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Moderate salinity enhances nutritional quality but suppresses growth in spinach (*Spinacia oleracea*): a trade-off between stress adaptation and yield

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ABSTRACT:
Soil salinity is an increasing constraint to leafy vegetable production, often limiting crop yield while simultaneously altering nutritional composition. Understanding the balance between growth suppression and stress-induced nutritional enhancement is therefore critical for sustainable spinach (*Spinacia oleracea*) cultivation in saline agroecosystems. This study investigated the growth and biochemical responses of spinach to incremental salinity stress (0–6 dS/m NaCl) under controlled conditions. The growth parameters (plant height, the number of leaves, and leaf area), proximate composition (moisture, ash, protein, carbohydrates, crude fat, and fibre), and mineral dynamics (Ca^{2+}, Fe^{2+}, K^{+}, Mg^{2+}) were evaluated using a completely randomised design, supported by ANOVA and robust regression analyses. Salinity reduced vegetative performance overall, with the leaf number declining by approximately 50% at 6 dS/m and plant height showing a net reduction of 13% relative to the control at harvest, despite increases observed at intermediate salinity levels. Leaf expansion exhibited a hormetic response, with moderate salinity (2 dS/m) temporarily enhancing leaf area during the early growth stages. Bulk biochemical analysis revealed salinity-driven trade-offs, where ash (+33%) and protein (+42%) contents increased significantly ($p < 0.001$), while carbohydrate content declined by 17% ($R^2 = 0.946$). Mineral composition displayed salinity-dependent shifts, with Fe^{2+} peaking at 2 dS/m (20.63 mg/L) before declining at higher salinity, partial recovery of K^{+} uptake at 6 dS/m (59.91 mg/L), and relatively stable Ca^{2+} and Mg^{2+} concentrations. Moisture and crude fibre contents were not significantly affected ($p > 0.05$). Robust regression confirmed threshold-dependent responses, indicating that moderate salinity (2–4 dS/m) can enhance micronutrient availability without severely disrupting ionic homeostasis. These findings highlight a trade-off between nutritional quality enhancement and growth suppression under salinity stress and support precision irrigation and salinity-resilient breeding strategies to optimise spinach production in saline environments.

Keywords: mineral dynamics, nutritional trade-offs, proximate composition, salinity stress, *Spinacia oleracea*

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INTRODUCTION

Spinach (*Spinacia oleracea* L.) is a nutrient-dense leafy green vegetable recognised for its rich profile of vitamins, minerals, and phytochemicals which contribute to health benefits, including antioxidant, anti-cancer, and anti-obesity properties. As a result, spinach is acknowledged as a highly functional food with significant health benefits attributed to its diverse nutritional composition. Numerous studies have highlighted the health benefits of spinach and its role in dietary strategies aimed at mitigating chronic diseases (Mokhtari *et al.* 2021; Tan *et al.* 2024; Manzoor *et al.* 2025). For instance, increased intake of vegetables, including spinach, correlates with reduced risks of cardiovascular diseases, cancer, and all-cause mortality, with a notable summary relative

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risk of 0.92 per 200g/day for coronary heart disease (Aune *et al.* 2017). This protective effect is attributed to the bioactive compounds abundant in leafy greens. Furthermore, the association between vegetable consumption and improved mental health outcomes suggested that the phytonutrients in spinach may alleviate psychological distress and enhance mood regulation (Głąbska *et al.* 2020). In addition, the American Heart Association (AHA) advocates for dietary patterns prioritising nutrient-dense foods like spinach, emphasising their role in cardiovascular health when integrated into whole-food-based, minimally processed diets. Beyond individual health, plant-centric diets rich in spinach align with broader public health objectives, as such dietary frameworks not only reduce chronic disease morbidity, but also promote sustainable food systems (Mozaffarian 2016).

Despite these benefits of spinach, its cultivation, particularly for commercial purposes, mostly depends on irrigation, for which the water mostly comes from effluents of different sources and sometimes from lakes and rivers of low water quality. Other agronomic practices, such as the excessive use of NPK-based fertilisers to promote vegetative growth, along with the ongoing challenges presented by global climate change, pose significant threats to spinach cultivation. These practices can lead to fluctuations in soil salinity levels exceeding the physiological tolerance of the plants (Abdolahi Arshad *et al.* 2024; Meena *et al.* 2025). Soil salinity has been reported to significantly affect the nutritional composition of leafy vegetables. A previous study indicates that low to moderate salinity can increase phenolic compounds and glucosinolates in *Brassica* vegetables, while maintaining macro- and micro-element homeostasis (Šamec *et al.* 2021). However, salt stress also alters metabolite profiles, decreasing the levels of flavonoids, amino acids, sugars, and lipid-related compounds, which can negatively affect nutritional quality (Kim *et al.* 2021). In addition, soil salinity has a strong positive correlation with the cadmium bioconcentration factor in leafy vegetables, potentially increasing heavy metal uptake in contaminated soils (Huang *et al.* 2020). To mitigate such salinity effects, various strategies can be employed, including chemical and biological amendments, fertiliser application, and sustainable agronomic practices like crop diversification and irrigation management (Syed *et al.* 2020).

Soil salinity significantly impacts spinach growth and nutritional quality. Increasing NaCl concentrations decrease plant growth due to mineral imbalance, reducing K^+, Ca^{2+}, and Fe^{2+} levels (Kim *et al.* 2021). However, spinach cultivars such as Raccoon can maintain NPK homeostasis even at low soil K^+ levels and favour K^+ absorption over Na^+ regardless of salinity (Ferreira *et al.* 2020). Salinity also affects metabolite profiles, decreasing levels of flavonoids, amino acids, and sugars, potentially reducing nutritional quality (Kim *et al.* 2021). Conversely, moderate salinity (30–60 mML^{-1} NaCl) may support plant growth under K-deficient conditions (Uçgun *et al.* 2020). Salt-tolerant spinach cultivars can be cultivated with recycled water of moderate salinity and less potassium than recommended, thereby reducing both financial inputs and environmental effects (Ferreira *et al.* 2020). Thus, understanding these effects is crucial for developing strategies to maintain spinach productivity and nutritional value in saline conditions (Sogoni *et al.* 2021). Therefore, this study aimed to investigate the effect of salinity (NaCl) on the growth, and proximate and mineral composition of spinach (*S. oleracea*). We hypothesised that increasing salinity (NaCl) would progressively inhibit spinach growth, manifested as reduced biomass and leaf area due to osmotic stress and ion toxicity. However, moderate salinity (2–4 dS/m) may enhance root plasticity as a hormetic response. Concurrently, salinity is expected to increase ash content through sodium (Na^+) and chloride (Cl^-) accumulation, while reducing carbohydrate reserves as photosynthetic efficiency decreases, with compensatory increases in protein content driven by osmoprotectant synthesis (e.g. proline).

Crude fibre and fat levels are anticipated to remain stable or rise marginally, reflecting structural adaptations to salinity. The mineral composition is predicted to shift, with Na^+ and Cl^- concentrations increasing linearly, while potassium (K^+), calcium (Ca^{2+}), and magnesium (Mg^{2+}) uptake declines due to ionic competition, and micronutrient availability (e.g. iron, zinc) diminishes at higher salinity (>6 dS/m) due to reduced solubility. Finally, growth suppression is expected to correlate strongly with tissue sodium accumulation, while increased protein and ash content may signal metabolic adjustments to salinity stress, highlighting the potential trade-offs between stress adaptation and nutritional quality.

MATERIALS AND METHOD

Experimental site and soil sampling. The pot experiment was carried out in the Botanical Garden of the Department of Plant Biology, Federal University Dutse (Fig. 1). Bulk sandy loam topsoil (0–20 cm depth) was collected from an area within this site with no recent history of salinity stress. Composite sampling was conducted using a sterile auger. The collected soil was air-dried, homogenised, and passed through a 2-mm sieve prior to disinfestation. Soil solarisation was performed *ex situ* by spreading the soil in plastic trays as a 5–7 cm thick layer, covering it with transparent polyethylene sheets, and exposing it to direct sunlight for 21 consecutive days (Al-Shammary *et al.* 2019). The trays were kept outdoors under ambient conditions to ensure effective heat accumulation. Following solarisation, the soil was allowed to cool to ambient temperature before use. The physico-chemical soil properties were determined after solarisation and prior to compost amendment to characterise the growth substrate used in the experiment. The soil test was carried out at the soil science laboratory, Faculty of Agriculture, Federal University Dutse. The solarised soil was subsequently mixed with compost as described in Section 2.2 and transferred into experimental pots.

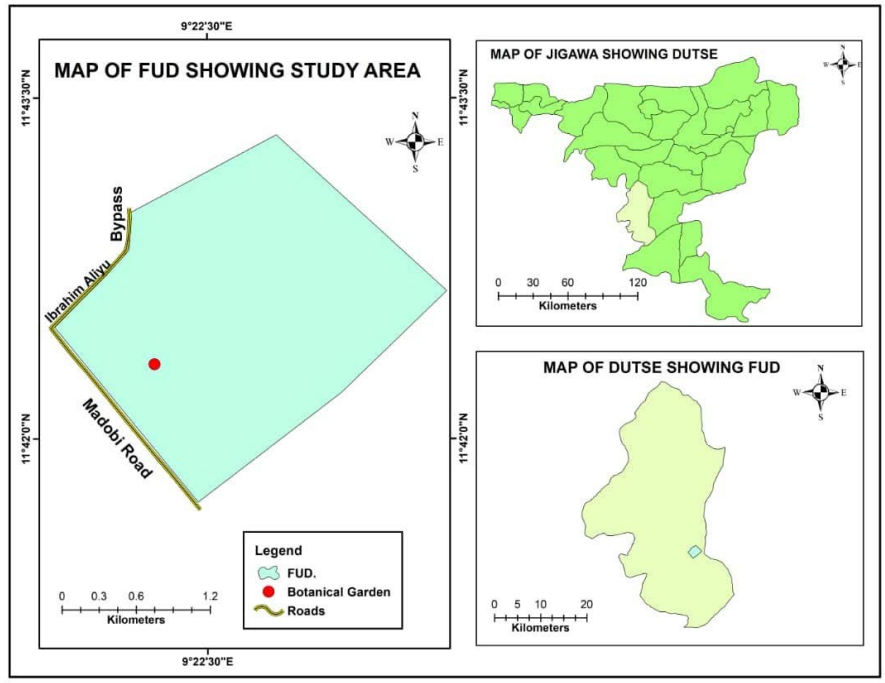

Fig. 1. Map of the study area (experimental site) showing the botanical garden in Federal University Dutse (FUD), Jigawa State, Nigeria.

Soil preparation. Prior to potting, the solarised sandy-loam soil was thoroughly mixed with compost at a ratio of 2:1 (soil:compost, v/v) to improve organic matter content and nutrient availability and placed in 15 × 15 cm pots, leaving about 3–5 cm for water application. The planting pots were perforated at the base to ensure proper drainage and avoid excess water accumulation which could cause seed decay or similar effects. Since compost was uniformly incorporated across all treatments and salinity was the only experimental variable, post-amendment soil analysis was not conducted. Water (500–800 mL) was applied twice a day, in the morning and evening, for three consecutive days to allow the soil to settle and unwanted seeds or weedy plants to germinate, which were immediately removed when observed. These prepared pots were subsequently used for growing spinach in the experiment.

Seed sowing and agronomic practices. Prior to planting in the prepared pots, spinach seeds were sourced and sown in a pre-nursery plot to facilitate germination. One spinach variety (*Dan Hausa*) was used, selected because of its wide coverage as the most cultivated and consumed spinach in the region (Jigawa State, Nigeria). Two weeks after seed emergence in the pre-nursery, the young seedlings were carefully transplanted into the prepared pots. Four seedlings were planted per pot, which were later thinned to two seedlings per pot, retaining those plants with no signs of transplanting shock. Each pot was treated as a replicate, hence, three replications were used per treatment. Watering and other agronomic practices were carried out to maintain the plants until treatment application (Sogoni *et al.* 2021).

Preparation of salt (NaCl) concentrations and application. Each salt concentration was prepared by determining the electrical conductivity (EC) of the solution using an EC meter (Bhuyan *et al.* 2023). Briefly, granulated NaCl was gently added to distilled water using a spatula and stirred gently until dissolved, followed by determination of its EC value until the desired level was obtained. Where the EC level exceeded the required EC, distilled water was gently added until the EC was adjusted to the required concentration. This protocol was repeated to obtain salinity levels of 2, 4 and 6 dS/m, corresponding approximately to 0, 20–25, 40–50 and 60–70 mM NaCl, respectively, based on standard EC–NaCl conversion under soil solution conditions. Approximately 500–800 mL of the prepared salt concentrations was added to each pot as irrigation water every seven days for a period of eight weeks.

Experimental design. The experiment was conducted using a completely randomised design with four salinity treatments (0, 2, 4, and 6 dS/m). Each treatment consisted of three biological replicates, with each replicate represented by one pot containing a single spinach plant (n = 3 plants per treatment). The growth parameters were measured repeatedly on the same plants at weeks 2, 4, and 8 after treatment initiation. For the biochemical and mineral analyses, leaf tissues were collected from each biological replicate and analysed in technical triplicate, with mean values used for statistical analysis.

Determination of the growth parameters. Vegetative growth parameters, namely plant height, number of leaves and leaf size, were considered for data collection. The plant height was measured using a transparent calibrated meter rule and expressed in centimetres. The number of leaves was directly counted and expressed as a numerical value. The leaf size was determined according to the method described by Han *et al.* (2023) with slight modifications. Briefly, because of the oval to oblong shape of the spinach leaves, an elliptical model using R Studio was used to compute the leaf size from the measurements of the leaf length and width and expressed in cm^2. Each measurement was re-

peated three times at weekly intervals up to the six weeks after planting, at which time the maximum vegetative growth of the spinach was observed.

Determination of bulk biochemical composition. Bulk biochemical composition (commonly referred to as proximate composition), namely, moisture, ash, protein, and carbohydrate content were analysed at the Biochemistry Laboratory, Federal University Dutse. Moisture content was determined using the oven-drying (gravimetric) method (Alakangas 2016). Briefly, a clean flat platinum dish was dried in an oven at 105°C and then cooled in a desiccator. This dish was weighed (W_1), and 5 g of the spinach leaf sample was placed in the dish and weighed accurately (W_2). The dish and its contents was then transferred into an oven at 105°C for 3 hours. After drying, the dish was left in the oven for an additional half an hour before it was allowed to cool again in the desiccator, and its weight was then determined and expressed as W_3. The moisture content was calculated as follows:

$$\text{Moisture Content (\%)} = \frac{w_2 - w_3}{w_2 - w_1} \times 100$$

where W_1 is the empty dish weight, W_2 is the dish + fresh sample weight, and W_3 is the dish + dried sample weight.

The dry ashing method was used to determine the ash content (Alakangas 2016). A clean silica dish was dried and cooled in a desiccator and weighed (W_1), and 5 g of dried spinach sample was weighed accurately into the dish (W_2). The dish was then transferred using a pair of tongs into a muffle furnace at 500°C until complete ashing was achieved (grey-coloured ash). The dish containing the ash was cooled in a desiccator and weighed (W_3). The ash content was calculated as follows:

$$\text{Ash Content (\%)} = \frac{w_3 - w_1}{w_2 - w_1} \times 100$$

where W_1 is the empty crucible weight, W_2 is the crucible + dry sample weight, and W_3 is the crucible + ash weight.

The spinach leaf samples (5 g) were first dried in a forced-air oven at 105°C until constant weight was obtained. The fat content was determined by Soxhlet extraction using petroleum ether for 6 hours (Carpenter 2010). The protein content was determined using the Kjeldahl method following digestion with concentrated sulphuric acid and catalytic copper sulphate (Zikalala *et al.* 2017). The carbohydrate content was calculated by difference, subtracting the percentages of moisture, fat, protein, and ash from 100%. The crude fibre was determined using an enzymatic-gravimetric method involving sequential acid and alkaline digestion, filtration, drying, and ashing (Agiang *et al.* 2016).

Atomic absorption spectroscopy (AAS) analysis. A total of 0.5 g of the dried and powdered spinach leaf sample was weighed and transferred to a digestion flask. A mixture of 5 mL of concentrated nitric acid (HNO_3) and 2 mL of perchloric acid ($HClO_4$) was added to the sample. The digestion was carried out on a hot plate at 120–140°C until a clear solution was obtained. The digested sample was then cooled to room temperature and filtered using Whatman No. 42 filter paper. The filtrate was diluted to 50 mL with deionised water and stored in labelled polyethylene bottles for AAS analysis. The concentrations of calcium (Ca^{2+}), iron (Fe^{2+}), potassium (K^{+}), and magnesium (Mg^{2+}) in the digested spinach leaf samples were determined using a PerkinElmer AAnalyst 400 Atomic Absorption Spectrophotometer (PerkinElmer Inc., USA) under standard operating conditions (Dauda *et al.* 2023). Calibration curves were established using standard solutions of each element prepared in deionised water. The wavelengths used for element detection were 422.67 nm, 248.33

nm, 404.41 nm, and 202.58 nm for Ca^{2+}, Fe^{2+}, K^{+}, and Mg^{2+}, respectively. A hollow cathode lamp was used for each element, and the instrument was operated in flame mode using an acetylene-air mixture. The absorbance of each sample was recorded, and the corresponding element concentrations were obtained by interpolation from the calibration curves. The mineral concentrations were quantified in acid-digested leaf samples and are reported as mg L^{-1} of digest solution. Biomass-normalised values (e.g. mg g^{-1} dry weight) were not calculated due to the fixed-volume extraction protocol; therefore, the mineral data are interpreted comparatively across treatments rather than as absolute tissue accumulation.

Data analysis. The data obtained was subjected to statistical analysis using R Studio version 4.4.2. Analysis of Variance (ANOVA) was used to compare the means between treatments, and Tukey's Honestly Significant Difference was used as a *post hoc* test to separate the mean differences within treatments at $P \leq 0.05$ significance. Principal component analysis (PCA) was conducted separately for the bulk biochemical composition (ash, crude protein, carbohydrates, crude fat, crude fibre, and moisture) and the mineral composition data (Ca^{2+}, Fe^{2+}, K^{+}, and Mg^{2+}) to identify multivariate response patterns to the salinity treatments. Prior to PCA, the variables were standardised (z-score transformation) to account for differences in the measurement scales. The treatment-wise clustering and variable loadings were interpreted to assess salinity-driven trade-offs and nutrient redistribution. Linear regression analysis was used to model the relationship between salinity levels and proximate compositions. To model the relationship between salinity levels (the predictor variable) and nutrient concentrations (the response variables), robust regression analysis was performed using the Huber–M-estimator approach in the rlm function of the MASS package in R. This method was chosen due to its ability to handle potential outliers and heteroscedasticity in the data.

The regression equation was expressed as:

$$Y = \beta_0 + \beta_1 X + \varepsilon$$

where:
Y is the nutrient concentration (Ca^{2+}, Fe^{2+}, K^{+}, Mg^{2+}),
X is the salinity level,
β_0 and β_1 are the regression coefficients,
ε is the error term.

RESULTS

The effects of salinity on the vegetative growth parameters (plant height, number of leaves and leaf size) of spinach. Figure 2A illustrates the effects of salinity and growth duration on spinach plant height. Across all the treatments, plant height increased significantly over time ($p \leq 0.05$), indicating active vegetative growth from week 2 to week 8. At harvest (week 8), the plants grown under non-saline conditions (0 dS/m) attained the greatest height (52.67 cm), which was significantly higher ($p \leq 0.05$) than those grown at 2 dS/m (30.67 cm). Although plants exposed to 4 and 6 dS/m reached heights of 41.0 cm and 46.0 cm, respectively, these values were significantly lower than those of the control, indicating the- overall suppressive effect of salinity on plant elongation despite partial compensatory growth at higher salinity levels. These results demonstrate that increasing salinity reduced final plant height relative to the control, with significant differences observed among salinity treatments at week 8.

The number of leaves per plant was also significantly influenced by both salinity level and growth duration (Fig. 2B). Leaf number increased significantly over time within each treatment ($p \leq 0.05$); however, higher salinity

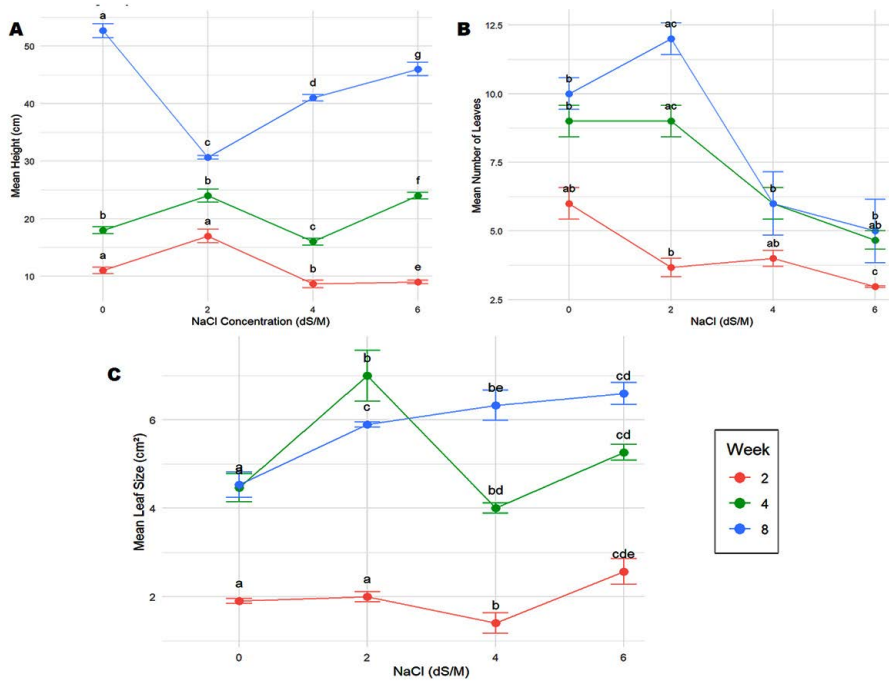

Fig. 2. The effects of different NaCl concentrations (ds/m) on (A) plant height (cm), (B) number of leaves and (C) size of leaf (cm²) of spinach (*Spinacia oleracaea*) at different weeks of exposure.

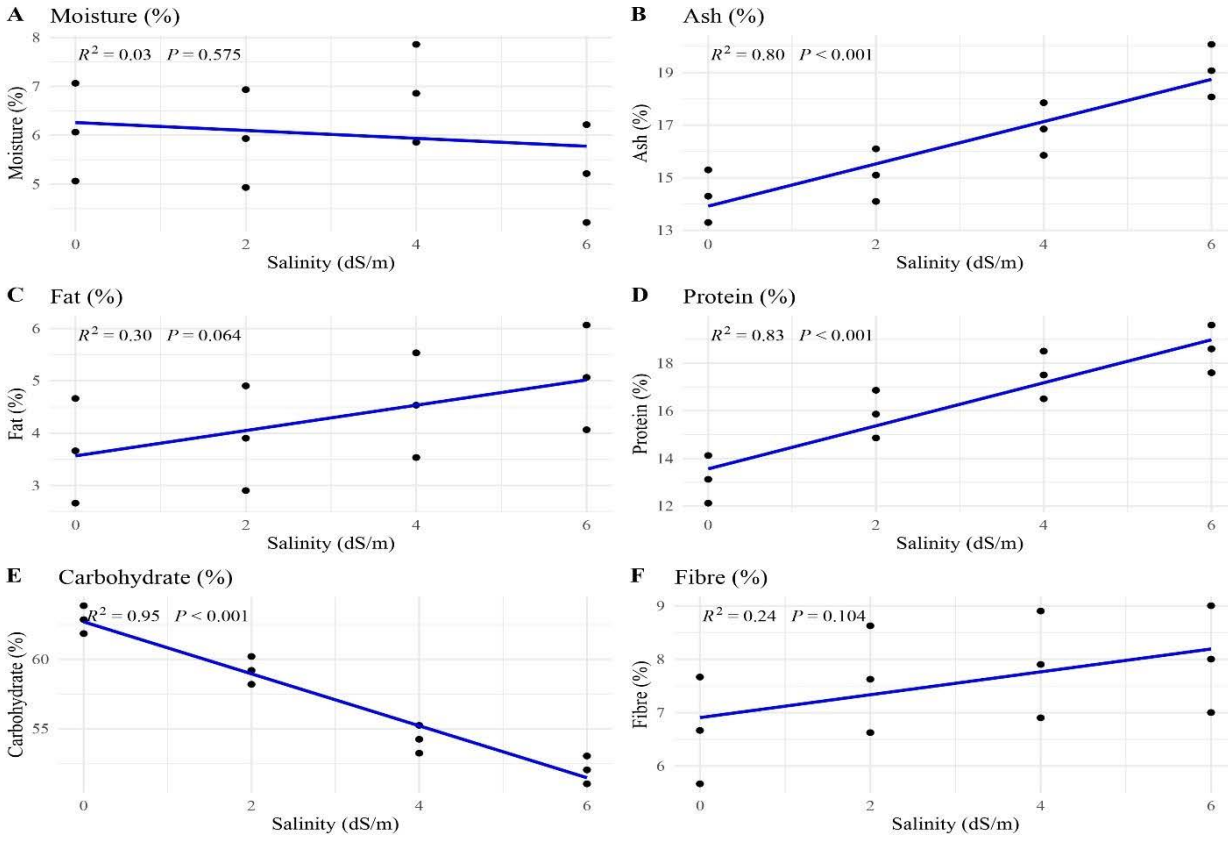

Fig. 3. Linear regression of the effect of salinity on (A) moisture content, (B) ash content, (C) crude fat content, (D) protein content, (E) carbohydrate content and (F) crude fibre content of the spinach leaves after treatment at different salinity levels. Each data point represents the mean of three independent biological replicates per salinity level. Regression lines are shown to visualise the response trends across the salinity gradient; traits with low R^2 and nonsignificant slopes indicate relative stability across treatments.

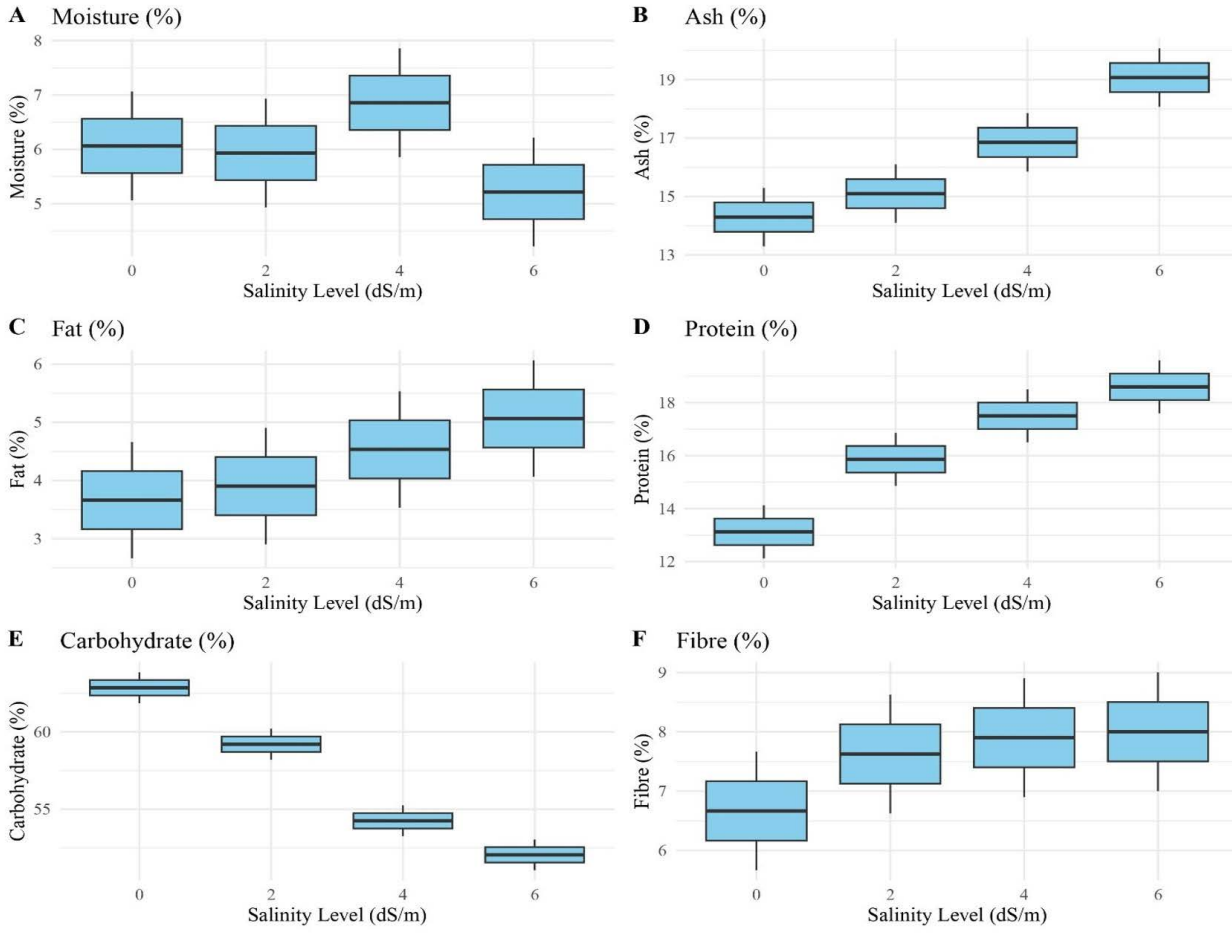

Fig. 4. Boxplot of the effect of salinity on (A) moisture content, (B) ash content, (C) crude fat content, (D) protein content, (E) carbohydrate content and (F) crude fibre content of the spinach leaves after treatment at different salinity levels.

levels consistently reduced leaf proliferation. At week 8, the plants grown at 2 dS/m produced the highest number of leaves (12.0), which was significantly greater than those grown at 4 dS/m (6.0) and 6 dS/m (5.0). In contrast, the plants exposed to 6 dS/m recorded the lowest leaf numbers throughout the experimental period, differing significantly from the control and moderate salinity treatments ($p \leq 0.05$). These findings indicate that salinity markedly constrained leaf initiation and development, particularly at higher salinity levels.

Leaf size exhibited a salinity- and time-dependent response (Fig. 2C). While the leaf area increased significantly with plant age across treatments ($p \leq 0.05$), the salinity effects differed with growth stage. At week 4, moderate salinity (2 dS/m) resulted in a significantly larger leaf area (7.0 cm^2) compared with the control and higher salinity treatments, indicating a transient stimulatory effect. However, by week 8, leaf size under higher salinity levels (4 and 6 dS/m) did not differ significantly from the control, suggesting that prolonged salinity exposure limited sustained leaf expansion. Overall, these results indicate a hormetic response, whereby moderate salinity temporarily enhanced leaf size, while higher salinity ultimately limited foliar growth.

The effects of salinity on the bulk biochemical composition of spinach. The bulk biochemical composition of spinach (*S. oleracea*) varied significantly across salinity levels (0–6 dS/M, Table 1). Linear regression analysis (Fig. 3A–F) demonstrated a strong positive association between salinity and ash content, which increased from 14.30 ± 0.03% (0 dS/M) to 19.07 ± 0.07% (6 dS/M);

Table 1. Biochemical bulk composition of spinach (*Spinacia oleracea*) under different NaCl concentrations (0–6 ds/m).

	Salinity Level (dS/M)			
Biochemical Composition (%)	0	2	4	6
Moisture	6.06±0.07[a]	5.93±0.09[a]	6.86±1.41[a]	5.22±0.30[a]
Ash	14.30±0.03[c]	15.10±0.01b[c]	16.85±0.07[ab]	19.07±0.07[a]
Crude Fat	3.66±0.06[a]	3.90±0.02[a]	4.54±0.13[a]	5.07±0.07[a]
Protein	13.13±0.02[c]	15.86±0.77[b]	17.50±0.07[ab]	18.59±0.95[a]
Carbohydrate	62.85±0.15[a]	59.21±0.76[b]	54.25±1.48[c]	52.05±0.16[c]
Crude Fiber	6.67±0.50[a]	7.63±0.05[a]	7.90±0.06[a]	8.00±0.04[a]

Mean ± SD followed by the same letter(s) are not statistically significant at $P \leq 0.05$.

($R^2 = 0.802$, $F(1,10) = 40.62$, $p < 0.001$; Fig. 3B). Similarly, protein content rose from 13.13 ± 0.02% to 18.59 ± 0.95% ($R^2 = 0.829$, $F(1,10) = 48.55$, $p < 0.001$; Fig. 3D), with distinct statistical groupings across salinity treatments (Table 1). In contrast, carbohydrate content exhibited a pronounced negative relationship with salinity, declining from 62.85 ± 0.15% to 52.05 ± 0.16% ($R^2 = 0.946$, $F(1,10) = 173.9$, $p < 0.001$; Fig. 3E), supported by non-overlapping variability in the boxplot distributions (Fig. 4E).

Crude fat displayed a marginal upward trend rising from 3.66 ± 0.06% to 5.07 ± 0.07% ($R^2 = 0.303$, $F(1,10) = 4.336$, $p = 0.064$; Fig. 3C), although no significant differences were observed among salinity groups (Table 1). Moisture content remained stable, varying from 6.06 ± 0.07% to 5.22 ± 0.30% ($R^2 = 0.032$, $F(1,10) = 0.335$, $p = 0.575$; Fig. 3A), consistent with the homogeneous groupings in Table 1 and the overlapping interquartile ranges observed in the boxplots (Fig. 4A). Similarly, crude fibre showed no significant salinity-dependent variation, ranging from 6.67 ± 0.50% to 8.00 ± 0.04% ($R^2 = 0.243$, $F(1,10) = 3.203$, $p = 0.104$; Fig. 3F), aligning with the nonsignificant statistical categorisations in Table 1 and the boxplot distributions (Fig. 4F). Principal component analysis (PCA) of the bulk biochemical composition (Fig. 5A) revealed a clear separation of the variables and treatments along two major axes, explaining 94.8% of the total variance (Dim1: 68.5%; Dim2: 26.3%). Along Dim1, carbohydrate content loaded positively, whereas protein, ash, crude fat, and crude fibre loaded negatively, indicating an opposing pattern of variation between carbohydrate accumulation and the other compositional traits. This axis therefore reflects a compositional trade-off associated with salinity intensity. The samples corresponding to moderate salinity treatments (e.g. S2) were positioned toward the negative side of Dim1, consistent with higher protein and ash content, while the samples from higher salinity treatments (e.g. S4 and S6) clustered toward the positive side, reflecting reduced nutrient accumulation. Dim2 was primarily driven by moisture content, separating the samples based on water-related variation rather than nutrient composition. Heatmap analysis (Fig. 5B) corroborated these patterns, showing elevated protein and ash levels in S2, whereas S4 and S6 exhibited uniformly lower values across most compositional traits. The broader spread observed in the control treatment (S0) suggests a transitional or heterogeneous compositional profile under non-saline conditions.

Residual standard errors across the models ranged from 0.899 (crude fat) to 1.097 (carbohydrate), reflecting variable precision in the salinity effect estimates. The regression trends for ash, protein, and carbohydrate (Fig. 3B, D & E) were supported by minimal overlap in the boxplot quartiles (Fig. 4B, D & E), while fat, moisture, and fibre exhibited greater distributional overlap (Fig. 4A, C & F).

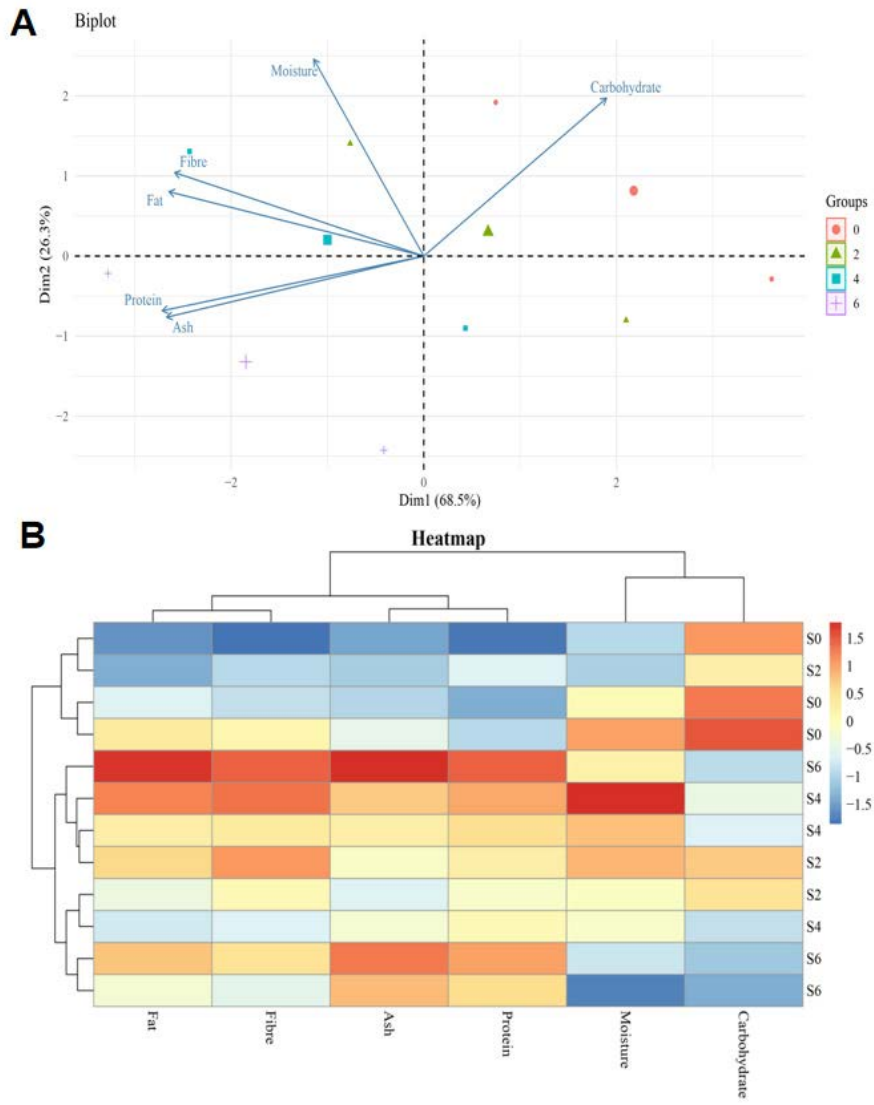

Fig. 5. Principal component analysis and a heatmap of proximate composition (%) of spinach (*S. oleracea*) exposed to different levels of salinity (ds/m). (A) A principal component analysis (PCA) biplot showing the distribution of the samples based on the proximate composition variables. The first two principal components (dim1 and dim2) explain the majority of variance. The vectors represent the contribution of each proximate parameter to the separation of the samples. (B) A heatmap showing the hierarchical clustering of the samples (rows) and proximate composition parameters (columns). Colour gradients represent standardised values, highlighting the patterns and clustering of similar profiles across treatments.

The effect of salinity on the mineral composition (Ca^{2+}, Fe^{2+}, K^{+}, and Mg^{2+}) of spinach. Figure 6 below presents the mean mineral concentrations (Ca^{2+}, Fe^{2+}, K^{+}, and Mg^{2+}) under different salinity levels, highlighting the effects of increasing salinity levels on nutrient availability. The mean calcium concentration in the digested leaf extracts (Fig. 6A) showed minimal variation across salinity treatments, ranging from 70.99 mg L^{-1} at 0 dS m^{-1} to 71.81 mg L^{-1} at 6 dS m^{-1}. While these values represent concentrations in the analytical extract rather than the biomass-normalised tissue content, they indicate that relative calcium availability in the leaf tissue was maintained across the salinity gradient. The minor variations suggest that Ca^{2+} availability is not significantly influenced by salinity stress in this range. A significant peak in Fe^{2+} concentration (Fig. 6B) was observed at 2 dS/m (20.63 mg L^{-1}), which was markedly higher than at 0 dS/m (6.66 mg/L). However, the Fe^{2+} levels drastically declined at 4 dS/m (5.54 mg/L) and remained low at 6 dS/m (6.1 mg/L). The mean K^{+} concentration (Fig. 6C) decreased significantly at 2 dS/m (51.02 mg/L) compared to 0 dS/m (60.44 mg/L), indicating that salinity stress may initially reduce K uptake. However, at 4 dS/m (59.1 mg/L) and 6 dS/m (59.91 mg/L), the K^{+} levels partially recovered, suggesting a potential adaptive mech-

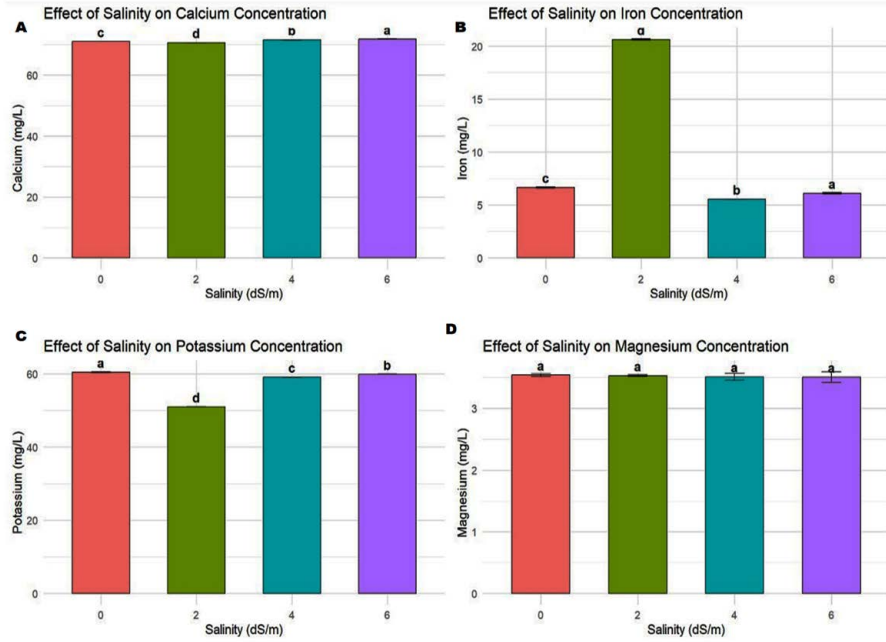

Fig. 6. The effect of salinity on mineral composition (Ca^{2+}, Fe^{2+}, K^{+}, and Mg^{2+}) in spinach. This figure illustrates the mean concentrations of (A) calcium (Ca^{2+}), (B) iron (Fe^{2+}), (C) potassium (K^{+}), and (D) magnesium (Mg^{2+}) at varying salinity levels (0, 2, 4, and 6 ds/m). The error bars represent the standard error (SE) of the mean. Different letters above the bars indicate statistically significant differences among the treatments ($p < 0.05$).

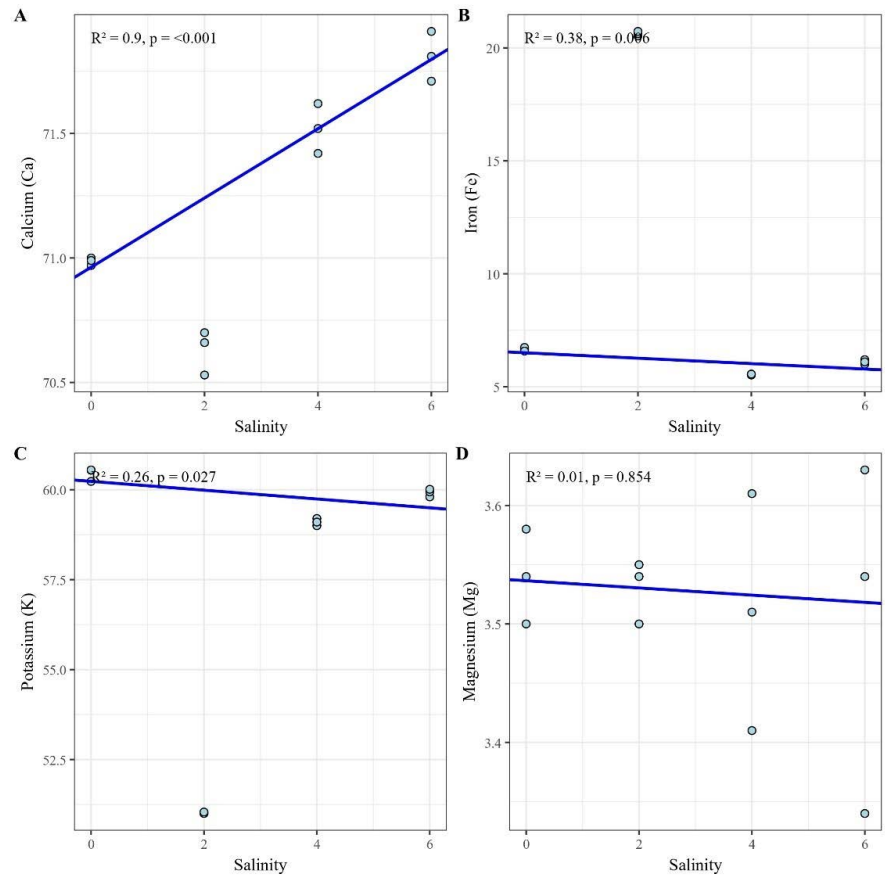

Fig. 7. Robust regression plots showing the relationships between the salinity levels (ds/m) and leaf concentrations of four essential minerals: (A) calcium (Ca^{2+}), (B) iron (Fe^{2+}), (C) potassium (K^{+}), and (D) magnesium (Mg^{2+}). Each plot includes the coefficient of determination (r^2) and associated p-value from robust linear regression.

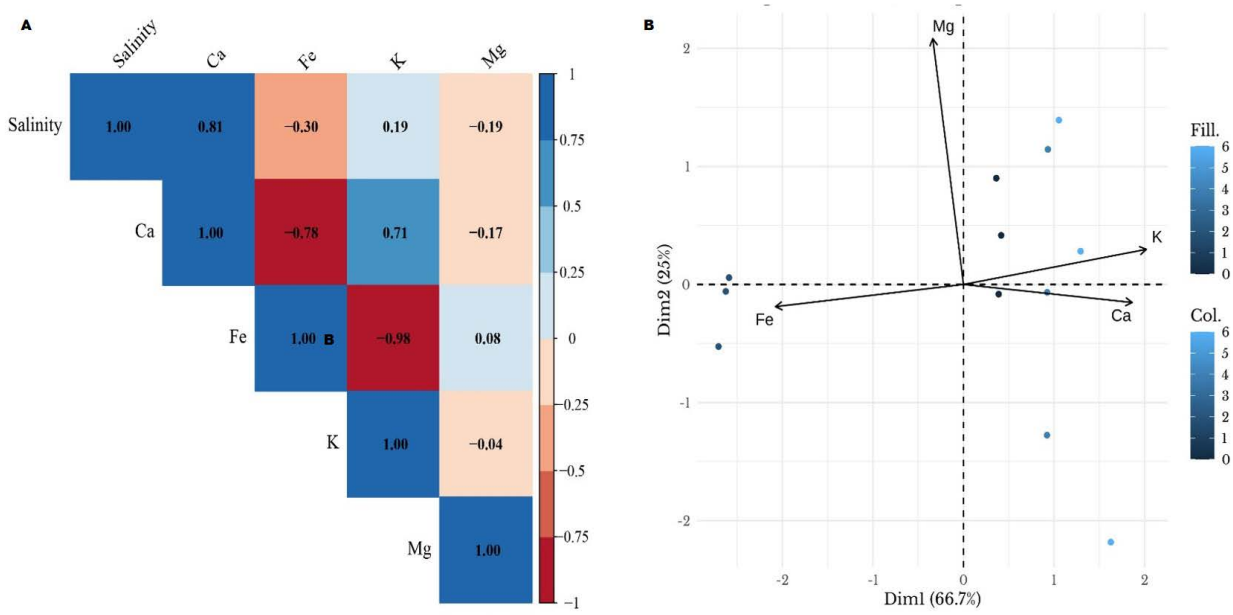

Fig. 8. A Pearson correlation heatmap (A) displaying the pairwise associations among the mineral concentrations, highlighting positive (blue) and negative (red) correlations. (B) A principal component analysis (PCA) biplot illustrating the multivariate distribution of the mineral concentrations across different salinity levels. The arrows represent variable loadings, and individual points represent observations coloured according to salinity level.

anism or compensatory uptake at higher salinity. Moreover, the Mg^{2+} levels as described in Fig. 6D remained relatively stable across all salinity levels, with minor fluctuations between 3.5 mg/L (0 dS/m) and 3.54 mg/L (6 dS/m). These small variations suggest that Mg^{2+} availability is not significantly affected by salinity stress in this experimental setup.

The robust regression plots (Fig. 7A–D) illustrate distinct trends in the response of mineral composition to increasing salinity. The calcium (Ca^{2+}) regression plot suggests a slight positive correlation between Ca^{2+} concentration and salinity, as indicated by the upward slope of the regression line. This implies that higher salinity levels might facilitate calcium uptake or retention in spinach leaves. In contrast, the iron (Fe^{2+}) plot (Fig. 7B) shows a sharp increase in Fe^{2+} concentration at moderate salinity (2 dS/m), followed by a notable decline at higher salinity levels. This suggests that moderate salinity may enhance Fe solubility or availability, while excessive salinity appears to negatively impact Fe absorption.

Similarly, the potassium (K^{+}) plot (Fig. 7C) reveals an initial decline at 2 dS/m, followed by recovery at 4 and 6 dS/m. This pattern indicates a potential osmotic adjustment mechanism in response to salinity stress, whereby K^{+} is regulated to maintain cellular function. Lastly, the magnesium (Mg^{2+}) plot exhibits relatively stable Mg^{2+} levels across all salinity treatments, suggesting that Mg^{2+} homeostasis in spinach is not significantly affected by salinity variations. The correlation heatmap analysis and PCA biplot (Fig. 8A & B) revealed moderate to strong negative correlations (r = -0.04 to -1.00) between salinity levels and mineral composition. Iron (Fe^{2+}) exhibited near-perfect negative correlations (r = -0.98), while magnesium (Mg^{2+}) displayed consistently moderate negative associations (r = -0.25 and -0.75, respectively). These results indicate strong inverse relationships between mineral composition and salinity levels in *S. oleracea* under the tested conditions.

DISCUSSION

Salinity-mediated growth suppression reflects stress sensitivity rather than adaptive vigour. The present findings demonstrate that increasing salinity imposes a clear constraint on spinach vegetative growth, consistent with the clas-

sification of *S. oleracea* as a salt-sensitive glycophyte. Although all the plants exhibited temporal increases in height, leaf number, and leaf area, salinity altered both the rate and allocation of growth, indicating that developmental progression under stress does not equate with optimal biomass accumulation. Similar growth suppression has been widely reported in cultivated spinach, in contrast to wild relatives such as *S. turkestanica*, which exhibit stronger ion compartmentalisation and enhanced osmotic tolerance mechanisms (Ribera *et al.* 2021).

The observed reduction in plant height under salinity likely reflects impaired cell elongation driven by osmotic stress and ionic imbalance. Salinity reduces cellular turgor and disrupts expansin-mediated cell wall loosening, thereby constraining longitudinal growth. Comparable reductions in stem elongation have been reported in salt-sensitive spinach cultivars and leafy vegetables such as lettuce and pak choi, whereas salt-tolerant chenopods maintain elongation through superior Na^+ sequestration and K^+ retention (Kumar *et al.* 2020; Shahid *et al.* 2020). While partial plant height recovery at higher salinity levels was observed, this response should not be interpreted as tolerance, but rather as delayed or compensatory growth which does not offset cumulative stress exposure.

Salinity constrains leaf initiation more strongly than leaf expansion. Leaf number proved more sensitive to salinity than plant height, indicating that salinity primarily disrupts meristematic activity and leaf initiation rather than overall shoot elongation. Reduced leaf production under saline conditions is consistent with salinity-induced inhibition of cell division, likely mediated by altered hormonal signalling and reduced carbon availability to developing meristems. Similar patterns have been reported in salt-sensitive spinach cultivars and *Brassica* species, where salinity suppresses cytokinin biosynthesis and transport, thereby limiting leaf primordia formation (Kumawat *et al.* 2022; Atta *et al.* 2023).

In contrast, leaf size exhibited a non-linear response to salinity, with moderate salinity transiently enhancing leaf expansion. This response resembles hormetic effects reported in other glycophytes, where mild stress induces short-term compensatory expansion, possibly through increased cell enlargement rather than increased cell number. However, sustained exposure to higher salinity ultimately constrained leaf expansion, likely due to reduced photosynthetic efficiency and impaired chloroplast function, as documented in spinach and related crops (Hameed *et al.* 2021; Balasubramaniam *et al.* 2023). Collectively, these findings suggest that salinity shifts the growth strategy of spinach from leaf proliferation toward limited compensatory expansion, with negative consequences for canopy development and yield.

Changes in bulk biochemical composition reflect concentration effects and metabolic reallocation, not direct synthesis. Salinity altered spinach bulk biochemical composition in a manner consistent with stress-induced metabolic trade-offs rather than the direct stimulation of biosynthesis. The increase in ash content under salinity most likely reflects the increased accumulation of inorganic ions, including Na^+ and Cl^-, as part of osmotic adjustment. This response aligns with observations in both cultivated spinach and its halophytic relatives, where ionic accumulation contributes to turgor maintenance, while also increasing total mineral residue (Ribera *et al.* 2021; Mallick *et al.* 2024).

The apparent increase in protein content must be interpreted with caution. The applied analytical method estimates total nitrogen rather than true protein fractions, and no amino acid profiling was conducted. Consequently, attributing this increase to specific compounds such as proline is not supported by the data. A more prudent explanation is that the elevated nitrogen

concentration likely reflects a concentration effect arising from reduced carbohydrate accumulation and overall biomass dilution under stress. Similar nitrogen concentration effects under salinity have been reported in spinach, rice, and mustard, where growth inhibition inflates nitrogen-based metrics without necessarily increasing protein synthesis (Kaur *et al.* 2022). Future studies incorporating amino acid profiling and enzymatic assays are required to determine whether osmoprotective nitrogenous compounds are actively synthesised.

The decline in carbohydrate content provides strong evidence for metabolic reallocation under salinity stress. Reduced photosynthetic efficiency, coupled with increased respiratory demand for stress mitigation, likely divert carbon away from storage pools. Comparable carbohydrate depletion under salinity has been documented in rice, tomato, and ornamental crops, reinforcing the interpretation that enhanced nutritional density under salinity may occur at the expense of caloric yield (Shahid *et al.* 2020; Mallick *et al.* 2024).

The moisture and crude fibre contents remained relatively stable across the salinity treatments, suggesting that spinach maintains tissue hydration and structural integrity despite ionic stress. This stability likely reflects conservative osmotic regulation and limited remodelling of cell wall architecture under the tested salinity range. Similar findings have been reported in salt-sensitive dicots, where the maintenance of cell wall composition is prioritised to preserve mechanical stability under stress (Dabravolski & Isayenkov 2023).

Mineral dynamics reveal threshold-dependent nutrient regulation. Salinity exerted distinct, element-specific effects on mineral composition, highlighting the complexity of nutrient regulation under ionic stress. Calcium stability across salinity levels suggests effective homeostatic control, consistent with its structural and signalling roles. In contrast, iron exhibited a pronounced peak under moderate salinity followed by a decline at higher levels, likely reflecting salinity-induced changes in rhizosphere chemistry and ion competition. Similar nonlinear Fe responses have been reported in spinach, wheat, and beet, underscoring the narrow range in which salinity may enhance micronutrient bioavailability (Houmani *et al.* 2024).

Potassium dynamics revealed an initial decline followed by recovery at higher salinity levels, indicating the activation of compensatory transport mechanisms. Although spinach is generally salt-sensitive, this recovery suggests the partial activation of K^+ retention strategies, possibly involving high-affinity transporters, as documented in *Arabidopsis* and moderately tolerant crops (Assaha *et al.* 2017; Gámez-Arjona *et al.* 2024). Magnesium stability further indicates the prioritisation of photosynthetic and enzymatic functions under stress.

Agronomic implications: nutritional gains versus yield penalties. Collectively, the results demonstrate a clear trade-off between nutritional enhancement and growth performance under salinity. Moderate salinity can transiently increase mineral density and nitrogen concentration, potentially improving micronutrient quality. However, these gains are accompanied by reduced leaf production and carbohydrate content, directly limiting yield and energy value. This trade-off mirrors findings in other leafy vegetables and reinforces the need to contextualise nutritional improvements within overall productivity frameworks.

From an applied perspective, salinity management strategies should aim to exploit narrow thresholds where nutritional benefits are maximised without incurring substantial yield losses. Precision irrigation, cultivar selection, and targeted nutrient supplementation may help reconcile these competing objec-

tives. However, translating these findings into practice will require field-scale validation and integration with genetic and physiological studies to identify spinach genotypes with improved stress resilience.

CONCLUSION

This study demonstrates that salinity within the range of 0–6 dS/m exerts a pronounced influence on spinach growth performance and nutritional composition, revealing a clear trade-off between vegetative productivity and nutrient enrichment. Increasing salinity suppressed plant height and leaf proliferation, confirming the salt-sensitive nature of cultivated spinach, while moderate salinity (2 dS/m) induced a transient enhancement of leaf expansion, indicative of short-term compensatory growth rather than sustained tolerance.

Alterations in proximate composition under salinity reflected stress-induced metabolic reallocation and concentration effects rather than direct biosynthetic enhancement. Increases in ash and nitrogen-derived fractions were accompanied by a marked decline in carbohydrate content, underscoring the cost of nutritional density in terms of biomass and energy yield. Mineral analyses further revealed threshold-dependent responses, with moderate salinity improving iron availability, potassium homeostasis recovering at higher salinity, and calcium and magnesium remaining largely stable, suggesting the selective regulation of ion uptake under stress.

From a bio-saline agriculture perspective, these findings highlight both opportunities and limitations for spinach cultivation in saline environments. Carefully managed moderate salinity may be exploited to enhance micronutrient density, particularly iron, without severely compromising mineral balance. However, the yield penalties associated with reduced leaf number and carbohydrate content emphasise the need for cautious application. Future prospects should therefore focus on integrating precision irrigation strategies, salinity-gradient management, and breeding programs targeting improved ion homeostasis, leaf retention, and carbon-use efficiency. Additionally, molecular and field-based studies are required to identify those genotypes capable of sustaining yield while maintaining nutritional quality under saline conditions. Such integrative approaches will be essential for advancing spinach production within bio-saline and climate-stressed agroecosystems.

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COMPREHENSIVE PLANT BIOLOGY

REZIME

Umereni salinitet unapređuje nutritivni kvalitet, ali suzbija rast spanaća (*Spinacia oleracea*): kompromis između adaptacije na stres i prinosa

Tijjani Mustapha, Fatima Sagir Nayaya, Mai-Abba Ishiyaku Abdullahi i Haris Nura Garba

Salinitet zemljišta predstavlja sve veće ograničenje u proizvodnji lisnatog povrća, jer smanjuje prinos, ali istovremeno može menjati i nutritivni sastav biljaka. Zbog toga je za održivu proizvodnju spanaća (*Spinacia oleracea*) u zaslanjenim agroekosistemima važno razumeti odnos između smanjenja rasta i mogućeg povećanja nutritivne vrednosti usled stresa. Povećan salinitet je generalno smanjio rast spanaća, pri čemu su broj listova i visina biljaka opadali sa porastom zaslanjenosti, dok je umeren stres u ranim fazama razvića pokazao prolazni stimulativni efekat na površinu lista. Istovremeno su uočene promene u biohemijskom sastavu, sa povećanjem sadržaja pepela i proteina i smanjenjem sadržaja ugljenih hidrata, što ukazuje na preraspodelu metabolizma u uslovima stresa. Mineralni sastav se menjao u zavisnosti od nivoa saliniteta, pri čemu je umeren stres mogao povoljno uticati na dostupnost pojedinih mikronutrijenata, dok su veće koncentracije dovodile do poremećaja u njihovom usvajanju, bez značajnih promena u sadržaju vlage i vlakana.

Ključne reči: mineralna dinamika, nutritivni kompromisi, približni sastav, stres soli, *Spinacia oleracea*