

Chitooligosaccharides Enhance Growth, Ion Homeostasis, and Antioxidant Defense in Potato under Saline-Alkaline Field Conditions

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Abstract

The biostimulant effect of chitooligosaccharides (COS) to improve the crop performance under abiotic stress conditions has been proven. The present study was conducted to evaluate the effects of foliar application of COS (0.1, 0.3, and 0.5 g/L) on potato (*Solanum tuberosum* L.) under saline-alkaline field conditions in Lianyungang, China during 2023–2024. The COS application greatly enhanced the shoot and root biomass. The maximum total weight (22.2 ± 0.8 g) was obtained with a concentration of 0.3 g/L. Reduction in Na^+ levels and K^+ buildup improved ion homeostasis leading to increased K^+/Na^+ ratio. In addition, the activities of antioxidant enzymes (SOD, POD and CAT) were significantly enhanced and the malondialdehyde and H_2O_2 contents were reduced by COS treatments. The level of osmoprotectants such as proline, soluble carbohydrates and proteins was shown to increase. These physiological benefits synergistically enhanced growth, stress resistance and yield under saline-alkaline conditions, indicating COS as a promising candidate for sustainable potato cultivation in marginal locations.

1. Introduction

Soil salinization and alkalinization are increasing in agricultural lands all over the world, especially in coastal and desert areas and severely affect the growth, yield and quality of crops such as potato (*Solanum tuberosum* L.) (Jaarsma et al., 2013; Khierallah & Jawad, 2017). Na^+ buildup and Na^+ suppression of K^+ uptake during saline-alkali stress impair ion homeostasis, lead to osmotic imbalance and oxidative stress and finally result in membrane lipid peroxidation (Alghamdi et al., 2022; Ali et al., 2021). These physiological abnormalities are one of the major constraints for tuber yield and plant growth (Tahir et al., 2019; Al-Taey et al., 2025).

Specifically, natural biostimulants like chitooligosaccharides (COS) have been explored as an eco-friendly strategy to enhance the plant tolerance to abiotic stressors (Liu et al., 2023; Wang et al., 2017). COS are low molecular weight oligochitosans obtained from chitosan. COS have better water solubility, biological activity and absorption in normal plant cells. Recent studies have demonstrated that COS can regulate numerous physiological processes of plants under stress situations, such as ion transport, antioxidant defence and osmolyte accumulation (Xu and Wei, 2023; Ye et al., 2023).

The COS enhanced salt tolerance via a cascade of physiological processes. The most important event is the re-establishment of ion homeostasis. COS enhances K^+ retention and reduces Na^+ absorption, therefore enhancing the K^+/Na^+ ratio in plant tissues (Zhao et al. 2025; Subramanian et al. 2023). Re-establishment of ionic homeostasis is the upstream signal of ionic toxicity and alleviation of osmotic imbalance. Additional defence responses are subsequently triggered. COS enhance the production of osmolytes (proline, soluble sugars, proteins, etc.) for osmoregulation and membrane protection (Xiong et al., 2009; Nandhini & Somasundaram, 2018). COS improves antioxidant capacity by increasing superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) activities, therefore lowering the formation of ROS (Shi et al., 2021; Lan et al., 2023). This concerted reaction is more stress resistant and cellular activity is sustained.

Exogenous treatment of COS has been found to boost seedling vigour and endogenous phytohormones in potato (Ye et al., 2023). Also, lipo-chitooligosaccharides were found to improve early growth of several crops (Tanaka et al., 2015). However, there are few publications about the application of COS to potato under saline-alkaline field conditions, especially in real farming systems with many stress variables. Few studies addressed the influence of COS on durability and stability of agricultural productivity with multi-year field testing.

The coastal degradation of Lianyungang in Jiangsu province, China is defined by saline-alkaline soils with high pH, low nutrient availability and high electrical conductivity (Table 1). These conditions are especially unfavourable for the growth of potatoes and other salt sensitive crops. The main objective is to develop sustainable and economic agronomic strategies for the improvement of potato resistance in marginal soils.

Table 1
Soil physicochemical properties of the experimental saline-alkaline field site compared with typical non-saline soil. Sampling Depth (0–20 cm)

Parameter	Saline-Alkaline Soil	Typical Soil
Soil Salinity (g/kg)	2.7	< 0.4
Electrical Conductivity (dS/m)	4.5	< 1.2
Soil pH	8.3	6.4–7.4
Total Nitrogen (%)	0.09	0.16–0.21
Total Phosphorus (%)	0.05	0.09–0.13
Total Potassium (%)	1.3	1.6–2.1

The present study was conducted to evaluate the effect of three concentrations of foliar application of COS (0.1, 0.3 and 0.5 g/L) on growth, yield attributes, ion uptake, osmolytes accumulation and antioxidant responses of potato under saline-alkaline field conditions during two successive growing seasons (2023 and 2024). The concept that COS therapy may reverse the physiological imbalances induced by salt through restoring ionic homeostasis, enhancing antioxidative defence and osmotic regulation leading to increased plant growth and yield has been examined. The results will provide vital insights into the physiological foundation and agronomic practicality of chitooligosaccharide as a biostimulator for potato under salt conditions.

2. Materials and methods

2.1. Field site and soil characteristics

Field trials were conducted throughout the growing seasons of 2023 and 2024 in the experimental station of Haizhou District, Lianyungang City, Jiangsu Province, China (34°36'N, 119°10'E). The land

features typical saline-alkaline agricultural soil with the characteristics of salinity, high pH and low nutrition. Before the investigation the physical and chemical properties of composite soil samples (0–20 cm depth) were examined. Saline-alkaline field soil salinity, electrical conductivity and pH value were 2.7 g/kg, 4.5 dS/m and 8.3, respectively. The nutrient analysis indicated that the content of total nitrogen, phosphorus and potassium was 0.09%, 0.05% and 1.3%, respectively (Table 1). These results are very different from the regular non-saline soils with salinity < 0.4 g/kg, EC < 1.2 dS/m and near neutral pH.

2.2. Experimental design and chitooligosaccharide treatments

The experiment was conducted in a randomised complete block design (RCBD) with four treatments and three replications of each treatment. Each plot was 5m × 2m with a buffer zone of 0.5m between adjacent plots. The treatments were: (1) control (application of distilled water), (2) COS-Low (0.1 g/L), (3) COS-Medium (0.3 g/L) and (4) COS-High (0.5 g/L). The COS used in this study was obtained from a commercial supplier (degree of polymerisation = 6–8) and its quality was controlled according to Liu et al. (2023). COS were applied as a foliar spray 20 days after transplanting and weekly thereafter for a total of four applications. Solutions were applied to potato leaves until run-off with a manual backpack sprayer in the early morning to avoid photodegradation. No other biostimulants or growth regulators were applied during the cultivation period.

2.3. Plant growth and yield measurements

At harvest (90 days following planting), five representative plants were randomly taken from each plot for determination of growth parameters. Shoot height was measured using a measuring tape and the number of leaves was counted manually. Root weight and shoot biomass were determined by carefully removing the roots from the soil and drying the shoots using paper towels and gentle washing. The number of tubers per plant was counted, and the fresh weight of tubers per plant was weighed. Tuber yield per plot (kg) was translated into yield per unit area (kg/m²) (Ali et al., 2021, Al-Taey et al., 2025).

2.4. Determination of ion content

Leaf samples were harvested at 60 days after seeding and dried at 70°C to a consistent weight. Dried tissues were homogenised and digested in a mixture of HNO₃ and HClO₄ (4:1, v/v). Na⁺, and K⁺ concentrations were determined using flame photometer (FP640, Shanghai Precision Instruments, China). K⁺/Na⁺ ratio was used as an ionic equilibrium (Tahir et al., 2019; Zhao et al., 2025).

2.5. Measurement of antioxidant enzyme activities and oxidative stress indicators

Fresh leaves samples were immediately frozen in liquid nitrogen for subsequent biochemical analysis. For enzyme extract preparation 0.5g of tissue was homogenised in 5 mL of phosphate buffer (pH 7.8) in ice and centrifuged at 12000 rpm for 20 min at 4°C. The supernatant was used for the enzymatic test.

SOD activity was determined by the capacity to inhibit the photochemical reduction of nitroblue tetrazolium (NBT) (Ye et al., 2023). Guaiacol was used as substrate for determination of the POD activity. The CAT activity was measured by H₂O₂ decomposition at 240 nm. Malondialdehyde (MDA) concentration was calculated using the thiobarbituric acid (TBA) reaction method, and hydrogen peroxide (H₂O₂) was measured spectrophotometrically at 390 nm (Shi et al., 2021, Lan et al., 2023).

2.6. Determination of osmolyte accumulation

Proline was estimated using acid ninhydrin method. Leaf tissue (0.5 g) was homogenised in 3% sulfosalicylic acid and centrifuged. The supernatant was treated with ninhydrin and glacial acetic acid and absorbance was measured at 520 nm (Xu and Wei, 2023). Soluble sugar content was estimated by anthrone method. Briefly, leaf tissue (0.5 g) was extracted in 80% ethanol and the supernatant reacted with anthrone reagent. Absorbance was measured at 620 nm. The soluble protein concentration was measured by Coomassie Brilliant Blue G-250 assay using bovine serum albumin as standard (Xiong et al., 2009; Nandhini & Somasundaram, 2018).

2.7. Statistical analysis

All data were presented as mean $\pm$ standard deviation (SD) derived from three biological replicates. Statistical significance was assessed via one-way ANOVA, succeeded by Duncan's multiple range test at $p < 0.05$, utilizing SPSS v22.0 software (IBM Corp., Armonk, NY, USA). Distinct letters within rows signify substantial variations among treatments.

3. Results

3.1. Effects of COS on potato growth and yield

COS treatment considerably increased shoot and root biomass of potato plants grown in saline-alkaline environments (Table 2). The total plant weight in COS-Medium (0.3 g/L) treatment was significantly increased to 21.9 ± 0.8 g and 22.2 ± 0.8 g in 2023 and 2024 respectively, compared with the control group ($P < 0.05$). Shoot and root weights were also increased under all COS treatments predominantly at medium and high dosages.

Table 2

Effects of chitooligosaccharide (COS) treatment on shoot weight, root weight, and total weight of potato under saline-alkaline field conditions in 2023 and 2024.

Parameters	Control	COS-Low (0.1 g/L)	COS-Medium (0.3 g/L)	COS-High (0.5 g/L)
2023				
Shoot weight (g)	13.2 ± 0.5 ^a	15.7 ± 0.6 ^b	18.1 ± 0.7 ^c	17.8 ± 0.5 ^b
Root weight (g)	2.7 ± 0.2 ^a	3.3 ± 0.2 ^b	3.8 ± 0.2 ^b	3.6 ± 0.2 ^b
Total weight (g)	15.9 ± 0.6 ^a	19.0 ± 0.7 ^b	21.9 ± 0.8 ^c	21.4 ± 0.6 ^b
2024				
Shoot weight (g)	13.6 ± 0.6 ^a	16.0 ± 0.7 ^b	18.3 ± 0.6 ^b	17.9 ± 0.6 ^b
Root weight (g)	2.8 ± 0.2 ^a	3.4 ± 0.2 ^b	3.9 ± 0.2 ^b	3.7 ± 0.2 ^b
Total weight (g)	16.4 ± 0.6 ^a	19.4 ± 0.7 ^b	22.2 ± 0.8 ^c	21.6 ± 0.7 ^b
Values are the mean ± SD (n = 3). Different superscript letters within each row indicate significant differences ($P < 0.05$).				

3.2. Ion homeostasis regulation

COS had considerable effects on Na⁺ and K⁺ concentrations in leaf tissues and consequently improved ionic balance (Table 3). Na⁺ concentrations were lower and K⁺ buildup was higher than the control in all COS treatments. The 0.3 g/L treatment considerably created the greatest K⁺/Na⁺ ratios, 2.55 ± 0.10 in 2023 and 2.68 ± 0.09 in 2024, which were more than 1.7 times the control values. The difference of ion balance suggested that COS induced specific ion absorption and homeostasis during salt stress.

Table 3

Effects of chitooligosaccharide (COS) treatment on Na⁺, K⁺ content and K⁺/Na⁺ ratio in potato under saline-alkaline field conditions in 2023 and 2024.

Parameters	Control	COS-Low (0.1 g/L)	COS-Medium (0.3 g/L)	COS-High (0.5 g/L)
2023				
Na ⁺ (mg/g FW)	8.3 ± 0.4 ^a	7.1 ± 0.3 ^a	6.2 ± 0.3 ^a	6.4 ± 0.3 ^a
K ⁺ (mg/g FW)	12.2 ± 0.6 ^a	14.1 ± 0.7 ^a	15.8 ± 0.8 ^a	15.3 ± 0.7 ^a
K ⁺ /Na ⁺ ratio	1.47 ± 0.08 ^a	1.99 ± 0.09 ^a	2.55 ± 0.10 ^a	2.39 ± 0.09 ^a
2024				
Na ⁺ (mg/g FW)	8.1 ± 0.4 ^a	6.9 ± 0.3 ^a	6.0 ± 0.3 ^a	6.3 ± 0.3 ^a
K ⁺ (mg/g FW)	12.4 ± 0.7 ^a	14.4 ± 0.7 ^a	16.1 ± 0.7 ^a	15.6 ± 0.6 ^a
K ⁺ /Na ⁺ ratio	1.53 ± 0.07 ^a	2.09 ± 0.08 ^a	2.68 ± 0.09 ^a	2.48 ± 0.08 ^a
Values are the mean ± SD (n = 3). Different superscript letters within each row indicate significant differences (<i>P</i> < 0.05).				

3.3. Enhancement of antioxidant defense and stress mitigation

Activities of antioxidant enzymes (SOD, POD and CAT) were improved after COS treatment (Table 4). The COS-Medium group showed the greatest enzyme activities in both years, with SOD activity of 158.7 ± 6.5 U/mg protein in 2023 and 160.3 ± 6.4 U/mg in 2024. Meanwhile, the oxidative stress indicators, malondialdehyde (MDA) and hydrogen peroxide (H₂O₂) levels were dramatically reduced in COS treated plants. The antioxidative impact of COS is shown by the decrease of MDA concentration to 3.9 ± 0.2 nmol/g in the COS-Medium group and H₂O₂ to 4.7 ± 0.3 µmol/g in 2023 from 5.6 ± 0.3 nmol/g and 6.8 ± 0.4 µmol/g in the control group.

Table 4

Effects of chitooligosaccharide (COS) treatment on antioxidant enzyme activities and oxidative stress indicators in potato under saline-alkaline field conditions in 2023 and 2024.

Parameters	Control	COS-Low (0.1 g/L)	COS-Medium (0.3 g/L)	COS-High (0.5 g/L)
2023				
SOD (U/mg protein)	128.5 ± 5.3 ^a	143.2 ± 6.1 ^a	158.7 ± 6.5 ^a	155.4 ± 6.2 ^a
POD (U/mg protein)	42.1 ± 2.1 ^a	47.8 ± 2.3 ^a	52.6 ± 2.4 ^a	51.9 ± 2.3 ^a
CAT (U/mg protein)	19.4 ± 1.0 ^a	22.6 ± 1.1 ^a	25.1 ± 1.2 ^a	24.6 ± 1.1 ^a
MDA (nmol/g FW)	5.6 ± 0.3 ^a	4.7 ± 0.2 ^a	3.9 ± 0.2 ^a	4.1 ± 0.2 ^a
H ₂ O ₂ (μmol/g FW)	6.8 ± 0.4 ^a	5.5 ± 0.3 ^a	4.7 ± 0.3 ^a	4.9 ± 0.3 ^a
2024				
SOD (U/mg protein)	130.2 ± 5.4 ^a	145.0 ± 6.3 ^a	160.3 ± 6.4 ^a	157.1 ± 6.1 ^a
POD (U/mg protein)	43.0 ± 2.0 ^a	48.3 ± 2.4 ^a	53.2 ± 2.5 ^a	52.3 ± 2.4 ^a
CAT (U/mg protein)	19.7 ± 1.1 ^a	23.0 ± 1.0 ^a	25.6 ± 1.2 ^a	24.9 ± 1.1 ^a
MDA (nmol/g FW)	5.4 ± 0.3 ^a	4.6 ± 0.2 ^a	3.8 ± 0.2 ^a	4.0 ± 0.2 ^a
H ₂ O ₂ (μmol/g FW)	6.6 ± 0.4 ^a	5.4 ± 0.3 ^a	4.5 ± 0.2 ^a	4.7 ± 0.3 ^a
Values are the mean ± SD (n = 3). Different superscript letters within each row indicate significant differences (<i>P</i> < 0.05).				

3.4. Accumulation of osmoprotectants

Proline, soluble sugars and soluble proteins were significant osmolites and their levels were dramatically enhanced by COS treatment (Table 5). The COS-Medium group had a proline concentration of 49.6 ± 2.0 μg/g FW in 2023, which was more than 50% more than the control. The concentrations of soluble sugar and protein were 22.3 ± 1.0 mg/g and 15.2 ± 0.7 mg/g respectively under the same treatment. The 2024 results were virtually the same as the previous year. The results indicated that COS might promote osmotic adjustment and maintain membrane stability under saline-alkaline stress.

Table 5

Effects of chitooligosaccharide (COS) treatment on proline, soluble sugar, and soluble protein contents in potato under saline-alkaline field conditions in 2023 and 2024.

Parameters	Control	COS-Low (0.1 g/L)	COS-Medium (0.3 g/L)	COS-High (0.5 g/L)
2023				
Proline ($\mu\text{g g}^{-1}$ FW)	32.4 $\pm$ 1.5 ^a	41.8 $\pm$ 1.7 ^b	49.6 $\pm$ 2.0 ^c	48.1 $\pm$ 1.9 ^b
Soluble sugar (mg g^{-1} FW)	15.7 $\pm$ 0.8 ^a	18.9 $\pm$ 0.9 ^b	22.3 $\pm$ 1.0 ^c	21.6 $\pm$ 1.1 ^b
Soluble protein (mg g^{-1} FW)	11.5 $\pm$ 0.6 ^a	13.4 $\pm$ 0.6 ^b	15.2 $\pm$ 0.7 ^b	14.9 $\pm$ 0.6 ^b
2024				
Proline ($\mu\text{g g}^{-1}$ FW)	33.1 $\pm$ 1.6 ^a	42.7 $\pm$ 1.6 ^b	50.2 $\pm$ 2.1 ^c	48.8 $\pm$ 2.0 ^b
Soluble sugar (mg g^{-1} FW)	16.0 $\pm$ 0.7 ^a	19.2 $\pm$ 0.9 ^b	22.6 $\pm$ 1.0 ^c	21.9 $\pm$ 1.0 ^b
Soluble protein (mg g^{-1} FW)	11.8 $\pm$ 0.5 ^a	13.6 $\pm$ 0.6 ^b	15.5 $\pm$ 0.7 ^b	15.0 $\pm$ 0.6 ^b
Values are the mean $\pm$ SD (n = 3). Different superscript letters within each row indicate significant differences ($P < 0.05$).				

4. Discussion

The present study showed that the foliar application of COS significantly mitigated the adverse effects of saline-alkaline stress on potato plants by increasing various physiological parameters, including biomass, ion homeostasis, antioxidant enzyme activities, and osmoprotectant levels. 1. We propose a mechanism of COS as a potent biostimulator to improve potato yield in saline agricultural conditions. Crucially these physiological reactions are not separate uncoupled processes but a hierarchically structured cascade. The important upstream regulatory event is the restoration of ionic balance. Biomass data (Table 2) showed that the highest shoot and root weights throughout the 2-year period were associated with the medium dose of COS (0.3 g/L), confirming a dose-response relationship. This increased growth is in line with recent studies demonstrating that COS enhances cell division and elongation and increases the efficiency of nutrient uptake (Ye et al., 2023; Subramanian et al., 2023). COS can promote biomass accumulation and tuber formation by modulating membrane permeability and activating stress-responsive genes, hence improving the transport of water and nutrients (Tanaka et al., 2015; Liu et al., 2023). The premise for stress reduction by COS is the maintenance of ion homeostasis. Saline-alkaline conditions are a serious physiological stress caused by ionic imbalance. As shown in Table 3, COS treatment significantly decreased the accumulation of Na^+ and increased the concentration of K^+ in leaf tissues, and higher ratios of K^+/Na^+ were identified. This is a crucial

adaptation stage since enzymatic activity and osmotic balance demand high K^+ concentrations and low Na^+ accumulation (Jaarsma et al., 2013; Zhao et al., 2025). Ali et al. (2021) also obtained similar results as they revealed that the biostimulant treatment induced the ion distribution in potatoes subjected to salt stress. COS might stimulate the production of certain ion transporters or change the activity of plasma membrane H^+ -ATPase, which favours K^+ retention and Na^+ exclusion. The main adaptive physiological response is the optimisation of intracellular K^+/Na^+ ratios. This removes ionic toxicity immediately and then osmotic pressure disturbance from salinity stress. Accumulation of osmoprotectants is the final index of alleviation of osmotic stress. Osmotic regulation and cellular protection are achieved by synthesis of osmoprotectants such as proline, soluble carbohydrates and proteins. Table 5 shows that all three osmolytes were significantly raised following treatment with COS notably at the medium dose. These chemicals improve the stability of proteins and membranes, enzymatic activity and turgor pressure under osmotic stress (Xu and Wei, 2023; Nandhini and Somasundaram, 2018). COS can induce osmolytes synthesis in maize and *Arabidopsis* by stimulating the metabolic enzymes or improving the phytohormonal signals (Subramanian et al., 2023; Ye et al., 2023). Increase of Na^+ in soil solution increases osmotic disequilibrium and directly induces osmolytes biosynthesis. Thus, COS supplementation should restore cellular K^+/Na^+ equilibrium, likely reducing transmembranous osmotic gradients and increasing the production of particular osmolytes. Finally, the ultimate outcome of the upstream ionic and osmotic changes is the alleviation of oxidative stress. Salt can cause oxidative stress via the buildup of reactive oxygen species (ROS). Table 4 shows the increase in SOD, POD and CAT activities after COS treatment suggesting the augmentation of the antioxidative defence system. This enzyme activity lowers oxidative damage as indicated by the low values of MDA and hydrogen peroxide (H_2O_2). The results are consistent with the results of Shi et al. (2021) and Lan et al. (2023) who found that COS increased the antioxidant enzyme systems in different crop species. COS may serve as a signalling molecule to induce ROS scavenging pathways or regulate the transcription of antioxidant genes (Xiong et al., 2009; Wang et al., 2017). Figure 1 shows a possible mechanistic flow chart for various physiological events. The first stage is the formation of ion homeostasis (increased K^+/Na^+ ratio) in saline-alkaline environment through injection of COS. This key advantage reduces osmotic stress and ionic toxicity, which would otherwise lead to an excessive production of ROS. This leads to a decrease in the need for high antioxidative enzyme activity to counteract oxidative damage and for adequate osmolyte production to sustain cell turgor and functioning. Each downstream response needs restoration of ion homeostasis in the upstream and ultimately boosts the overall plant resilience and productivity.

In conclusion, the application of COS under saline-alkaline conditions considerably increased the growth, physiological performance and stress tolerance of potatoes. These effects are attributed to the improved ion homeostasis, the higher accumulation of osmoprotectants and the improved antioxidant activity as outlined in Fig. 1. These findings support the use of COS as a sustainable biostimulator in salt-affected agricultural systems and provide a mechanistic basis for the future use of COS in agronomy. Only physiological signs were studied in the present experimental design. Further studies

such as photosynthetic properties and full spectrum nutritional profile could be conducted to understand the overall regulatory mechanisms of COS in stimulating plant growth.

Declarations

Author Contribution

Huiying Qian and Yanqiu Xia wrote the main manuscript text and prepared table s 1-5 and figure 1. Shengjun Wu reviewed the manuscript.

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Conflict of Interests

The authors have declared that no competing interests exist.

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Figures

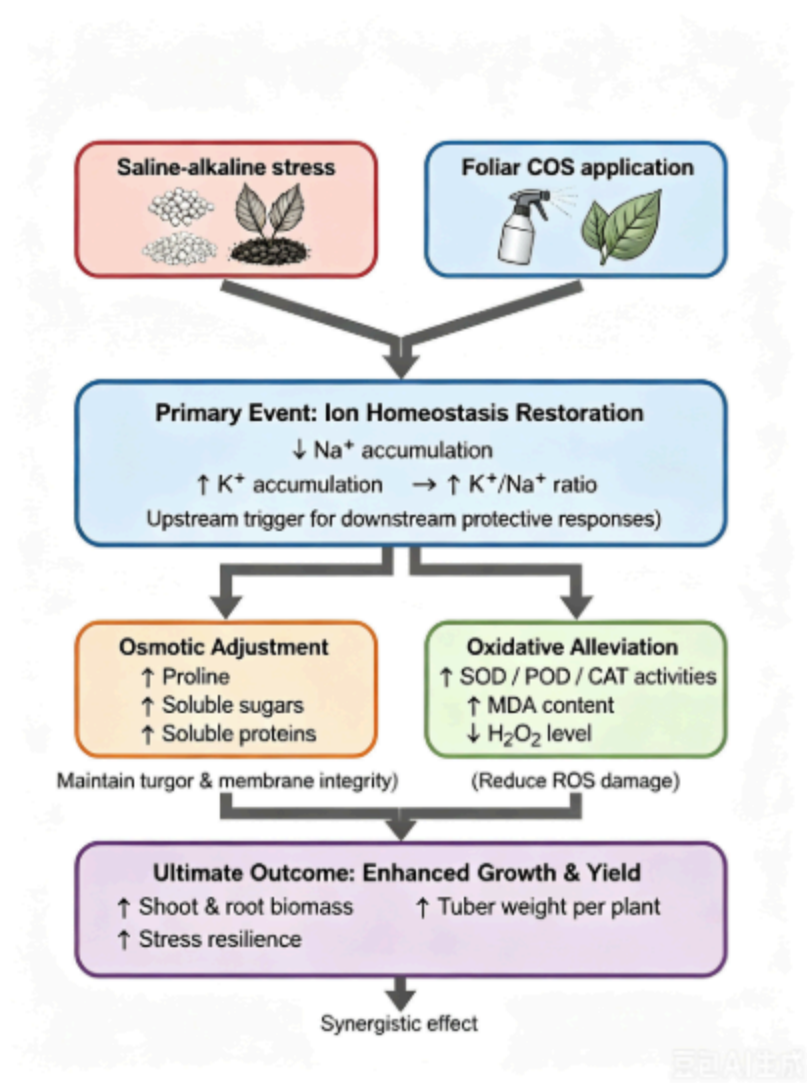


Figure 1

Proposed hierarchical mechanism of COS-mediated alleviation of saline-alkaline stress in potato. COS application sequentially: (1) restores ion homeostasis (↓Na⁺, ↑K⁺, ↑K⁺/Na⁺); (2) promotes osmotic adjustment (↑proline, ↑soluble sugars, ↑proteins); (3) alleviates oxidative stress (↑SOD/POD/CAT,

↓MDA/H₂O₂); and ultimately (4) enhances growth and tuber yield. Arrows indicate causal relationships from upstream to downstream events.