salinity and drought stress

Our results indicated that increasing salinity and drought stress stimulated both enzymatic and non-enzymatic antioxidant responses in plants (Figure 4). DPPH radical scavenging activity showed a

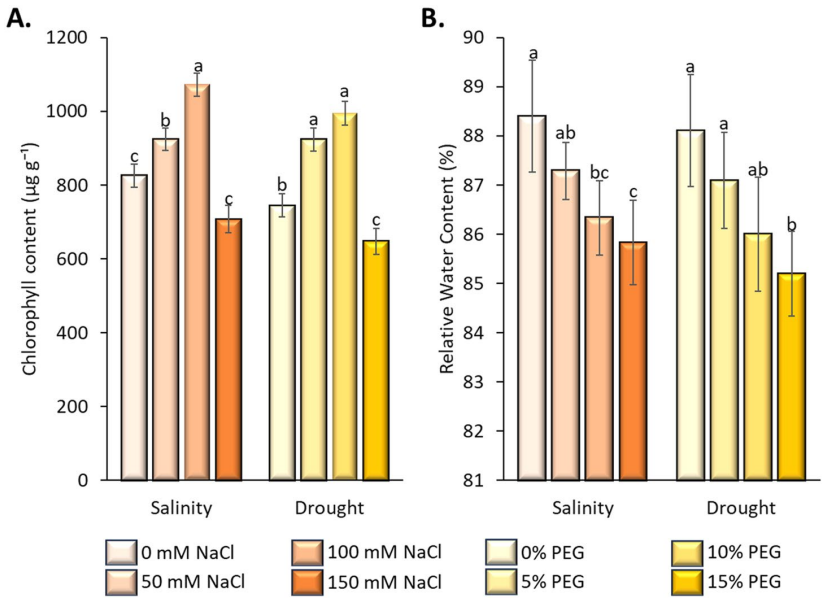


Figure 3. Physiological and antioxidant responses of maize under salinity and drought stress. (A) Total chlorophyll content, and (B) relative water content. Error bars represent standard deviations, and different letters indicate significant differences according to Tukey's test at $p < 0.05$.

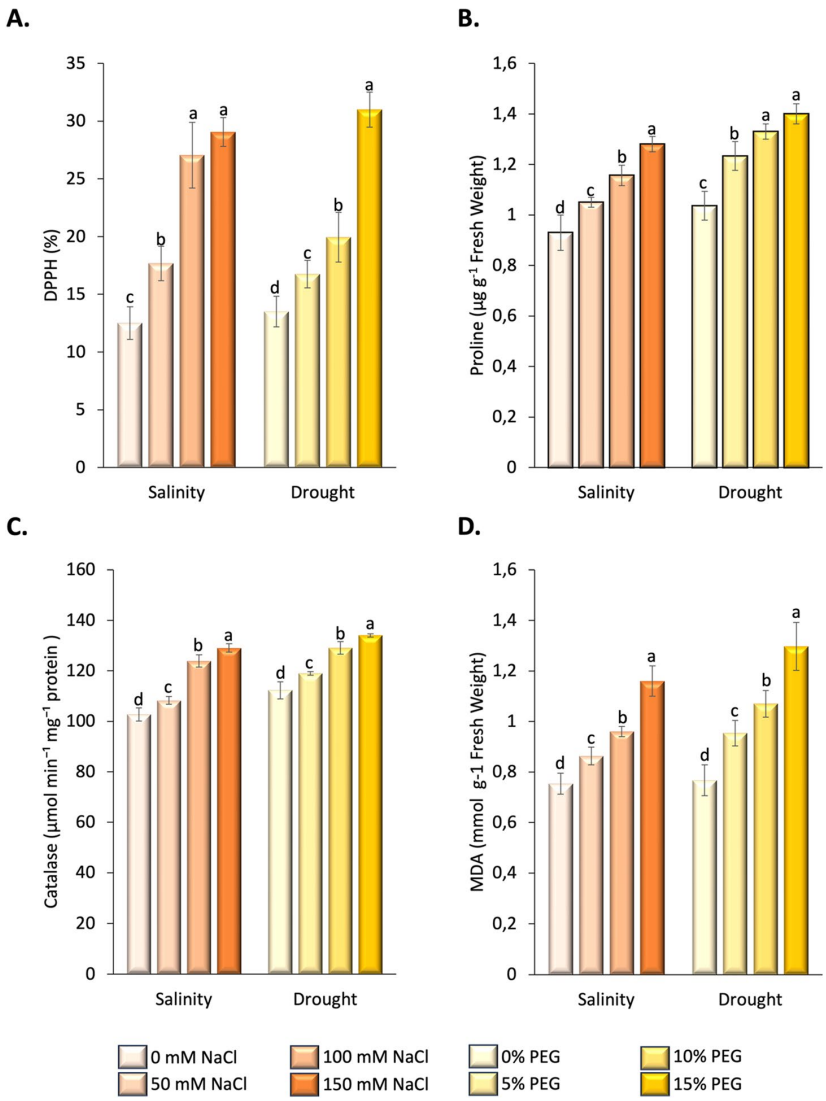


Figure 4. Antioxidant and oxidative stress responses of maize seedlings under salinity and drought stress. (A) DPPH radical scavenging activity, (B) proline content, (C) catalase (CAT) activity, and (D) malondialdehyde (MDA) content. Error bars represent standard deviations. Different letters above the bars indicate significant differences among treatments according to Tukey's test at $p < 0.05$.

clear increasing trend under stress conditions. Under salinity, DPPH increased from approximately 12% in the control to about 18% at 50 mM NaCl, then increased sharply to around 27–29% at 100–150 mM NaCl. Under drought condition, the increase was more gradual, from nearly 14% in the control to about 17% at 5% PEG and 20% at 10% PEG, before reaching approximately 31% at 15% PEG (Figure 4(A)). Proline accumulation exhibited a clear progressive response to increasing stress intensity (Figure 4(B)). Under salinity, proline content increased by 12.90%, 24.73%, and 37.63% at 50, 100, and 150 mM NaCl, respectively, relative to the control. Under drought, proline content increased by 20.39%, 29.13%, and 35.92% at 5, 10, and 15% PEG, respectively. These results indicated that drought induced a stronger osmotic adjustment response at low to moderate stress levels, whereas both stresses produced comparable increases under severe conditions. Catalase activity followed a similar increasing trend (Figure 4(C)). Under salinity, catalase activity increased by 4.85%, 20.39%, and 25.24% with increasing NaCl concentration. Under drought, catalase activity increased by 6.25%, 15.18%, and 19.64% at 5, 10, and 15% PEG,

respectively. These findings indicated that both salinity and drought activated enzymatic antioxidant defense systems, with salinity exhibiting a slightly greater increase at higher stress levels. MDA content, a marker of lipid peroxidation and membrane damage, increased markedly with stress severity (Figure 4(D)). Under salinity, MDA content increased by 14.67%, 28.00%, and 54.67%, whereas under drought it increased by 25.00%, 40.79%, and 71.05% across corresponding stress levels. The greater increase under drought suggested more severe oxidative membrane damage than under salinity.

Increasing salinity and drought stress induced a coordinated antioxidant response, reflected by the enhancement of both non-enzymatic and enzymatic defense systems (Fatima et al., 2025). The increase in DPPH radical scavenging activity indicated an upregulation of non-enzymatic antioxidants, suggesting that plants initially responded to elevate oxidative pressure by enhancing radical-scavenging capacity (Gulcin & Alwasel, 2023). This response is consistent with the disruption of cellular redox homeostasis under osmotic stress conditions, which promoted the accumulation of ROS and activates antioxidant pathways as a primary defense mechanism (Arif et al., 2020). However, despite this increase, the antioxidant response appeared insufficient to fully counterbalance ROS overproduction under severe stress conditions (Vennam et al., 2024). Under prolonged or high-intensity stress, antioxidant systems may become constrained by metabolic limitations, particularly due to reduced carbon assimilation and impaired secondary metabolite biosynthesis (Seleiman et al., 2021). As drought and salinity reduced photosynthetic efficiency and energy availability, the synthesis and regeneration of antioxidant compounds may have been restricted, potentially leading to an imbalance between ROS production and scavenging capacity (Azeem et al., 2023).

The concurrent increase in catalase activity further supported the activation of enzymatic antioxidant defense, specifically targeting hydrogen peroxide detoxification (Jomova et al., 2024). This indicated that both stress conditions triggered a multi-layered antioxidant response involving complementary pathways. In addition, the significant accumulation of proline reinforces this adaptive mechanism, as proline contributes to osmotic adjustment, redox buffering, and membrane stabilization under stress conditions (Per et al., 2017). Nevertheless, the substantial increase in MDA content indicated that antioxidant activation was not sufficient to prevent oxidative damage (Morales & Munné-Bosch, 2019). MDA accumulation reflected lipid peroxidation and membrane destabilization, suggesting that ROS levels exceeded the detoxification capacity of the antioxidant system. This finding suggested that drought imposed a stronger oxidative burden than salinity, likely due to its direct limitation on water availability and carbon metabolism. These findings indicated that although salinity and drought activated antioxidant defenses as protective strategies, the balance between ROS production and detoxification shifted toward oxidative damage at higher stress intensities.

Stress-induced reductions in root morphology and biomass

Salinity and drought stress consistently reduced root length and biomass, as depicted in Figure 5. Root length decreased progressively with increasing stress intensity (Figure 5(A)). Under mild stress conditions (50 mM NaCl or 5% PEG), the reduction was approximately 5–7% compared to the control. Root length further decreased by 10–15% at 100 mM NaCl or 10% PEG, whereas the highest stress levels (150 mM NaCl and 15% PEG) resulted in a 20–30% reduction, indicating strong inhibition of root elongation. A similar pattern was observed for fresh plant weight (Figure 5(B)): minor reductions of approximately 4–6% under mild stress; at 100 mM NaCl and 10% PEG, the reduction was 10–12%; and at the highest salinity and drought levels, the reduction was 20–25%. Plant dry weight followed the same pattern, remaining relatively stable under mild stress but decreasing by 10–15% under moderate stress and by 20–25% under 150 mM NaCl and 15% PEG (Figure 5(C)).

These patterns reflect well-known plant responses to salinity and drought, as indicated by reductions in root length, biomass, and overall growth. These responses reduced water uptake and turgor, thereby limiting nutrient availability and root development. Salinity likely constrained root elongation through osmotic stress and a possible ion-related component, which may disrupt ionic homeostasis and the activity of enzymes involved in cell expansion, consistent with reported reductions in root biomass under NaCl (Pandit et al., 2024). Drought reduced external water potential, limiting cell elongation and meristem activity while diverting carbohydrates away from roots, thereby reducing fresh and dry weights of maize (Nour et al., 2024). Although antioxidant capacity increased under stress, ROS accumulation may still exceed scavenging capacity under severe conditions, leading to oxidative

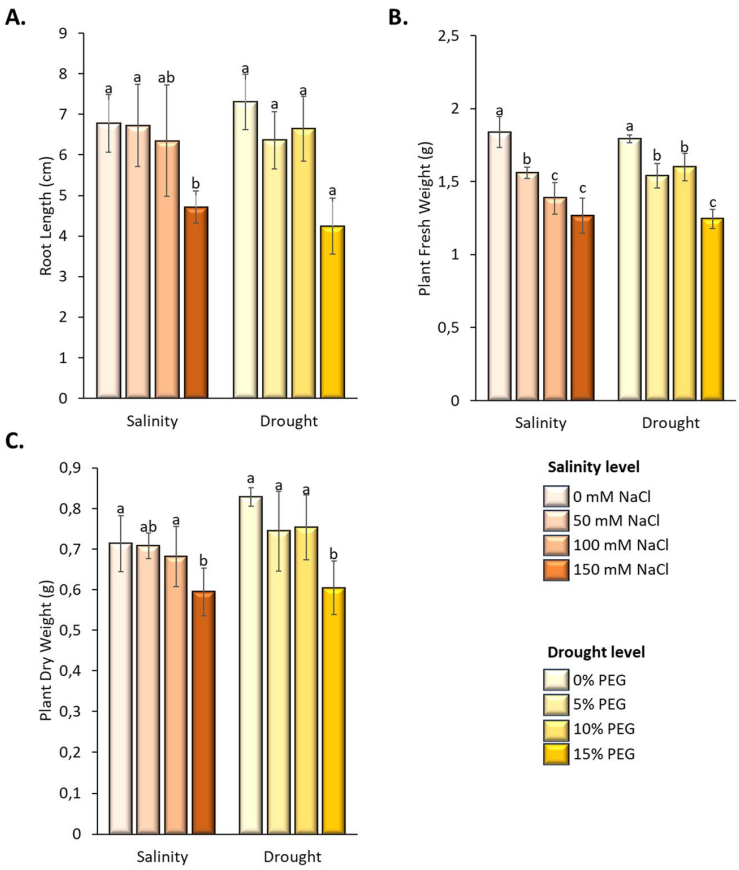


Figure 5. Root morphological and biomass traits of maize under salinity and drought stress. (A) Root length, (B) plant fresh weight, and (C) plant dry weight. Error bars represent standard deviations, and different letters indicate significant differences according to Tukey's test at $p < 0.05$.

damage in root tissues (Hosseini et al., 2025). Overall, root growth and biomass declined with increasing salinity and drought stress, supporting the role of osmotic stress as a primary driver of early growth inhibition, with salinity effects potentially intensified by an additional ion-related component (Arif et al., 2020).

Trait interrelationships under salinity and drought stress

Our results indicated that salinity and drought stress produced broadly similar, although not identical, correlation patterns among morphological, physiological, and biochemical traits (Figure 6). Under salinity stress (Figure 6(A)), growth-related traits, including plant height, leaf number, germination, root length, root weight, fresh weight, and dry weight, were strongly and positively correlated with one another (generally r = 0.68–1.00), indicating coordinated variation among plant growth attributes. Relative water content (RWC) was also positively associated with most of these traits (r = 0.61–0.99). In contrast, DPPH, proline, CAT, and MDA were strongly negatively correlated with growth-related traits and RWC; DPPH was negatively correlated with plant height (r = −0.73), fresh weight (r = −0.96), and RWC (r = −0.99). Similarly, proline, CAT, and MDA showed strong negative associations with most growth parameters, while remaining strongly positively correlated with each other (r = 0.87–0.99), suggesting a tightly coordinated biochemical stress response under saline conditions. Chlorophyll content showed weaker and less consistent associations, showing only moderate positive correlations with dry weight (r = 0.57) and weak or near-zero correlations with plant height, germination, RWC, and DPPH (r = 0.02–0.22).

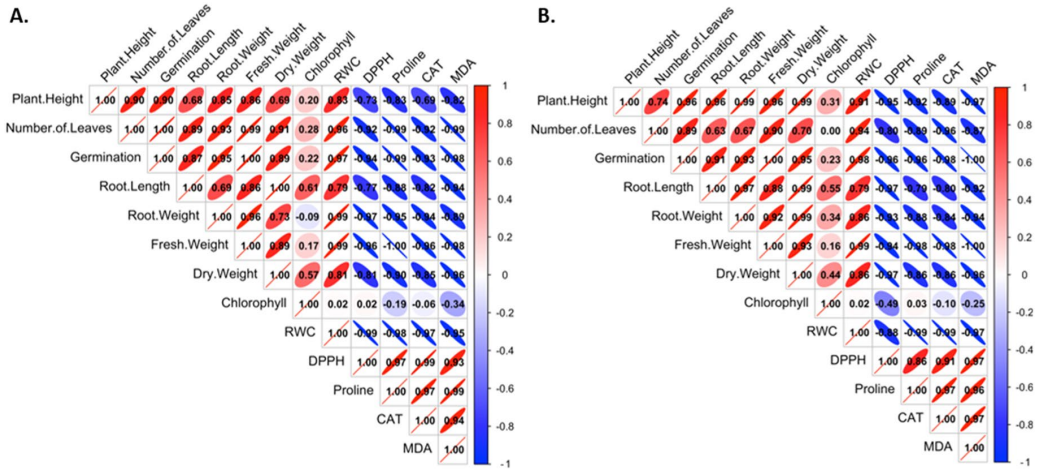


Figure 6. Pearson correlation matrix of physiological, morphological, and biochemical traits of maize under salinity and drought stress. (A) Under salinity stress and (B) under drought stress. The color scale represents correlation coefficients ranging from −1 to 1, where red indicates strong positive correlations and blue indicates negative correlations. The ellipse shapesdepict both the direction and strength of the correlations: elongated, narrow ellipses indicate stronger correlations (positive when slanted upward, negative when slanted downward), whereas circular shapes indicate weak or no correlation.

Under drought stress (Figure 6(B)), a comparable overall pattern was observed, but the negative relationships between stress-related biochemical traits and growth attributes were generally stronger. Growth-related traits again showed strong positive correlations with each other, with many coefficients exceeding 0.90, while RWC remained positively associated with most growth parameters (r = 0.79–0.99). In contrast, DPPH, proline, CAT, and MDA were strongly negatively correlated with plant growth and water status, with coefficients ranging approximately from −0.79 to −1.00. These biochemical traits were also strongly and positively correlated among themselves (r = 0.86–0.97), indicating that antioxidant and oxidative stress markers increased in parallel under drought condition. As in the salinity treatment, chlorophyll showed relatively weak correlations with most variables (r = 0.00–0.55), suggesting that it was less tightly linked to the coordinated growth-stress response. Overall, the results indicated that better growth performance and water status were associated with lower accumulation of stress-related biochemical markers, whereas enhanced antioxidant and oxidative stress responses were coupled with reduced growth under both salinity and drought stress.

The strong positive correlations between growth traits under both salinity and drought conditions indicated coordinate suppression of water uptake, cellular expansion, nutrient transport, and photosynthesis, resulting in simultaneous reductions in height, biomass, and root development, consistent with patterns reported in cereals (Seleiman et al., 2021). The close relationship between antioxidant activity (DPPH) and growth suggests a role for ROS detoxification in preserving cellular and growth stability under stress conditions (Wang et al., 2024b). However, the weak relationships between chlorophyll content and germination or RWC suggested that other mechanisms may mediate reductions in pigment content and initial seed responses.

Multivariate response patterns under salinity and drought

PCA revealed clear multivariate response patterns of sweet corn seedlings under both salinity and drought stress, as illustrated in Figures 7 and 8. The first principal component accounted for the largest proportion of variability under salinity and drought stress, at 82% and 83.7%, respectively (Figure 7(A,B)). Dim1 explained most of the variation and was primarily associated with growth- and biomass-related traits, including root length, fresh and dry weight, plant height, germination, leaf number, RWC, and DPPH activity. In contrast, chlorophyll contributed more strongly to Dim2, indicating a response partly distinct from other traits.

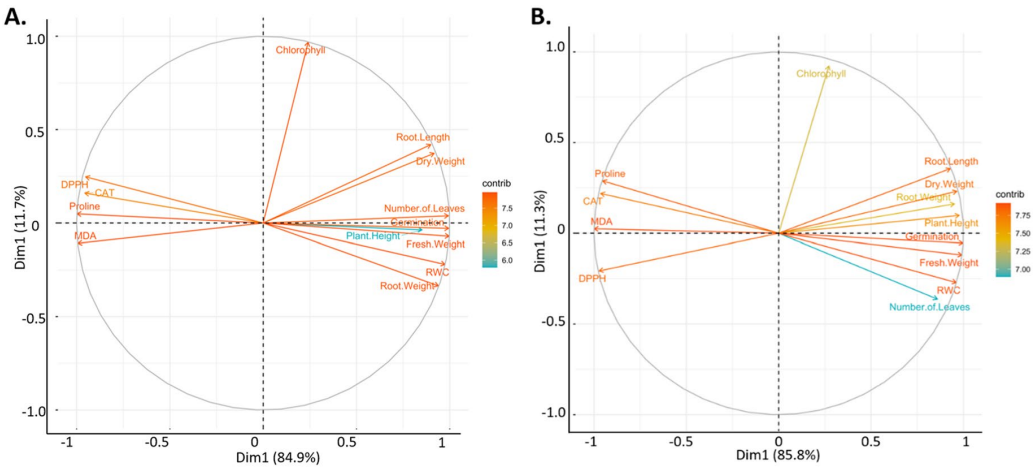


Figure 7. Principal Component Analysis (PCA) variable contribution biplot. Physiological and growth traits to PC1 and PC2 under (A) salinity stress and (B) drought stress. Vector colors represent the contribution of each trait to the principal components, with warmer tones (orange–red) indicating higher contributions and cooler tones (yellow-blue) indicating lower contributions.

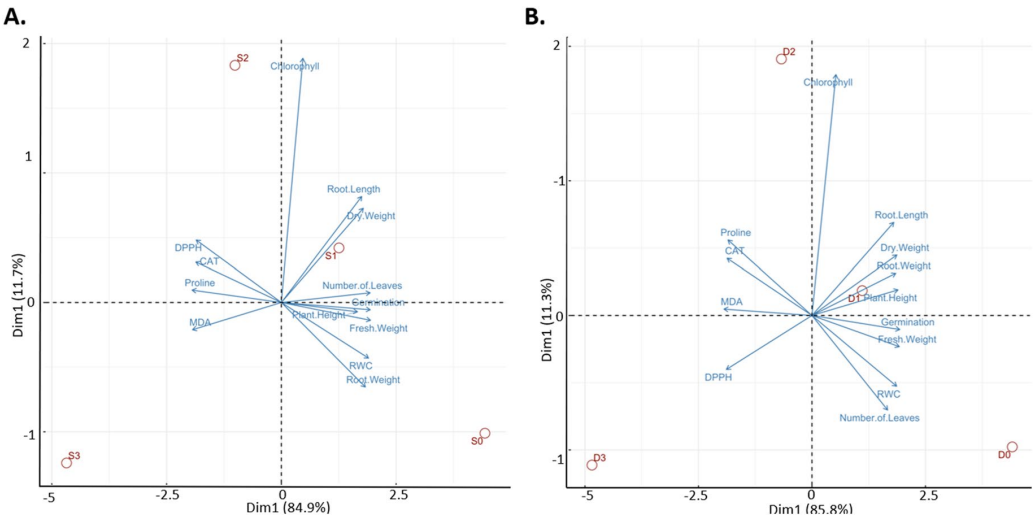


Figure 8. PCA observation biplot illustrating the multivariate clustering of treatments under (A) salinity stress (0–150 mM NaCl) and (B) drought stress (0–15% PEG), based on combined physiological and morphological responses. Arrows represent trait loadings, and sample positions indicate treatment clustering patterns based on similarities across variables.

Treatment ordination showed a clear dose-dependent along Dim1, with control treatments located at the positive end, severe-stress treatments at the negative end, and intermediate treatments positioned between them. Separation along Dim2 was influenced mainly by chlorophyll. Overall, PCA indicated that most traits responded in a coordinated manner to increasing stress intensity, particularly growth, biomass, water status, and DPPH activity. Chlorophyll showed a somewhat more independent pattern, suggesting that pigment responses do not fully parallel other traits under stress conditions. The increasing separation between treatments (S0-S3 and D0-D3) along the principal component axes is consistent with reports that increasing abiotic stress drives multivariate divergence from the control, reflecting cumulative effects on water status, photosynthesis, and redox homeostasis (Hosseini et al., 2025). These results indicated that PCA effectively summarized the major multivariate response patterns, with Dim1 representing coordinated variation in growth and biomass-related traits and Dim2 capturing additional variation associated with chlorophyll.

Although PCA and correlation analyses revealed coordinated physiological and biochemical responses to salinity stress, a key limitation of this study is that ion accumulation was not directly measured. Consequently, mechanisms related to Na^+ toxicity, K^+ depletion, and K^+/Na^+ imbalance which are commonly implicated in salinity-induced growth inhibition remain inferred from the observed response patterns and supporting literature rather than directly demonstrated in this study. Future studies incorporating ion profiling or tissue-level elemental analyses would provide a more mechanistic understanding of the ionic component of salinity stress in sweet corn seedlings.

Heatmap-based clustering of physiological responses to salinity and drought

The hierarchical clustering heatmaps separated treatments according to stress severity (Figure 9(A,B)), with red indicating higher standardized trait values and blue indicating lower values. Under salt stress (Figure 9(A)), the control treatment (0 mM NaCl) displayed colors ranging from red to orange, indicating higher levels of chlorophyll, antioxidant capacity, hydration status, and biomass. In contrast, 150 mM NaCl displayed predominantly blue values, indicating pronounced decreases in all traits under severe salinity stress, which may reflect both osmotic limitation and an additional ion-related component. The intermediate levels (50–100 mM NaCl) range from yellow to light blue, indicating a gradual dose-dependent decline. The same trend was observed under drought stress (Figure 9(B)), where 0% PEG displayed red, representing maximal physiological values, and 15% PEG was predominantly blue, indicating strong inhibition of hydration status, pigments, antioxidant capacity, and biomass.

These clustering patterns are consistent with reports that increasing salt and drought stress can simultaneously reduce several physiological traits, including photosynthetic performance, water status, antioxidant capacity, and biomass-related parameters (Ashraf & Harris, 2004; Chauhan et al., 2023). Studies in maize and other cereals have similarly reported coordinated declines in chlorophyll content, RWC, biomass, and antioxidant activity under stress, which can also be visualized using heatmap clustering (Talebzadeh & Valeo, 2022). Thus, the heatmaps support a gradient-like response, in which deeper blue values are associated with greater physiological impairment under the tested salinity and drought levels. Although the clustering patterns provide clear evidence of coordinated physiological impairment under increasing stress levels, the absence of exogenous regulatory treatments, such as biostimulants or plant growth regulators limits the interpretation of potential mitigation mechanisms. Incorporating such treatments in future studies would enable a more comprehensive understanding of plant adaptive strategies and stress alleviation under salinity and drought stress.

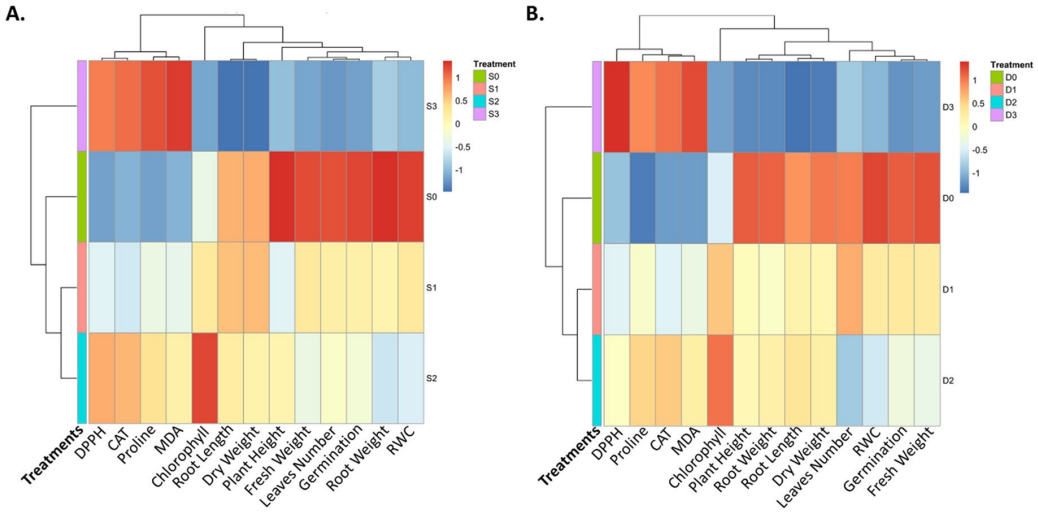


Figure 9. Hierarchical clustering heatmap of morphological, physiological, and biochemical traits of maize under salinity and drought stress. (A) Under salinity stress (S0-S3) and (B) under drought stress (D0-D3). Color gradients represent standardized values (z-scores), with red indicating higher values and blue indicating lower values across treatments.

Conclusion

This study demonstrates that both PEG-induced drought and NaCl-induced salinity reduced early maize seedling performance in a dose-dependent manner, primarily through osmotic stress, with salinity showing a stronger effect due to an additional ionic component. Stress conditions reduced germination, growth, chlorophyll content, and water status, while simultaneously increasing antioxidant responses that were insufficient to prevent oxidative damage under severe stress. Multivariate analysis confirmed that growth, biomass, and antioxidant traits were closely linked and declined together with increasing stress intensity. These findings highlight the critical role of osmotic stress in early maize development and demonstrate that enhanced antioxidant responses do not fully prevent oxidative damage under high stress conditions. This underscores the need for improved stress-resilient crop management strategies, including the potential use of biostimulants or plant growth regulators, to sustain productivity under climate variability, and to support sustainable agriculture and climate adaptation goals (SDG 2 and SDG 13).

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Author contributions

CRediT: **Nur Izzatul Maulidah**: Conceptualization; **Andi Kurniawan**: Data curation, Writing – original draft; **Ikhwan Adhirakha Mullatif**: Data curation; **Akhmad Rizal Oktafian**: Data curation; **Agung Nur Muhammad**: Data curation; **Mohd Fauzihan Karim**: Data curation; **Ridho Victory Nazara**: Data curation.

Disclosure statement

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Data availability statement

The raw data supporting the findings of this study are available from the corresponding author upon reasonable request.

References

Aebi, H. (1984). Catalase *in vitro*. *Methods in Enzymology*, *105*, 121–126. https://doi.org/10.1016/S0076-6879(84)05016-3

Alamer, K. H., Perveen, S., Khaliq, A., Zia Ul Haq, M., Ibrahim, M. U., & Ijaz, B. (2022). Mitigation of salinity stress in maize seedlings by the application of vermicompost and sorghum water extracts. *Plants (Basel, Switzerland)*, *11*(19), 2548. https://doi.org/10.3390/plants11192548

Argentel-Martínez, L., Peñuelas-Rubio, O., Pérez-López, L., Aguilera, J. G., Steiner, F., Zuffo, A. M., & Ratke, R. F. (2024). Assessing salinity, drought and high temperature stress in maize (*Zea mays* L.) and wheat (*Triticum aestivum* L.) varieties: Theoretical combination as multifactorial stress. *Journal of Agronomy and Crop Science*, *210*(6), e70001. https://doi.org/10.1111/jac.70001

Arif, Y., Singh, P., Siddiqui, H., Bajguz, A., & Hayat, S. (2020). Salinity induced physiological and biochemical changes in plants: An omic approach towards salt stress tolerance. *Plant Physiology and Biochemistry: PPB*, *156*, 64–77. https://doi.org/10.1016/j.plaphy.2020.08.042

Ashraf, M. P. J. C., & Harris, P. J. (2004). Potential biochemical indicators of salinity tolerance in plants. *Plant Science*, *166*(1), 3–16. https://doi.org/10.1016/j.plantsci.2003.10.024

Azeem, M., Pirjan, K., Qasim, M., Mahmood, A., Javed, T., Muhammad, H., Yang, S., Dong, R., Ali, B., & Rahimi, M. (2023). Salinity stress improves antioxidant potential by modulating physio-biochemical responses in *Moringa oleifera* Lam. *Scientific Reports*, *13*(1), 2895. https://doi.org/10.1038/s41598-023-29954-6

Barrs, H. D., & Weatherley, P. E. (1962). A re-examination of the relative turgidity technique for estimating water deficits in leaves. *Australian Journal of Biological Sciences*, *15*(3), 413–428. https://doi.org/10.1071/BI9620413

Bates, L. S., Waldren, R. P., & Teare, I. D. (1973). Rapid determination of free proline for water-stress studies. *Plant and Soil*, *39*(1), 205–207. https://doi.org/10.1007/BF00018060

Burlett, R., Trueba, S., Bouteiller, X. P., Forget, G., Torres-Ruiz, J. M., Martin-StPaul, N. K., Parise, C., Cochard, H., & Delzon, S. (2025). Minimum leaf conductance during drought: Unravelling its variability and impact on plant survival. *The New Phytologist*, *246*(3), 1001–1014. https://doi.org/10.1111/nph.70052

Chauhan, J., Prathibha, M. D., Singh, P., Choyal, P., Mishra, U. N., Saha, D., Kumar, R., Anuragi, H., Pandey, S., Bose, B., Mehta, B., Dey, P., Dwivedi, K. K., Gupta, N. K., & Singhal, R. K. (2023). Plant photosynthesis under abiotic stresses: Damages, adaptive, and signaling mechanisms. *Plant Stress*, *10*, 100296. https://doi.org/10.1016/j.stress.2023.100296

Fatima, H., Khan, A., Nadeem, M., Khalofah, A., & Abbas, T. (2025). Induction of salinity tolerance in maize (*Zea Mays* L.) by exogenous application of ascorbic acid and gibberellic acid. *Scientific Reports*, *15*(1), 38273. https://doi.org/10.1038/s41598-025-22174-0

Gechev, T., Mehterov, N., Denev, I., & Hille, J. (2013). A simple and powerful approach for isolation of Arabidopsis mutants with increased tolerance to H_2O_2-induced cell death. *Methods in Enzymology*, *527*, 203–220. https://doi.org/10.1016/B978-0-12-405882-8.00011-8

Gulcin, İ., & Alwasel, S. H. (2023). DPPH radical scavenging assay. *Processes*, *11*(8), 2248. https://doi.org/10.3390/pr11082248

He, X., Zhu, J., Gong, X., Zhang, D., Li, Y., Zhang, X., Zhao, X., & Zhou, C. (2025). Advances in deciphering the mechanisms of salt tolerance in Maize. *Plant Signaling & Behavior*, *20*(1), 2479513. https://doi.org/10.1080/15592324.2025.2479513

Hosseini, S., Moogouei, R., Teymoori, S., Moogouei, R., Borghei, M., Latinwo, O., & Katam, K. (2025). Biochemical changes and phytoextraction potential of quinoa and wheat for their resilience to salt stress. *Scientific Reports*, *15*(1), 37589. https://doi.org/10.1038/s41598-025-17012-2

Hu, D., Li, R., Dong, S., Zhang, J., Zhao, B., Ren, B., Ren, H., Yao, H., Wang, Z., & Liu, P. (2022). Maize (*Zea mays* L.) responses to salt stress in terms of root anatomy, respiration and antioxidative enzyme activity. *BMC Plant Biology*, *22*(1), 602. https://doi.org/10.1186/s12870-022-03972-4

Ikram, M., Khalid, B., Batool, M., Ullah, M., Zitong, J., Rauf, A., Rao, M. J., Rehman, H. U., Kuai, J., Xu, Z., Zhao, J., Wang, J., Zhou, G., & Wang, B. (2025). Secondary metabolites as biostimulants in salt stressed plants: Mechanisms of oxidative defense and signal transduction. *Plant Stress*, *16*, 100891. https://doi.org/10.1016/j.stress.2025.100891

Jomova, K., Alomar, S. Y., Alwasel, S. H., Nepovimova, E., Kuca, K., & Valko, M. (2024). Several lines of antioxidant defense against oxidative stress: Antioxidant enzymes, nanomaterials with multiple enzyme-mimicking activities, and low-molecular-weight antioxidants. *Archives of Toxicology*, *98*(5), 1323–1367. https://doi.org/10.1007/s00204-024-03696-4

Kumar, V., Srivastava, A. K., Sharma, D., Pandey, S. P., Pandey, M., Dudwadkar, A., Parab, H. J., Suprasanna, P., & Das, B. K. (2024). Antioxidant defense and ionic homeostasis govern stage-specific response of salinity stress in contrasting rice varieties. *Plants (Basel, Switzerland)*, *13*(6), 778. https://doi.org/10.3390/plants13060778

Kurniawan, A., Noviandi, W. D., Maulidah, N. I., Mullatif, I. A., Rahmandhias, D. T., Karim, M. F., & Shyu, D. J. (2025). Mitigating drought stress effects in tomato through seed priming and foliar application of salicylic acid: Impacts on germination and plant growth. *Journal of Ecological Engineering*, *26*(4), 369–383. https://doi.org/10.12911/22998993/200337

Lichtenthaler, H. K. (1987). [34] Chlorophylls and carotenoids: Pigments of photosynthetic biomembranes. In *Methods in enzymology* (Vol. 148, pp. 350–382). Academic Press. https://doi.org/10.1016/0076-6879(87)48036-1

Mahpara, S., Zainab, A., Ullah, R., Kausar, S., Bilal, M., Latif, M. I., Arif, M., Akhtar, I., Al-Hashimi, A., Elshikh, M. S., Zivcak, M., & Zuan, A. T. K. (2022). The impact of PEG-induced drought stress on seed germination and seedling growth of different bread wheat (*Triticum aestivum* L.) genotypes. *PloS One*, *17*(2), e0262937. https://doi.org/10.1371/journal.pone.0262937

Morales, M., & Munné-Bosch, S. (2019). Malondialdehyde: Facts and artifacts. *Plant Physiology*, *180*(3), 1246–1250. https://doi.org/10.1104/pp.19.00405

Nour, M. M., Aljabi, H. R., Al-Huqail, A. A., Horneburg, B., Mohammed, A. E., & Alotaibi, M. O. (2024). Drought responses and adaptation in plants differing in life-form. *Frontiers in Ecology and Evolution*, *12*, 1452427. https://doi.org/10.3389/fevo.2024.1452427

Pandit, K., Kaur, S., Kumar, M., Bhardwaj, R., & Kaur, S. (2024). Salinity stress: Impact on plant growth. In *Advances in food security and sustainability* (Vol. 9, pp. 145–160). Elsevier. https://doi.org/10.1016/bs.af2s.2024.07.002

Per, T. S., Khan, N. A., Reddy, P. S., Masood, A., Hasanuzzaman, M., Khan, M. I. R., & Anjum, N. A. (2017). Approaches in modulating proline metabolism in plants for salt and drought stress tolerance: Phytohormones, mineral nutrients and transgenics. *Plant Physiology and Biochemistry: PPB*, *115*, 126–140. https://doi.org/10.1016/j.plaphy.2017.03.018

Pienaar, B. C., Majeke, B. M., Wittenberg, M. F., Adetunji, A. E., Nephali, L., Tugizimana, F., & Rafudeen, M. S. (2025). Mitigating salt stress in maize using *Ecklonia maxima* seaweed extracts. *Plant Stress*, *16*, 100828. https://doi.org/10.1016/j.stress.2025.100828

Qiao, M., Hong, C., Jiao, Y., Hou, S., & Gao, H. (2024). Impacts of drought on photosynthesis in major food crops and the related mechanisms of plant responses to drought. *Plants*, *13*(13), 1808. https://doi.org/10.1371/journal.pone.0262937

Sajid, M., Ahmed, S., Sardar, R., & Yasin, N. A. (2025). Insight into polyethylene glycol-mediated physiochemical, nutritional, and antioxidative defense modulations in salt-stressed *Raphanus sativus* L. *Physiology and Molecular Biology of Plants*, *31*(4), 659–674. https://doi.org/10.1007/s12298-025-01585-3

Salama, H. S. A. (2019). Yield and nutritive value of maize (*Zea mays* L.) forage as affected by plant density, sowing date and age at harvest. *Italian Journal of Agronomy*, *14*(2), 1383. https://doi.org/10.4081/ija.2019.1383

Seleiman, M. F., Al-Suhaibani, N., Ali, N., Akmal, M., Alotaibi, M., Refay, Y., Dindaroglu, T., Abdul-Wajid, H. H., & Battaglia, M. L. (2021). Drought stress impacts on plants and different approaches to alleviate its adverse effects. *Plants (Basel, Switzerland)*, *10*(2), 259. https://doi.org/10.3390/plants10020259

Talebzadeh, F., & Valeo, C. (2022). Evaluating the effects of environmental stress on leaf chlorophyll content as an index for tree health. In *IOP conference series: Earth and environmental science* (Vol. 1006(1), p. 012007). IOP Publishing. https://doi.org/10.1088/1755-1315/1006/1/012007

Taulavuori, E., Hellström, E., Taulavuori, K., & Laine, K. (2001). Comparison of two methods used to analyse lipid peroxidation from *Vaccinium myrtillus* (L.) during snow removal, reacclimation and cold acclimation. *Journal of Experimental Botany*, *52*(365), 2375–2380. https://doi.org/10.1093/jexbot/52.365.2375

Valko, M., Leibfritz, D., Moncol, J., Cronin, M. T., Mazur, M., & Telser, J. (2007). Free radicals and antioxidants in normal physiological functions and human disease. International *Journal of Biochemistry and Cell Biology*, *39*(1), 44–84. https://doi.org/10.1016/j.biocel.2006.07.001

Vennam, R. R., Bheemanahalli, R., Reddy, K. R., Dhillon, J., Zhang, X., & Adeli, A. (2024). Early-season maize responses to salt stress: Morpho-physiological, leaf reflectance, and mineral composition. *Journal of Agriculture and Food Research*, *15*, 100994. https://doi.org/10.1016/j.jafr.2024.100994

Wang, P., Liu, W. C., Han, C., Wang, S., Bai, M. Y., & Song, C. P. (2024a). Reactive oxygen species: Multidimensional regulators of plant adaptation to abiotic stress and development. *Journal of Integrative Plant Biology*, *66*(3), 330–367. https://doi.org/10.1111/jipb.13601

Wang, X., Chen, Z., & Sui, N. (2024b). Sensitivity and responses of chloroplasts to salt stress in plants. *Frontiers in Plant Science*, *15*, 1374086. https://doi.org/10.3389/fpls.2024.1374086