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Anion-Mediated Modifications in Rhizospheric Bacterial Composition and Morphological Plasticity of Celosia argentea L. in Sodic-Saline Soil Conditions

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ABSTRACT

This study investigated the effects of sodic-saline soil conditions on the growth and development of *Celosia argentea* L., with a focus on the role of anions in modifying rhizospheric bacterial composition and plant morphological plasticity. The experiment was conducted in a controlled environment, with soil salinization achieved using different sodium salts (sodium sulfate, sodium chloride, sodium carbonate, sodium phosphate, and sodium nitrate) at varying concentrations (50, 500, and 5000 ppm). The results showed that sodic salinity significantly impacted plant growth, with reductions in plant height (up to 49% at 5000 ppm NaCl), leaf count (up to 38.8% at 5000 ppm Na_2CO_3), and foliar yield (up to 54.2% at 5000 ppm NaCl). However, plants treated with phosphate and nitrate anions exhibited improved growth parameters, with increases in seed weight per plant (up to 28% at 50 ppm $NaNO_3$) and foliar yield (up to 18% at 50 ppm Na_3PO_4). Interestingly, nitrate and sulfate treatments demonstrated some mitigating effects on salinity stress, suggesting good potential for enhancing plant performance. Furthermore, the study examined the impact of sodic salinity on the rhizospheric bacterial community. Five dominant rhizospheric bacterial isolates were identified, i.e., *Klebsiella aerogenes*, *Serratia marcescens, Escherichia coli, Bacillus safensis*, and *Enterobacter cloacae*. These isolates exhibited potential plant growth-promoting traits, such as nitrogen fixation, phosphate solubilization, and the production of phytohormones. These findings highlight the significant impact of anion composition on plant responses to sodic salinity and highlight the importance of understanding the rhizosphere microbiome in mitigating the detrimental effects of salinity stress.

Abbreviation: Organic matter (OM), Plant Growth Promoting Rhizobacteria (PGPR), Sodium carbonate (CO), Sodium chloride (CL), Sodium nitrate (NO), Sodium phosphate (PO), Sodium sulfate (SO), Total organic carbon (TOC)

Introduction

Soil salinization presents a critical threat to global food security, contributing to soil degradation and accelerating desertification (Bechtaoui et al., 2020). Traditional remediation methods have often proven inadequate, prompting more sustainable, eco-friendly alternatives. The use of organic amendments, beneficial microorganisms, and integrated soil management strategies has shown promise in enhancing soil fertility and improving crop tolerance to salinity. Furthermore, the incorporation of advanced biotechnological tools—such as molecular marker-assisted breeding and genome editing—offers a comprehensive and effective framework for mitigating salt stress. These approaches support environmental sustainability, ensure food sufficiency, and promote the long-term viability of agricultural systems (Begum et al., 2019). This study seeks to contribute to the development of innovative, sustainable strategies for addressing complex challenges posed by soil salinization.

The global agricultural sector faces numerous challenges, chief among them being the need to ensure sufficient food production for a rapidly growing population projected to reach 8 billion by mid-century (Boukhari et al., 2020). One of the most pressing threats to global food security is soil salinization, which is increasingly exacerbated by population growth. This phenomenon affects extensive areas of irrigated land, particularly in arid and semi-arid regions (Chernane et al., 2015). The consequences of soil salinization are far-reaching, including degradation of soil health, deterioration of water quality, and inhibited plant growth, all of which compromise the resilience of ecosystems (Egamberdieva et al., 2019).

In response to these challenges, researchers are investigating innovative and sustainable solutions, such as the utilization of resilient tropical plants like *Celosia argentea* (commonly known as silver cock's comb). This nutrient-dense leafy vegetable, also valued as an ornamental crop, demonstrates remarkable adaptability to diverse environmental conditions and requires only moderate soil moisture. The species' rapid growth rate, resilience, and rich nutritional profile make it a promising candidate for cultivation in resource-constrained regions (Mahanty et al., 2017). Additionally, its potential roles as a biofertilizer and phytoremediator warrant further investigation.

Cultivating *C. argentea* in tropical zones may contribute significantly to strategies aimed at enhancing global food security, combating soil salinization, and advancing sustainable agricultural practices. Achieving these outcomes, however, depends on effective management of salt-affected soils, which in turn requires a thorough understanding of their chemical properties, classification, and influence on plant growth (Saha et al., 2017). Accurate soil assessment and comprehensive water quality testing are critical for diagnosing salinity and sodicity problems (Etesami et al., 2017; Jha, 2017; Young, 2017). Such evaluations enable land managers to devise and implement targeted reclamation strategies that restore soil health, improve crop productivity, and reinforce ecosystem resilience.

Organic farming presents a holistic approach to sustainable agriculture by fostering ecological balance and offering effective strategies to mitigate soil salinity. By eliminating the use of synthetic fertilizers and pesticides, organic practices prioritize soil health, enhance soil structure, and stimulate microbial activity (Jithesh et al., 2019; Jha et al., 2019). This approach enriches organic matter content, improves soil quality, reduces bulk density, and increases water infiltration. Beneficial microorganisms and natural soil amendments play a critical role in stabilizing mineral particles and detoxifying saline soils.

Among these, arbuscular mycorrhizal (AM) fungi form symbiotic associations with plant roots, facilitating nutrient exchange and supporting the overall health of agricultural ecosystems. This mutualistic relationship enhances plant access to essential inorganic nutrients, thereby improving growth and resilience (Abbott et al., 2018; Al-Ghamdi and Elansary, 2018). AM fungi can contribute significantly to soil structure, fertility, and quality, while also strengthening plant defenses against salinity stress. Their integration into sustainable agricultural systems supports ecological balance and minimizes environmental degradation.

Plant Growth-Promoting Rhizobacteria (PGPR) further enhance plant growth in the rhizosphere through multiple mechanisms, including the synthesis of phytohormones, solubilization of phosphorus, and improved nutrient availability—particularly phosphate (Bechtaoui et al., 2020; Begum et al., 2019). PGPR also mitigate the adverse effects of abiotic stresses, especially salinity, and their inoculation has been shown to increase photosynthetic pigment levels, nutritional value, and crop productivity under saline conditions.

Additionally, seaweed extracts have emerged as potent biostimulants that improve plant growth and productivity. These extracts promote root development, energy storage, and the activation of defense mechanisms, enabling plants to better withstand salinity and other abiotic stresses (Gupta and Pandey, 2019; Gusain et al., 2015). Treatment with seaweed extracts triggers the expression of key stress-responsive genes, thereby enhancing crop resilience and overall growth performance.

The synergistic interactions between beneficial microorganisms, particularly Plant Growth-Promoting Rhizobacteria (PGPR) and arbuscular mycorrhizal (AM) fungi, represent a promising avenue for advancing sustainable agriculture. These microorganisms enhance crop yields, improve tolerance to abiotic stresses, and facilitate phosphorus solubilization, thereby supporting environmentally friendly farming practices (Dalal et al., 2019; Digruber et al., 2018). By adopting organic farming systems and harnessing the potential of these microbial allies, farmers can effectively mitigate soil salinity, maintain crop quality, and promote environmental sustainability.

This study specifically investigates the impact of salt stress on plant growth and development, morphological characteristics, soil microbial composition, and post-harvest resilience. It aims to evaluate the influence of associated anions on the morphological responses and rhizospheric bacterial communities of *Celosia argentea* cultivated in sodic-salinized soils.

Materials and Methods

Location

The experiment was conducted at the Botanical Garden, Department of Plant Biology and Biotechnology, University of Benin, Benin City, Edo State, during the 2023-2024 growth season spanning from July in 2023 to January in 2024.

Experimental design

Soil preparation

Forty-four (44) plastic bowls were obtained, and each bowl (radius 1: 23.6 cm, and radius 2: 18.5 cm, surface area: 1749.97 cm^2, volume ≈ 25,919 cm^3 or 25.9 L) was filled with 15 kg of sun-dried soil from the botanical garden (Table 1). Soil was bulked, mixed, and evenly distributed among the bowls to ensure uniformity. Soils were analyzed for soil physicochemical parameters according to methods described by Bouyoucos (1692), Page et al. (1982), Sparks et al. (1996), and Bray and Kurtz (2010).

Table 1. Physicochemical characteristics of soil samples used in the present study.

Characteristics	Sample 1	Sample 2	Sample 3	Sample 4	Mean
pH	5.85	5.60	5.75	5.79	5.75
Electric conductivity (µS cm^{-1})	131.38	89.20	109.15	119.28	112.25
Org. carbon (%)	0.45	0.12	0.48	0.42	0.37
Total nitrogen (%)	0.04	0.01	0.04	0.04	0.03
Org. matter (%)	0.77	0.21	0.83	0.72	0.63
Exchangeable acidity (meq 100 g^{-1} of soil)	0.48	0.40	0.70	0.54	0.53
Na (mg kg^{-1})	0.01	0.01	0.01	0.01	0.01
K (mg kg^{-1})	0.06	0.04	0.06	0.06	0.05
Ca (mg kg^{-1})	0.15	0.09	0.16	0.15	0.14
Mg (mg kg^{-1})	0.09	0.05	0.08	0.08	0.08
Av. phosphorus (mg kg^{-1})	20.97	13.44	21.16	20.20	18.94
Fe (%)	0.0101	0.0158	0.0086	0.0073	0.0105
Clay	9.28	9.00	9.00	9.15	9.11
Silt	2.95	2.70	3.08	2.96	2.92
Sandy	87.78	88.30	87.93	87.88	87.97

Seeding and salinization

Celosia argentea seeds (0.5 g) were broadcast over a 1603.45±50.72 cm^2 area of top soil surface in each bowl. Sodic salinized soils varied in associated anions: sodium sulfate (Na_2SO_4), sodium chloride (NaCl), sodium carbonate (Na_2CO_3), sodium phosphate (Na_3PO_4), and sodium nitrate ($NaNO_3$). Three concentrations of each salt solution were prepared: 5000, 500, and 50 ppm. The corresponding mass/volume concentrations were:

- Na_2SO_4: 5, 0.5, and 0.05 g L^{-1}
- NaCl: 5.85, 0.585, and 0.0585 g L^{-1}
- Na_2CO_3: 5.3, 0.53, and 0.053 g L^{-1}
- Na_3PO_4: 6.45, 0.645, and 0.0645 g L^{-1}
- $NaNO_3$: 5.75, 0.575, and 0.0575 g L^{-1}

Each treatment was replicated 5 times to ensure reliable results.

Salt solution application

Soils were initially saturated with salt solutions and left to attenuate for 2 d. Post-planting, a watering schedule was established, with each bowl receiving 500 mL of sodium salt solution every 2 d.

Morphological parameters

Plant morphological traits, including plant density, stem length, root length, leaf count, leaf area, and root weight, were systematically measured. Plant density was assessed by counting the number of plants within a defined area at the time of harvest. Stem length was measured from the soil surface to the tip of the main stem using a ruler or measuring tape. Root length was determined by carefully excavating each plant, washing away the adhering soil, and measuring the longest root from the crown to the tip. Leaf count was recorded by counting all fully expanded leaves per plant. Leaf area was measured either using a leaf area meter or estimated by tracing individual leaves onto graph paper and counting the enclosed squares. Root weight was obtained by separating the root system from the shoot, thoroughly washing the roots to remove soil particles, and measuring their fresh weight using a digital balance.

Rhizosphere bacterial composition

The composition of the bacterial community in the rhizospheric soil was elucidated through a comprehensive and integrated approach that combined conventional microbiological techniques with advanced molecular biology methods. This multifaceted strategy enabled a thorough characterization of the bacterial community, offering detailed insights into its structure, diversity, and potential functional roles.

Bacterial isolates were obtained from rhizospheric soil samples using well-established microbiological protocols (Cheesebrough, 2000), involving both selective and non-selective culture media to maximize the recovery of diverse bacterial taxa. The isolates were then characterized through a series of morphological and biochemical assessments, including Gram staining, analysis of cellular morphology, and biochemical profiling. Biochemical tests—such as catalase and oxidase assays, along with API profiling—provided essential information on the metabolic traits of the isolates, facilitating their preliminary taxonomic classification.

Following phenotypic characterization, molecular identification was conducted using PCR-mediated amplification and sequencing of the 16S rRNA gene, a widely recognized marker for bacterial taxonomy and phylogenetic analysis. The 16S rRNA gene, due to its conserved and variable regions, serves as an ideal target for accurate bacterial identification. Amplification was performed using universal primers 27F and 1492R, and the resulting PCR products were sequenced using Sanger sequencing technology, following the protocols outlined by Sambrook and Russel (2001).

The obtained sequence data were analyzed using MEGA (Molecular Evolutionary Genetics Analysis) software (Posada, 2009) to infer phylogenetic relationships among the bacterial isolates. Phylogenetic trees were constructed to visually represent the evolutionary affiliations of the isolates. Additionally, the sequence data were compared against reference databases such as GenBank and the Ribosomal Database Project (RDP) to achieve taxonomic resolution at the genus and species levels (Saitou and Nei, 1987; Calmin et al., 2008). This comparative analysis employed bioinformatics tools to align query sequences with database references and calculate similarity coefficients, ensuring robust and accurate taxonomic identification.

Evaluation of plant growth-promoting characteristics

To evaluate the plant growth-promoting (PGP) characteristics of bacterial isolates, the initial steps involved culturing and standardizing the isolates under controlled laboratory conditions. Phosphate solubilization was assessed using a qualitative assay, wherein bacterial isolates were cultivated on a medium containing insoluble phosphate. The formation of a clear halo around the bacterial colonies was considered indicative of phosphate solubilization activity (Nautiyal, 1999). Similarly, nitrogen fixation capacity was evaluated qualitatively by inoculating the isolates onto a nitrogen-free medium; observable bacterial growth under these conditions was recorded as a positive indication of nitrogen-fixing ability, following the protocol of Bashan and Holguin (1997).

Salinity tolerance was assessed by monitoring the growth of bacterial isolates on media supplemented with 7.5% NaCl. The “Growth (%)” column in the results represents the proportion of sub-cultured isolates within each genus that exhibited visible growth under saline conditions. These qualitative and semi-quantitative analyses provided an overview of the prevalence of key PGP traits—such as phosphate solubilization, nitrogen fixation, and salinity tolerance—among the tested bacterial genera. The reported trait percentages (e.g., “Positive” or “Negative” for phosphate solubilization and nitrogen fixation) correspond to the fraction of isolates within each genus that expressed the respective characteristic.

Data analysis

Data analysis was performed using GraphPad Prism version 6 and SPSS version 21. Following data cleaning, transformation, and normalization, descriptive statistics—including means and standard errors—were calculated. Analysis of Variance (ANOVA) was conducted to identify significant differences among treatments. When significant effects were detected, post-hoc comparisons were carried out using the Least Significant Difference (LSD) test to separate treatment means.

Results

The physicochemical properties of the soil samples analyzed in this study are summarized in Table 1. The soils exhibited a slightly acidic pH, with a mean value of 5.75. Organic matter content was relatively low, as indicated by a mean total organic carbon (TOC) of 0.375% and an organic matter (OM) content of 0.63%, alongside a correspondingly low nitrogen concentration (Table 1). These characteristics likely reflect nutrient leaching associated with the soil’s proximity to water-accumulating areas. The box-and-whisker plot presented in Figure 1 depicts the number of emergent seedlings per 0.5 g of broadcasted seeds after three weeks (see Table 2). Notably, the results demonstrate a consistent emergence pattern across all treatments, with a minimum of 60 seedlings emerging per 0.5 g of seeds in the treatment group. This robust seedling emergence rate suggests that the experimental conditions were favorable for germination (Fig. 2).

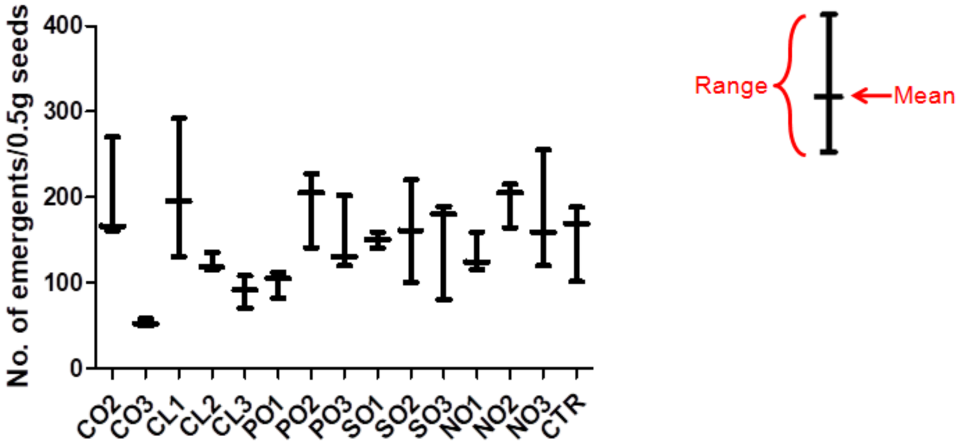


Fig. 1. Box and whiskers plot showing number of emergent per 0.5 g of seeds broadcasted after 3 weeks
CO carbonate, CL chloride, PO phosphate, SO sulfate, NO nitrate of sodium, CTR control
Category 3 = 5000 ppm (sodic- saline), Category 2 = 500 ppm (sodic), Category 1 = 50 ppm (slightly sodic), Surface area of soil in bowl = 1749.97 cm^2 (r = 23.6cm).

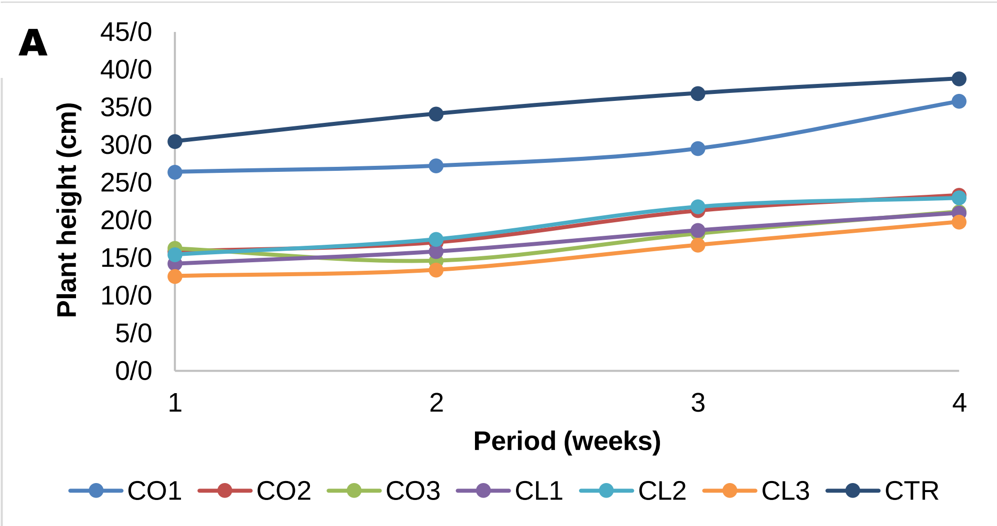
Table 2. Plant morphological parameters at 6 weeks in sodic soil compared to control.

Plant Characteristics	Sodic soil	Control soil	t-value	P value	Summary
Plant height (cm)	24.85±2.71	34.85±2.86	2.907	$P < 0.05$	*
No. leaves/plant	29.17±0.81	49.55±6.09	5.925	$P < 0.001$	***
Leaf area (cm^2)	19.11±0.24	30.93±3.72	3.434	$P < 0.01$	**
Seed wt. per plant (g)	0.542±0.05	0.69±0.03	0.0430	$P > 0.05$	ns
Above ground biomass	14.58±0.31	21.61±1.62	2.043	$P > 0.05$	ns
Foliar yield (g)	4.128±0.25	6.914±0.55	0.8097	$P < 0.05$	ns

Fig. 2. *Celosia argentea* emergents after 6 d following sowing with 0.5 g seeds in the control and in soils affected with 500 ppm NaCl (CL2).

The preliminary salinity study revealed significant growth impairment in plants cultivated in sodic soil compared to those grown in control soil. Specifically, plant height decreased by 28.6% under sodic conditions, measuring 24.85 cm versus 34.85 cm in the control. In addition, the number of leaves per plant was significantly reduced from 45 to 29 ($P < 0.001$), representing a 35.6% decrease. Foliar yield also declined significantly, from 6.914 g to 4.128 g ($P < 0.05$), indicating a 40.4% reduction. These findings suggest that sodicity imposes substantial stress on plant growth and development, negatively affecting key morphological traits. The observed reductions in plant height, leaf count, and foliar yield reflect compromised productivity and an increased susceptibility to environmental stressors.

In the second phase of the experiment, sodicity was varied based on the predominant anions. Figures 3–6 illustrate the effects of these treatments on plant growth parameters over a four-week period. The results confirm the detrimental impact of salinity on plant development, as treated plants exhibited reduced growth relative to the control. However, plants treated with PO and NO showed comparatively improved growth across key parameters, including plant height (Fig. 3), number of leaves (Fig. 4), leaf area (Fig. 5), and stem girth (Fig. 6). These findings indicate that PO and NO treatments may mitigate the negative effects of salinity on plant growth, offering potential benefits for improving plant development under saline conditions.



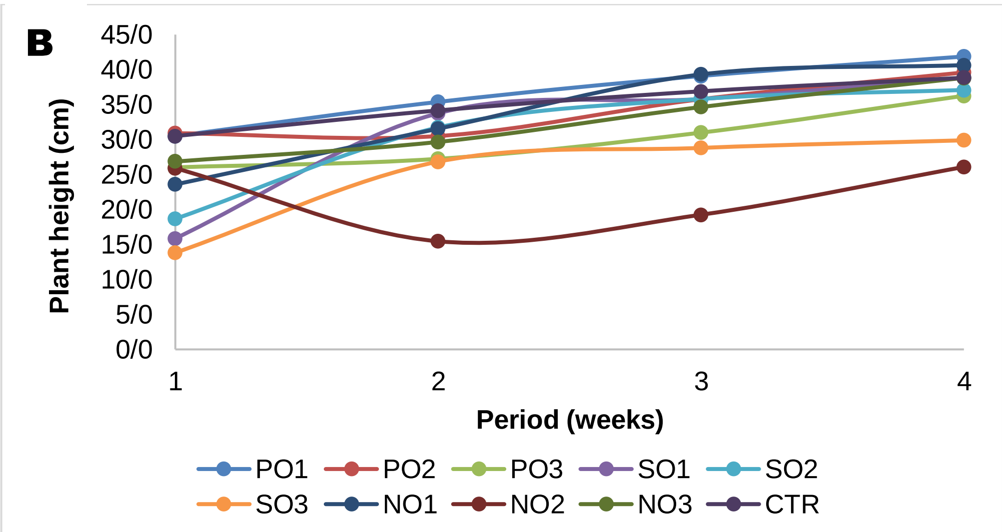


Fig. 3. Plant height of *Celosia argentea* after exposure to anion treatment.

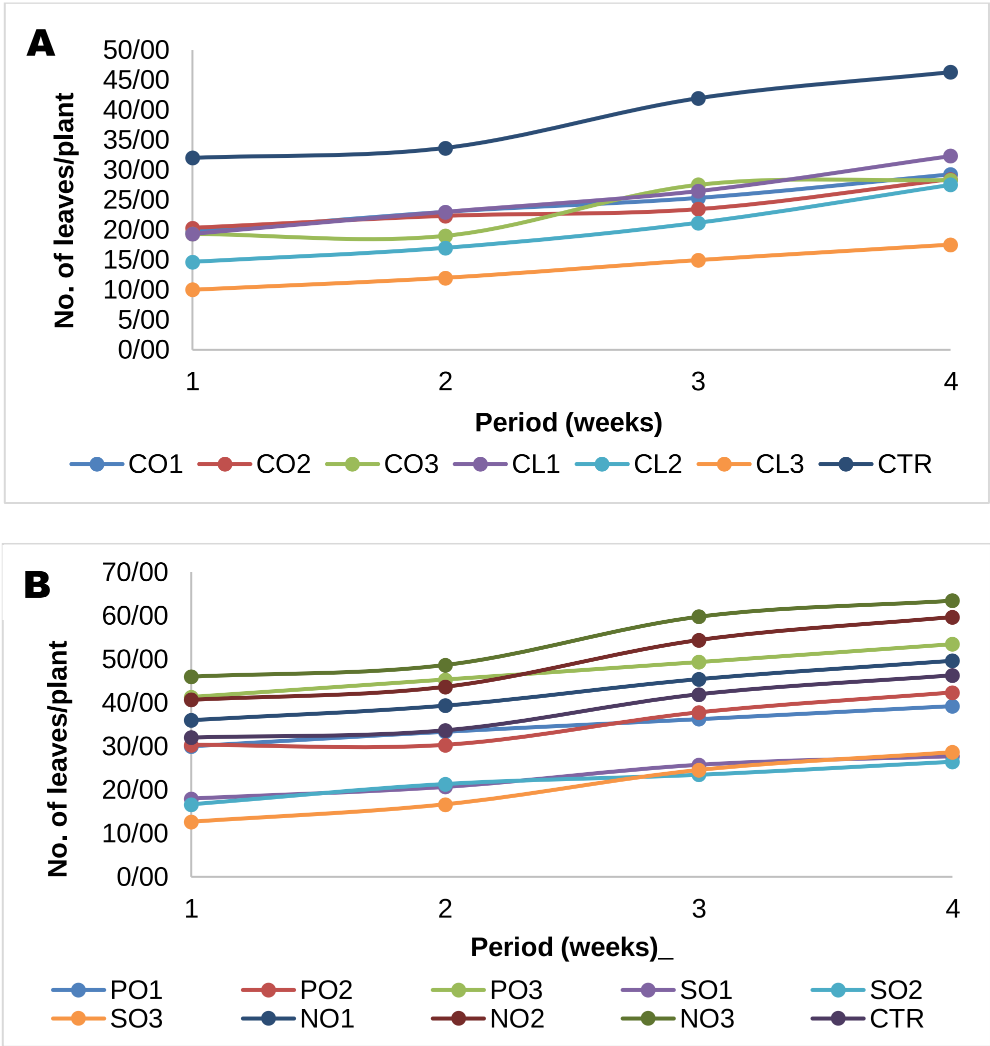
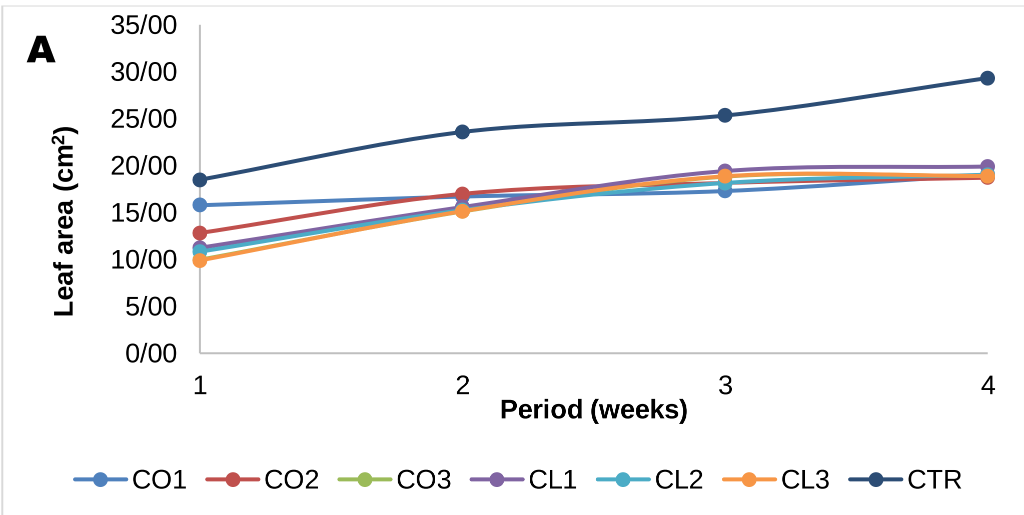


Fig. 4. Number of leaves per plant of *Celosia argentea* after exposure to anion treatment.



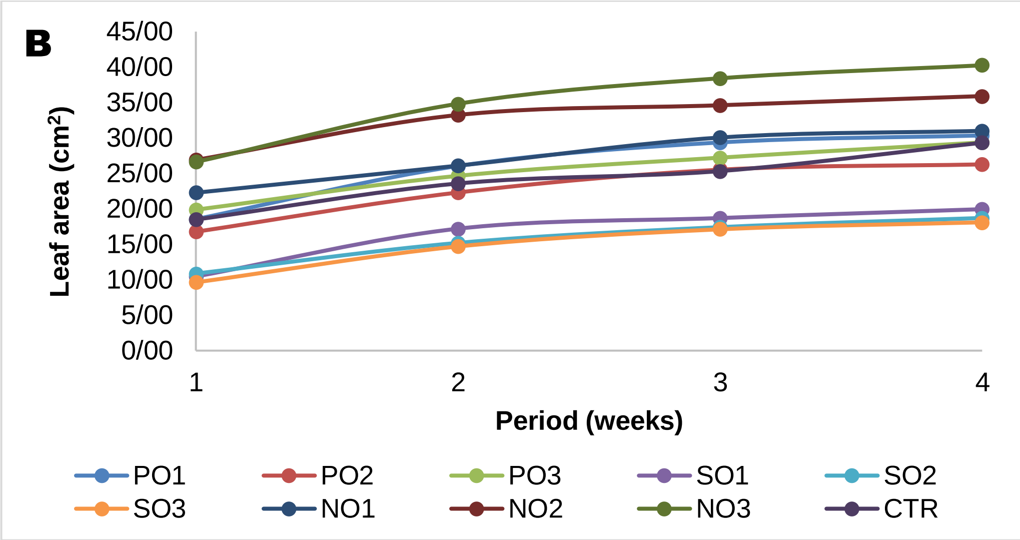


Fig. 5. Leaf area of *Celosia argentea* after exposure to anion treatment.

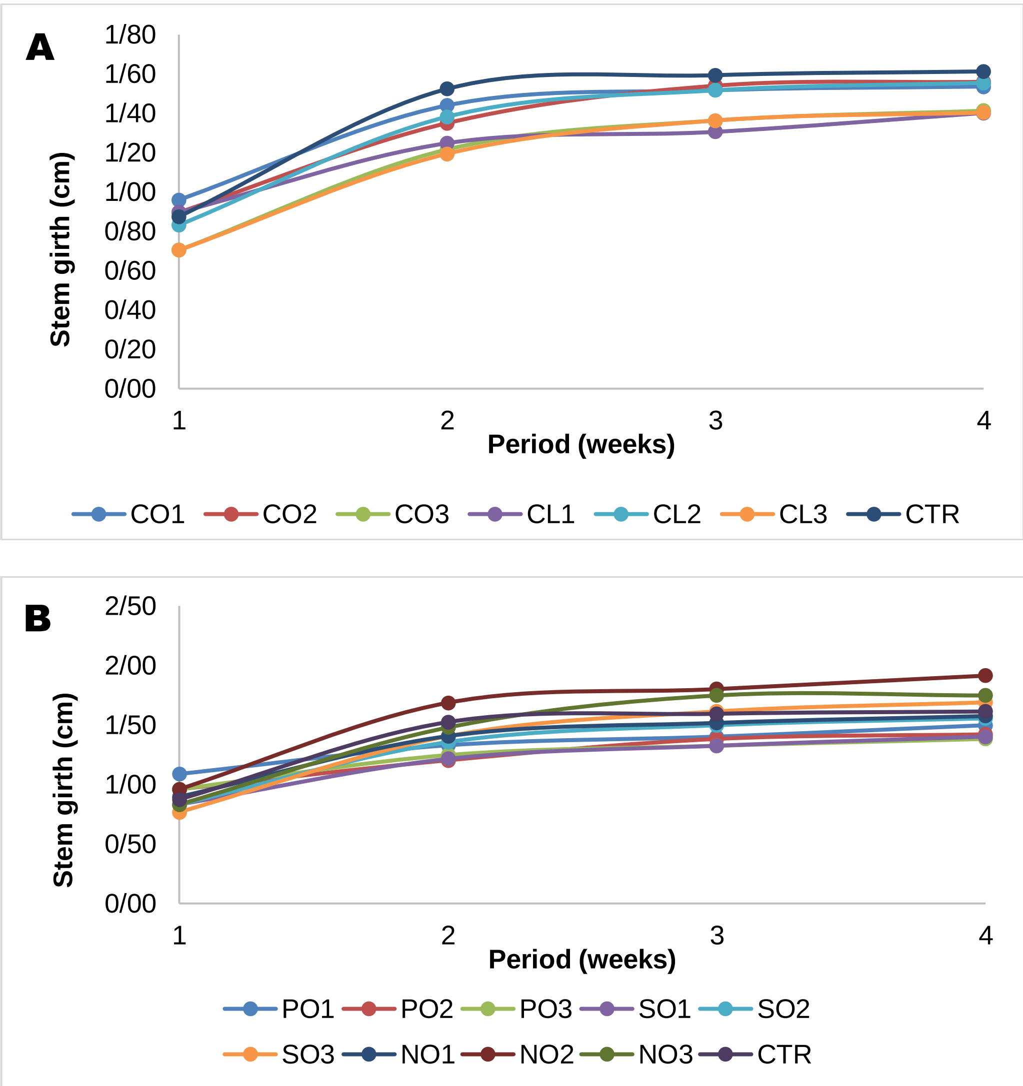


Fig. 6. Stem girth of *Celosia argentea* after exposure to anion treatment. CO carbonate, CL chloride, PO phosphate, SO sulfate, NO nitrate of sodium, CTR control. Category 3 = 5000 ppm (sodic- saline), Category 2 = 500 ppm (sodic), Category 1 = 50 ppm (slightly sodic).

Morphological evaluation of *Celosia argentea* at six weeks revealed significant variations in plant height and leaf count across the different treatments (Table 3). Control plants exhibited the greatest height (38.83 cm), while those grown in sodic soils (CO2, CO3, CL1, CL2, and CL3) showed marked reductions. Notably, the most substantial decline in plant height was observed in the CL3 treatment, which contained 5000 ppm sodium chloride; plants in this group reached only 19.81 cm, representing a 49% reduction compared to the control. Leaf count also decreased significantly in sodic soils amended with sodium carbonate (ranging from 28.33 to 29.26) and sodium chloride. Similarly, sulfate-sodic soils showed comparable reductions in leaf count, ranging from 26.44 to 28.64.

Table 3. Morphological traits of *Celosia argentea* at 6 weeks after sowing.

	Plant height (cm)	No. leaves/plant	Leaf area (cm^2)	Stem girth (cm)
CO1	35.81	29.26*	19.05	1.54
CO2	23.34*	28.45*	18.71	1.56
CO3	21.15*	28.33*	18.89	1.41
CL1	20.98*	32.32*	19.89	1.4
CL2	22.97*	27.54*	19.03	1.56
CL3	19.81*	17.53*	18.89	1.4
PO1	41.87	39.23	30.36	1.5
PO2	39.59	42.37	26.27	1.42
PO3	36.26	53.45	29.37	1.38
SO1	38.82	27.72*	19.95	1.4
SO2	37.09	26.44*	18.71	1.56
SO3	29.89	28.64*	18.12	1.69
NO1	40.64	49.65	31.06	1.57
NO2	26.08	59.71*	38.91*	1.91
NO3	38.82	63.45*	41.25*	1.75
CTR	38.83	46.31	28.33	1.61
LSD (0.05)	13.02	12.43	8.33	0.53
p-value	0.057	0.042	0.009	0.294

Values do not compare with the control on the same column ($P < 0.05$). CO carbonate, CL chloride, PO phosphate, SO sulfate, NO nitrate of sodium, CTR control. Category 3 = 5000 ppm (sodic-saline), Category 2 = 500 ppm (sodic), Category 1 = 50 ppm (slightly sodic).

In contrast, stem girth remained relatively stable across treatments, ranging from 1.38 to 1.91 cm, with no significant differences observed. Control plants produced an average of 46 leaves per plant. These results indicate that sodicity—particularly at high sodium chloride concentrations—substantially affects the growth of *Celosia argentea*, as evidenced by reductions in plant height and leaf count.

Table 4 presents above-ground plant yield parameters following exposure to sodic salinity under various anionic compositions. Notably, the type of anion in sodic soil did not significantly influence the number of days to flowering, which ranged from 53.46 to 63.65 days across treatments, remaining statistically comparable to the control (55.32 days; P > 0.05). This suggests that sodic salinity, irrespective of anion type, does not alter flowering time in *Celosia argentea*. However, seed weight per plant varied significantly among treatments. Compared to the control (0.65 g), reductions were observed in CO2 (0.35 g; 46% decrease), CL1 (0.48 g; 26% decrease), and CL3 (0.488 g; 25% decrease). In contrast, treatments with SO1 (0.77 g; 18% increase) and NO1 (0.83 g; 28% increase) resulted in enhanced seed weights. These findings suggest that certain anions, particularly sulfate and nitrate, may mitigate the negative effects of sodicity or even enhance seed production in *Celosia argentea* under saline conditions.

Foliar yield and leaf count were significantly affected by sodic salinity under varying anionic compositions. Foliar yield, measured as the dry weight of above-ground plant material in grams, decreased in soils containing carbonate, chloride, phosphate, and sulfate anions. In contrast, sodic soils associated with nitrate showed no significant change in foliar yield (P > 0.05). Similarly, the number of leaves per plant declined by 36.82–38.88% in carbonate-associated sodic soils. However, a slight increase of 3.5% in leaf number was observed in soils amended with 50 ppm sodium phosphate (Table 5).

Table 4. Above-ground plant yield parameters.

	Day to flowering (d)	Seed wt. per plant (g)	Above ground biomass (g DW plant^{-1})	Foliar yield (g DW plant^{-1})
CO1	58.81	0.580	13.420*	4.46*
CO2	59.63	0.350*	14.920*	3.58*
CO3	56.82	0.640	14.496*	4.32*
CL1	59.32	0.480*	15.032*	4.63*
CL2	63.65	0.660	15.013*	3.65*
CL3	61.25	0.488*	11.681*	3.26*
PO1	53.46	0.640	17.722	4.76*
PO2	55.32	0.658	18.134	5.35*
PO3	54.36	0.636	20.775	6.53
SO1	57.54	0.770*	14.282*	5.43*
SO2	55.43	0.543*	14.742*	4.04*
SO3	56.48	0.670	15.993	5.03*
NO1	50.58	0.830*	20.785	6.36
NO2	54.78	0.680	24.320	8.03
NO3	54.32	0.620	25.206	7.92
CTR	55.32	0.650	21.730	7.23
LSD (0.05)	13.24	0.103	6.436	1.424
p-value	0.184	0.337	0.032	0.006

Values do not compare with the control on the same column ($P < 0.05$). CO carbonate, CL chloride, PO phosphate, SO sulfate, NO nitrate of sodium, CTR control. Category 3 = 5000 ppm (sodic-saline), Category 2 = 500 ppm (sodic), Category 1 = 50 ppm (slightly sodic).

Table 5. Comparative changes due to treatment exposure.

Code	Plant height	No. leaves/ plant	Leaf area	Stem girth	Above ground biomass	Foliar yield	Day to flowering	Seed weight per plant
	Percentage change, Δ%							
CO1	-7.79	-36.82	-35.05	-4.62	-38.2	-37.8	6.3	-10.8
CO2	-39.9	-38.56	-36.23	-3.11	-31.3	-49.8	7.7	-46.2
CO3	-45.52	-38.82	-35.60	-12.24	-33.3	-39.7	2.7	-1.5
CL1	-45.96	-30.25	-32.17	-12.94	-30.8	-35.5	7.2	-26.2
CL2	-40.84	-40.62	-35.12	-3.40	-30.9	-48.8	15.1	1.5
CL3	-49.01	-62.15	-35.60	-12.83	-46.2	-54.2	10.7	-25.0
PO1	7.83	-15.29	3.50	-6.98	-18.4	-33.7	-3.4	-1.5
PO2	1.95	-8.51	-10.42	-11.75	-16.6	-25.6	0.0	1.2
PO3	-6.62	15.42	0.13	-14.14	-4.4	-9.5	-1.7	-2.2
SO1	-0.02	-40.14	-31.97	-12.94	-34.3	-24.6	4.0	18.5
SO2	-4.49	-42.9	-36.21	-3.40	-32.2	-43.5	0.2	-16.5
SO3	-23.02	-38.16	-38.28	4.94	-26.4	-30.0	2.0	3.1
NO1	4.66	7.21	5.70	-2.21	-4.3	-11.9	-8.6	27.7
NO2	-32.83	28.93	22.42	18.87	11.9	10.9	-1.0	4.6
NO3	-0.02	37.01	37.22	8.52	16.0	9.3	-1.8	-4.6

Negative values indicate percentage reduction compared to the control; while positive values indicate percentage increase compared to the control. CO carbonate, CL chloride, PO phosphate, SO sulfate, NO nitrate of sodium, CTR control. Category 3 = 5000 ppm (sodic-saline), Category 2 = 500 ppm (sodic), Category 1 = 50 ppm (slightly sodic).

The extent of foliar yield reduction varied among the different anionic treatments. Carbonate-associated sodic soils exhibited reductions ranging from 37.8% to 49.8%, while chloride-associated sodic soils showed the most pronounced decline at 54.2%. These findings indicate that specific anions, particularly chloride and carbonate, intensify the adverse effects of sodic salinity on foliar yield and leaf number in *Celosia argentea*. The differential plant responses to various anions underscore the importance of considering anion type when assessing or mitigating the impacts of sodic salinity on plant growth.

Due to unforeseen circumstances, the plants were left unattended for an additional seven weeks without irrigation, resulting in an unintentional drought stress experiment. Although data were not collected on relative water content (RWC) of leaves, soil moisture levels, or atmospheric water potential during this period, significant reductions in plant growth parameters were observed (Table 6), along with visible symptoms of water stress, such as leaf wilting and reduced stomatal conductance. These observations strongly suggest that the plants experienced drought stress; however, we acknowledge that the absence of quantitative data on RWC, soil water content, and atmospheric water potential represents a limitation of this aspect of the study.

Table 6. Resilience at 15 weeks (plants were exposed to simulated drought only during the last 6 weeks).

	Av. Resilient plant height (cm)	No. of remaining green plant standing	Total No of green leaves remaining per bowl	Av. No. of leaves per plant
CO1	19.2	3.66*	18.72*	5.11
CO2	41.2*	5.49	29.67*	9.57
CO3	24.3	3.66*	41.16	11.25
CL1	18.4	2.75*	26.88*	8.67
CL2	21.1	2.75*	35.43	11.43
CL3	32.1*	4.58*	45.57	14.70
PO1	34.5*	2.75*	47.74	15.40
PO2	16.9	6.41	38.75	12.50
PO3	12.7	5.49	35.84	11.56
SO1	13.7	5.49	23.56*	7.60
SO2	17.6	8.24	14.11*	4.55
SO3	16.0	6.41	24.57*	3.83
NO1	28.5*	9.16	24.16*	2.64
NO2	32.4*	7.33	42.23	15.75
NO3	23.7	10.99	38.13	12.30
CTR	17.8	8.24	43.06	14.44
LSD (0.05)	9.28	3.12	12.42	NA
P-value	0.085	0.138	0.015	NA

Values do not compare with the control on the same column ($P < 0.05$). CO carbonate, CL chloride, PO phosphate, SO sulfate, NO nitrate of sodium, CTR control. Category 3 = 5000 ppm (sodic-saline), Category 2 = 500 ppm (sodic), Category 1 = 50 ppm (slightly sodic).

The results revealed significant differences in plant resilience across treatments. Notably, plants cultivated in soils containing nitrate and sulfate anions demonstrated enhanced drought tolerance, retaining 60–70% of their initial biomass. In contrast, those grown in carbonate- and chloride-amended soils exhibited substantial biomass loss, maintaining only 20–30% of their original biomass. These findings suggest that certain anions—particularly nitrate and sulfate—may confer increased drought resilience in *Celosia argentea*, enabling the plants to better withstand unintended periods of water scarcity (Fig. 7).

The analysis of plant resilience under drought conditions revealed pronounced differences among treatments. Notably, plant height in CO2 (41.2 cm), CL3 (32.1 cm), and NO3 (32.4 cm) treatments showed significant increases compared to the control (17.8 cm), suggesting that sodic soils containing specific anions—carbonate, chloride, and nitrate—enhanced plant resilience under drought stress. Variation was also observed in the number of surviving plant stands following drought exposure. While the control retained 8 plants, CO-sodic soils maintained between 3 and 5 plants, and CL-sodic soils retained 3 to 4 plants. In contrast, no significant changes in plant survival were observed in sulfate- (SO) and nitrate- (NO) sodic soils.

Additionally, the total number of green leaves per bowl decreased significantly in CO1, CO2, CL1, CL2, SO1, SO2, and SO3 treatments compared to the control (43.06 leaves). These findings indicate that specific anions influence drought resilience in *Celosia argentea*, particularly in terms of plant height and survival, with nitrate- and sulfate-associated treatments offering greater protection against drought-induced stress (Fig. 8).

Fig. 7. *Celosia argentea* emergents at (**A**) three weeks; (**B**) 25 d after sowing.

The Effect Index was calculated to assess the overall impact of treatments on plant growth, incorporating data from all measured parameters throughout the study. This comprehensive analysis revealed differential responses to treatments under sodic-salinized conditions. Notably, nitrate-treated plants (NO) demonstrated enhanced overall development relative to the control. In contrast, plants grown in sodic soils amended with phosphate (PO), sulfate (SO), carbonate (CO), and chloride (CL) anions generally exhibited poor performance. The most pronounced negative effects were observed in carbonate- and chloride-affected soils, which showed substantial reductions in plant growth and development (Fig. 9). These findings underscore the distinct and varying impacts of specific anions on plant performance under sodic-salinized conditions.

Fig. 8. Picture of experimental plots at 10 weeks of sowing, including exposure to 3 weeks of drought.

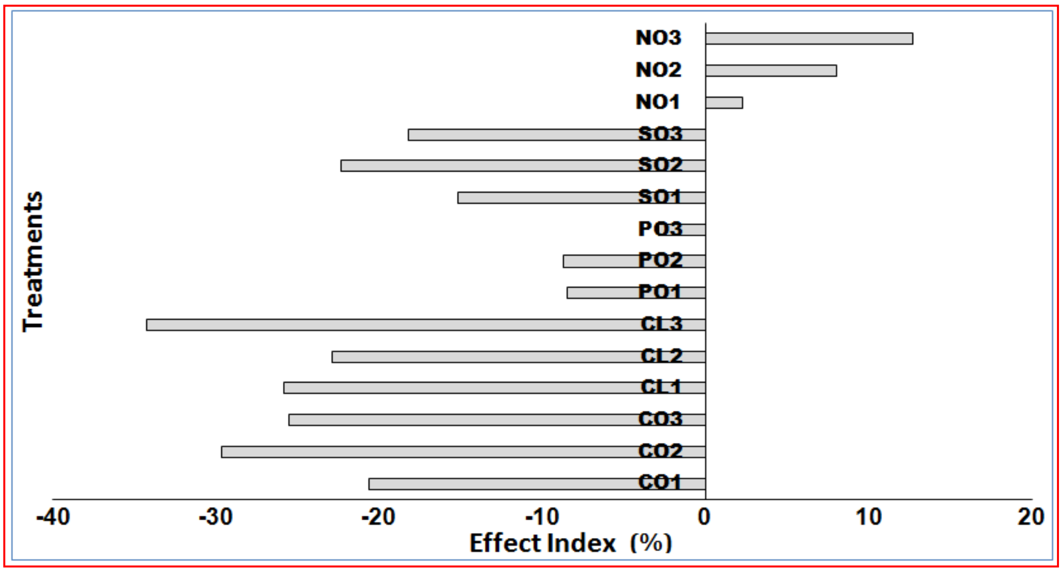


Fig. 9. Effect index (to measure which, based on measured characteristics were more affected). CO carbonate, CL chloride, PO phosphate, SO sulfate, NO nitrate of sodium, CTR control. Category 3 = 5000 ppm (sodic-saline), Category 2 = 500 ppm (sodic), Category 1 = 50 ppm (slightly sodic).

Figures 10 and 11 present the heterotrophic rhizosphere and total heterotrophic bacterial counts after seven weeks, ranging from 4.96–5.87 log_{10} cfu g^{-1} and 4.99–5.48 log_{10} cfu g^{-1}, respectively. Notably, comparisons between sulfate-sodic soils and the control revealed no significant differences in either heterotrophic bacterial counts or total rhizosphere bacterial counts. These results suggest that sodic conditions involving sulfate anions do not adversely affect bacterial populations, thereby maintaining microbial community stability within the rhizosphere of *Celosia argentea*.

Five dominant rhizospheric bacterial isolates were recovered from plant samples subjected to various treatments. Preliminary identification based on morphological and biochemical characteristics indicated the presence of *Klebsiella* sp., *Pseudomonas aeruginosa*, *Escherichia coli*, *Bacillus subtilis*, and *Enterobacter aerogenes*. However, subsequent molecular characterization revealed distinct identities for each isolate. The confirmed species were *Klebsiella aerogenes* strain AUH-KAM-9, *Serratia marcescens* strain PPM4, *Escherichia coli* strain UNIBEN19, *Bacillus safensis* subsp. *safensis* strain N32, and *Enterobacter cloacae* strain BGK-4 (Figs. 10–12; Table 7). These findings emphasize the importance of molecular techniques for accurate bacterial identification, highlighting potential discrepancies between initial morphological and biochemical assessments.

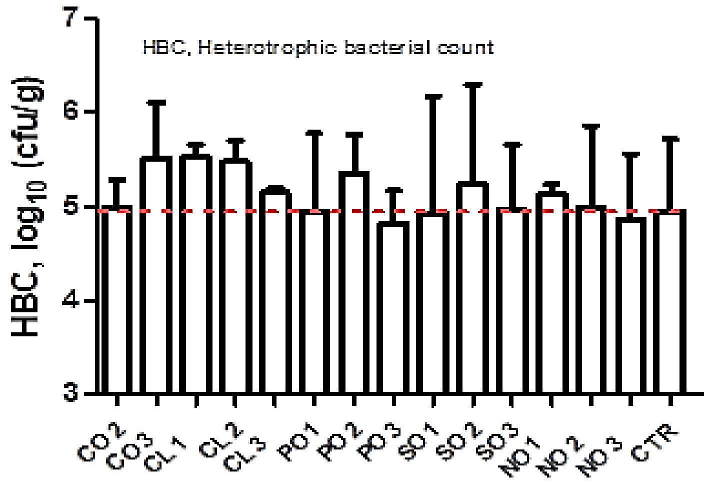


Fig. 10. Heterotrophic rhizospheric bacterial counts obtained from plant roots at 7 weeks after sowing.

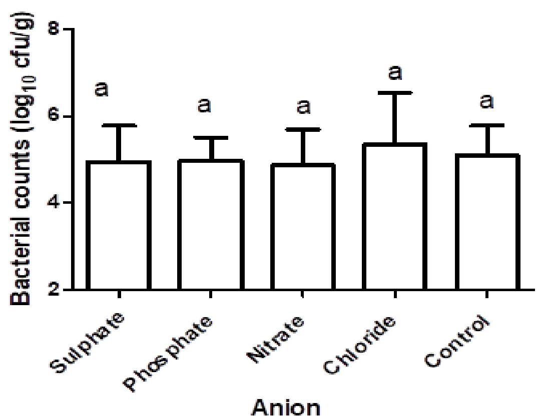


Fig. 11. Heterotrophic bacterial counts.

The plant growth-promoting (PGP) potential of bacterial isolates associated with the rhizosphere of the test plant was evaluated. Notably, all isolates demonstrated the ability to produce ammonia and indole-3-acetic acid, both key indicators of PGP activity. Furthermore, with the exception of *Enterobacter cloacae*, the remaining isolates—*Klebsiella aerogenes*, *Serratia marcescens*, *Escherichia coli*, and *Bacillus safensis*—exhibited nitrogen-fixing and phosphate-solubilizing capabilities, suggesting their potential to enhance plant nutrition and growth (Table 8). These results underscore the beneficial role of these rhizospheric bacteria in promoting plant development and highlight their potential applications in sustainable agricultural practices.

(a) Control samples (b) Phosphate samples (c) Carbonate samples

(d) Nitrate samples (e) chloride samples (f) sulphate samples

Fig. 12. Bacterial isolates from rhizosphere samples obtained from various treatment regimens.

Table 7. Molecular identification of the bacterial isolates in the plants rhzosphere.

Code	Scientific Name	Total Score	Query Cover	Percent Identity	Accession number
BA1	*Klebsiella aerogenes* strain AUH-KAM-9	1136	100	100.00	CP048598.1
BA2	*Serratia marcescens* strain PPM4	2719	100	99.80	JQ308604.1
BA3	*Escherichia coli* strain UNIBEN19	2555	100	100.00	MN317310.1
BA4	*Bacillus safensis*subsp. safensis strain N32	2569	99	99.58	MN555373.1
BA5	*Enterobacter cloacae* strain BGK-4	2679	99	99.87	OP648170.1

Table 8. Test for plant growth promotion among rhizospheric bacterial isolates.

Isolate	Sub-cultured Isolates	Salinity Tolerance (7.5%)	Nitrogen fixation	Phosphate solubilization	Ammonia
Bacillus (n = 5)	CTR, CO3, CL3	Growth (100%)	Negative (20%), Positive (80%)	Negative (80%), Positive (20%)	Positive (20%), Negative (80%)
E. coli (n = 23)	NO3, SO1, SO3, PO1, CTR, CO1, CL1, NO1, NO3	Growth (83.6%) NG (17.4%)	Negative (4.3%), Positive (95.7%)	Negative (4.3%), Positive (95.7%)	Negative (69.6%), Positive (30.4%)
Enterobacter (n = 5)	PO1, CO3, CL3	Growth (80%); NG (20%)	Positive (40%), Negative (60%)	Positive (40%), Negative (60%)	Positive (60%), Negative (40%)
Klebsiella (n = 7)	PO1, PO3, CTR, CL3, NO1, NO3	Growth (100%)	Negative (85.7%), Positive (14.3%)	Negative (85.7%), Positive (14.3%)	Negative (57.2%), Positive (42.8%)
Serratia (n = 8)	SO1, SO3, PO3, CTR, CO1, CL3	Growth (87.5%), NG (12.5%)	Negative (87.5%), Positive (12.5%)	Negative (87.5%), Positive (12.5%)	Positive (62.5%), Negative (37.5%)
Total	48	48	48	48	48
Percentage(-)	NA	12.5	12.5	12.5	12.5
Percentage(+)	NA	87.5	87.5	87.5	87.5

Percentage(-) percentage reductions, Percentage(+) percentage increase compared to the total. CO carbonate, CL chloride, PO phosphate, SO sulfate, NO nitrate of sodium, CTR control. Category 3 = 5000 ppm (sodic-saline), Category 2 = 500 ppm (sodic), Category 1 = 50 ppm (slightly sodic).

Discussion

This study confirmed significant growth impairment in *Celosia argentea* by assessing the impact of salinity on the species' growth and development. The findings align with previous research that highlights salinity's detrimental effects on plant growth and productivity (Bayabil et al., 2020; Kibria & Hoque, 2019; Kalaji et al., 2016). Salinity stress initiates a cascade of physiological disruptions—ionic, oxidative, and osmotic—which collectively hinder plant development and reduce yield (Mohinani et al., 2021).

This investigation focused particularly on the effects of sodic soils, characterized by sodium concentrations exceeding 500–1000 ppm, to elucidate how different anions associated with sodium salts influence soil salinization. Preliminary trials using 5000 ppm NaCl revealed the deleterious impact of sodic-salinized soils on plant growth. Seed emergence rates varied significantly across treatments: soils treated with NaCl exhibited markedly reduced emergence (<150 seeds 0.5 g^{-1}), whereas $NaNO_3$-treated soils displayed comparatively higher emergence rates (150–267 seeds 0.5 g^{-1}). These results indicate that NaCl and Na_2CO_3-based salinity significantly impair seedling performance.

This research emphasizes the critical importance of sodium salt type in salinization studies, given its demonstrable influence on plant development. Addressing the agricultural challenges posed by salinity requires the implementation of innovative, salt-specific strategies to mitigate its adverse effects and sustain crop productivity. Salinity severely compromises plant development by disrupting water uptake and balance, resulting in pronounced growth inhibition (Shahid et al., 2020). Moreover, this stressor impedes seed germination and early seedling development, particularly during key stages of the plant life cycle (Chaturvedi et al., 2017).

A comprehensive understanding of salinity's impacts is essential for the advancement of resilient agricultural practices. Salinity stress adversely affects plants in multiple ways, including reduced growth and yield, impaired metabolic activity, and diminished absorption of water and essential minerals (Ali et al., 2017). In response, plants modulate gene expression and metabolic pathways—such as the phenylpropanoid biosynthesis pathway—to enhance salt tolerance (Zhu et al., 2021; Zhang et al., 2013). Compounds such as salicylic acid have been shown to promote plant growth and induce salt-responsive gene expression under saline conditions (Zheng et al., 2018). Additionally, biochar and arbuscular mycorrhizal fungi have demonstrated the capacity to alleviate the negative effects of salinity on plant growth, potentially by enhancing salt ion absorption (Porcel et al., 2021; Alotaibi, 2022).

Detailed analysis of plant growth data revealed significant treatment-based variation. Notably, plants exposed to sodic soils amended with nitrate exhibited superior growth relative to the control. Conversely, treatments containing phosphate (PO_4), sulfate (SO_4), carbonate (CO_3), and chloride (Cl^-) anions resulted in diminished growth performance, with CO_3^- and Cl^--dominated soils exerting the most pronounced inhibitory effects.

Understanding the underlying mechanisms of plant responses to salinity stress is essential for developing effective mitigation strategies and enhancing plant productivity under saline conditions. Identifying the key determinants of salinity tolerance will enable the optimization of plant growth and development in increasingly challenging environments.

Five predominant rhizospheric bacteria were isolated from plant samples subjected to various treatments. Preliminary identification suggested the presence of *Klebsiella* spp., *Pseudomonas aeruginosa*, *Escherichia coli*, *Bacillus subtilis*, and *Enterobacter aerogenes*. However, subsequent molecular characterization revealed their precise taxonomic identities as *Klebsiella aerogenes* AUH-KAM-9, *Serratia marcescens* PPM4, *Escherichia coli* UNIBEN19, *Bacillus safensis* subsp. *safensis* N32, and *Enterobacter cloacae* BGK-4, underscoring the critical importance of molecular verification in microbial identification.

Rhizospheric bacteria play an essential role in plant survival, particularly in vegetable crops, as they significantly influence plant growth and development (Compant et al., 2010; Mhlongo et al., 2018). These beneficial microorganisms enhance plant performance through mechanisms such as drought tolerance (Sati et al., 2023), increased resistance to salinity stress (Yang et al., 2020), and the modulation of rhizosphere bacterial diversity (Duan et al., 2021). Moreover, they contribute to the regulation of root-associated microbial communities, particularly in halophytic plant species (Li et al., 2022).

The rhizosphere functions as a dynamic center of microbial activity, enriched by root exudates that support diverse bacterial populations (Chiranjeevi et al., 2020). The rhizospheric microbiome exerts substantial influence over plant metabolism, growth, and yield (Baskaran et al., 2022). It comprises both beneficial and pathogenic organisms, each playing a role in shaping plant health and productivity (Mhlongo et al., 2018). A nuanced understanding of the intricate plant-microbe interactions within this zone is therefore essential for the development of strategies aimed at improving crop productivity.

Members of the genera *Bacillus*, *Pseudomonas*, and *Klebsiella* are commonly found in the rhizosphere, indicating their prominent roles in allelopathy and plant growth promotion (Zuluaga et al., 2021). These bacteria are particularly relevant to the survival and resilience of vegetable crops under abiotic and biotic stress. For instance, *Bacillus amyloliquefaciens* FZB42 has demonstrated plant growth-promoting and protective properties under pathogen pressure (Chowdhury et al., 2013). Understanding such microbial interactions is essential for leveraging their potential in sustainable agriculture.

Molecular studies have identified both *Klebsiella* and *Bacillus* species as beneficial agents that promote growth in tomato plants (Helal et al., 2022). The role of *Klebsiella variicola* in maize seedling development (Yang & Yang, 2020) further supports the relevance of *Bacillus*, *Pseudomonas*, and *Klebsiella* species in the *Celosia* rhizosphere. Harnessing these bacterial communities holds promise for enhancing crop resilience and advancing sustainable agricultural practices.

This study provides key insights into plant responses under sodic-salinity conditions, highlighting the significant role of dominant anions in shaping plant growth patterns. The results reveal that plant growth and yield are markedly inhibited in sodic-salinity environments where chloride and carbonate anions predominate. This finding emphasizes the importance of anion composition in determining plant tolerance to sodic-salinity stress.

Importantly, the research identifies a promising alleviator of salinity stress: the presence of nitrate ions significantly enhances plant morphological growth, even under sodic-saline conditions, with growth performance surpassing that of the control. This observation suggests that nitrate ions may exert salinity-alleviating effects, meriting further investigation into their physiological and molecular roles.

Uncovering the mechanisms by which nitrate mitigates salinity stress could have transformative implications for improving crop productivity and advancing global food security strategies. By elucidating the benefits of nitrate ions, researchers may develop targeted interventions to enhance plant resilience in saline environments, contributing to sustainable agricultural practices and food systems.

Conclusion

This study offers novel insights into the anion-specific modulation of *Celosia argentea*'s response to sodic-saline stress. While sodic salinity broadly impedes plant growth, our findings reveal that the associated anion significantly determines the severity of this inhibition. Specifically, high concentrations of chloride (5000 ppm NaCl) resulted in the most pronounced reduction in plant height, with a decline of 49%, whereas carbonate (Na_2CO_3) treatments led to a significant decrease in leaf count, reaching up to 38.8%. In contrast, nitrate and phosphate treatments partially mitigated the adverse effects of sodicity, with nitrate notably enhancing seed weight per plant by as much as 28%. These findings are significant, as they underscore the potential for manipulating anion composition in salt-affected soils to alleviate stress in *C. argentea*, and potentially in other agriculturally relevant crops. Additionally, the identification of rhizospheric bacterial isolates with plant growth-promoting traits presents promising opportunities for the development of bio-based strategies aimed at enhancing plant resilience under saline conditions.

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Author contributions

Conceptualization, BI; methodology, BI and DEE; software, BI and FAI; validation, BI, FAI and BOE; formal analysis, BI; investigation, DEE, UNN and BOE; resources, all authors provided the resources; data curation, DEE and UNN; writing—original draft preparation, FAI, DEE and BI; writing—review and editing, BI, FAI, DEE, UNN and BOE; visualization, BI.; supervision, BI and BOE; project administration, BI and BOE; funding acquisition, Nil. All authors have read and agreed to the published version of the manuscript.

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Conflict of Interest

The authors indicate no conflict of interest in this work.

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