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Exogenous manganese application improves salinity stress in tomato (*Solanum Lycopersicum* L.) by modulating biochemical and physiological responses

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Abstract
Salinity stress is one of the most devastating environmental constraints limiting tomato (*Solanum lycopersicum* L.) productivity worldwide. It induces osmotic stress, ion toxicity, and oxidative damage, severely disrupting plant growth and development. Manganese (Mn) is a crucial micronutrient involved in photosynthesis, enzyme activation, and antioxidant defence systems. This study investigates the potential role of exogenous manganese application in mitigating the adverse effects of salt stress in tomato plants. Salinity stress was imposed using NaCl at concentrations of 0, 10, 25, 50, and 100 mM, while Mn was applied as $MnCl_2 \cdot 4H_2O$ at concentrations of 10, 20, and 50 µM. Salinity significantly reduced seed germination, plant growth, biomass production, and photosynthetic pigment content. The highest salinity level (100 mM NaCl) reduced germination percentage by more than 50% and markedly decreased shoot and root development. Chlorophyll-a and chlorophyll-b contents declined substantially with increasing salt concentration. Salinity stress also induced oxidative stress, as evidenced by increased H_2O_2 accumulation, proline content, and alterations in antioxidant enzyme activities. Mn supplementation of 20 µM Mn proved most effective in improving germination, shoot and root growth, biomass accumulation, and chlorophyll retention under saline conditions, enhanced antioxidant defence mechanisms and improved physiological performance, thereby reducing salinity-induced damage. In contrast, 50 µM Mn showed comparatively lower effectiveness, suggesting the existence of an optimum Mn concentration for stress mitigation. The findings demonstrate that exogenous manganese application can improve salinity tolerance in tomato by maintaining saline conditions. Therefore, Mn supplementation may represent a practical strategy for improving tomato productivity in salt-affected soils.

Keywords: Tomato, Salinity Stress, Manganese, Photosynthesis, Enzyme activation, Antioxidant

Introduction

Plant stress is one of major problem that cause significant economic loss for growers, reduction of crop yield and quality (cattivelli *et al*., 2008) [6]. Ensuring an adequate food supply for India's rapidly increasing population remains one of the most critical challenges. Nearly 200 million people in the country continue to experience chronic malnutrition, primarily due to insufficient food availability (Glick, 2014) [9]. Plant stress refers to external influences that induce abrupt physiological and metabolic changes, thereby affecting growth, flowering, seed germination, development, respiration, photosynthesis, senescence, cellular functions, and gene expression, which collectively diminish crop yield and performance (Flexas *et al*., 2005) [8]. According to Rhodes and Nadolska-Orczyk (2001) [16], stress is defined as any external factor or stimulus that negatively impacts plant growth, productivity, reproductive success, or survival. Plant stress refers to a condition in which plants grow under unfavourable or suboptimal environmental circumstances. Such stress arises from a variety of biotic factors including pathogens, insects, pests, and weeds and abiotic factors such as temperature extremes, nutrient deficiencies, nutrient toxicities, and herbicide exposure.

Abiotic stress refers to environmental factors that limit plant growth and productivity below their optimal potential. Plants exhibit complex and dynamic responses to such stresses, which can be reversible (elastic) or irreversible (plastic). These responses vary depending on the specific tissue or organ experiencing the stress (Dinneny *et al*., 2008) [7]. Among the various abiotic stresses, salinity is one of the most critical factors limiting crop productivity, as it induces ionic imbalance, osmotic stress, and multiple secondary stresses in glycophytic plants. At present, climate change combined with poor irrigation practices is contributing to increased sodium chloride (NaCl) accumulation in agricultural soils, further degrading arable land (Carillo *et al*., 2011) [5].

Manganese (Mn) is an essential micronutrient for plants, crucial for numerous physiological and biochemical functions. As an essential micronutrient, manganese (Mn) plays a vital role in supporting plant growth and development, and it enhances tolerance to salinity stress by restricting the absorption and movement of salt within the plant. Under saline conditions, the application of manganese improves ion balance, strengthens the antioxidant defence system, and enhances the glyoxalase pathway in rice seedlings, thereby increasing their tolerance to salt stress. Numerous studies have demonstrated that manganese contributes to improved salinity tolerance in several crops, such as sunflower (Jabeen and Ahmad, 2011) [12] and mung bean (Shahi and Srivastava, 2018). Manganese (Mn) significantly contributes to photosynthesis, as it is indispensable for the water-oxidizing system of Photosystem II. Adequate manganese (Mn) is vital in this process because it aids in the photolysis (light-splitting) of water molecules, thereby providing energy for photosynthesis (Alejandro *et al*., 2020) [1].

Tomato (*Solanum lycopersicum* L.) is among the most extensively cultivated and consumed vegetables across the globe (Campestrini *et al*., 2019 [4]; Li *et al*., 2021). It ranks

as the second most important vegetable crop after potato. Worldwide, tomatoes are grown on nearly 4.92 million hectares, producing about 186.11 million tons annually. Major tomato-growing states in India include Maharashtra, Bihar, Karnataka, Uttar Pradesh, Odisha, Andhra Pradesh, Madhya Pradesh, and Assam. They are a rich source of essential minerals such as potassium, phosphorus, magnesium, and iron, which are vital for proper nerve and muscle function. Tomatoes also provide significant amounts of vitamins A, B, and C, ranking as the third major dietary source of vitamin C and the fourth for vitamin A due to their beta-carotene (pro-vitamin A) content. Tomato plants are generally considered moderately sensitive to salinity, although their tolerance varies depending on the growth stage and cultivar. Salt stress disrupts key physiological processes, ultimately reducing overall growth and productivity. High salinity levels cause noticeable changes in plant morphology, such as reduced shoot and root biomass, shorter plant height, and a decline in total leaf area (Ikram *et al*., 2024) [11].

Salinity stress influences nearly all growth characteristics, causing noticeable changes in plant morphology throughout all developmental stages, including reductions in plant height, alterations in root-to-shoot ratios, decreases in leaf area, and fewer branches, leaves, and flowers per plant (Roșca *et al*., 2023) [17]. Tomato production is often constrained by multiple factors, including biotic and abiotic stresses, the cultivation of low-yielding varieties, imbalanced fertilizer application, and inadequate insect and pest management, all of which can significantly reduce crop performance. To achieve maximum productivity, tomato plants must receive appropriate and balanced nutrition throughout their growth cycle (Ullah *et al*., 2020) [19]. Tomato plants exhibit moderate tolerance to salinity, and while certain external stressors may enhance the accumulation of beneficial bioactive compounds in the fruits, exposure to high levels of salt stress ultimately leads to significant reductions in yield (Rouphael *et al*., 2018 & Moles *et al*., 2019) [15, 18].

Materials and Methods

1. Plant Material and Experimental Design

The present study was conducted to investigate the role of exogenous manganese (Mn) in alleviating salinity stress in tomato (*Solanum lycopersicum* L.). Seeds of tomato Saksham (hybrid) were procured from a local seed market in Mathura, Uttar Pradesh, India. The experiment was conducted under controlled conditions using a Completely Randomized Design (CRD) with three replications. Salinity stress was imposed using sodium chloride (NaCl), while manganese supplementation was provided in the form of manganous chloride tetrahydrate ($MnCl_2 \cdot 4H_2O$; molecular weight = 197.91 g mol^{-1}). NaCl solutions were prepared at concentrations of 0 (control), 10, 25, 50, and 100 mM by dissolving the required quantities of NaCl in distilled water and making the final volume up to 1 L. Manganese solutions were prepared at concentrations of 0, 10, 20, and 50 µM using $MnCl_2 \cdot 4H_2O$ dissolved in distilled water.

2. Germination Analysis and Growth Measurements

Seeds were placed in sterilized glass Petri dishes lined with filter paper and moistened with distilled water. The Petri dishes were incubated in darkness at 25 ± 1°C. Germination was recorded after 48 h, and seeds with radicle emergence of at least 2 mm were considered germinated. Seedlings were carefully uprooted and washed thoroughly with distilled water to remove adhered soil particles. Shoot length and root length were measured using a graduated scale and expressed in centimeters (cm). Fresh biomass was determined immediately after harvesting using a digital electronic balance. For dry biomass determination, plant samples were oven-dried at 60°C for 48 h until constant weight was obtained.

3. Determination of Photosynthetic Pigments

Photosynthetic pigments were estimated according to the method described by Arnon (1949) [2]. Fresh leaf tissue (0.5 g) was homogenized in 80% acetone and centrifuged at 10,000 rpm for 10 min. The absorbance of the supernatant was recorded at 663, 645, and 470 nm using a UV–Visible spectrophotometer. Chlorophyll-a and chlorophyll-b contents were calculated using Arnon's equations, while carotenoid content was estimated following the method of Lichtenthaler.

4. Determination of Proline Content and Antioxidant Enzyme Assays

Proline content was determined following the method of Bates *et al*. (1973) [3]. Fresh leaf tissue (0.5 g) was homogenized in 3% sulfosalicylic acid and reacted with acid ninhydrin reagent. The absorbance was recorded spectrophotometrically, and proline concentration was expressed as µmol g^{-1} fresh weight. Peroxidase (POD) and glutathione-S-transferase (GST) activities were determined spectrophotometrically according to the method described by Zhang (1992) [20]. Enzyme activities were expressed as units mg^{-1} protein.

5. Electrolyte Leakage (EL) and Hydrogen Peroxide (H_2O_2)

Electrolyte leakage (EL) was used as an indicator of membrane stability and cellular damage caused by salinity stress. Electrolyte leakage was determined according to the method of Gong *et al*. (1997) [10]. Fresh leaf discs were incubated in deionized water and electrical conductivity was measured before and after autoclaving. Electrolyte leakage was expressed as a percentage. Hydrogen peroxide content was measured according to the method of Patterson *et al*. (1984). The absorbance of the reaction mixture was recorded spectrophotometrically and expressed as µmol g^{-1} fresh weight.

6. Statistical Analysis

All data were subjected to one-way analysis of variance (ANOVA) using SPSS statistical software. Treatment means were compared using Duncan's Multiple Range Test (DMRT) at a significance level of $p < 0.05$. Data are presented as mean ± standard error (SE). Graphs were prepared using Origin Pro and Microsoft Excel software.

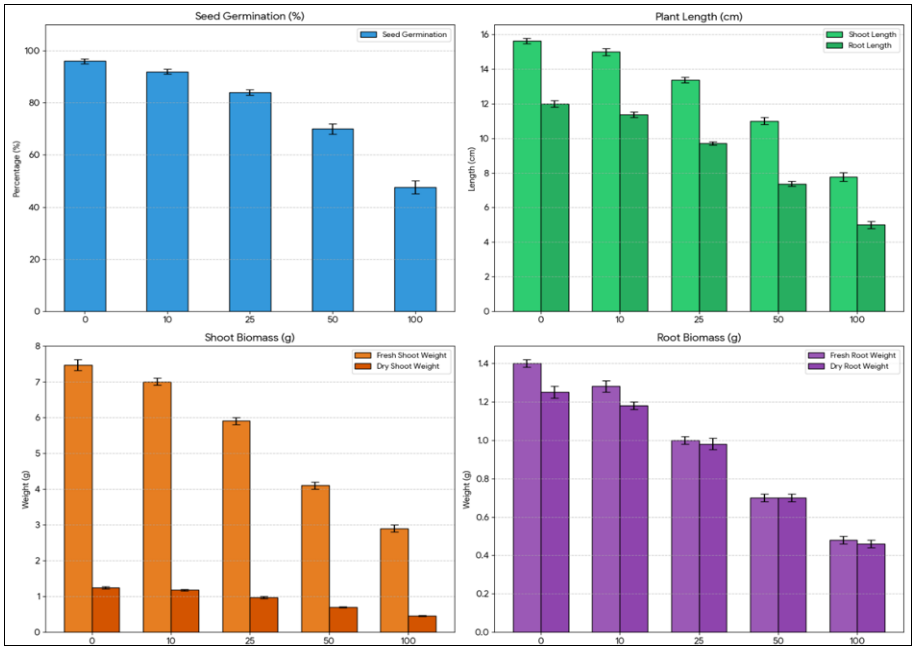
Results and Discussion

1. Effect of Salinity Stress and Manganese Application on Seed Germination and Growth Attributes

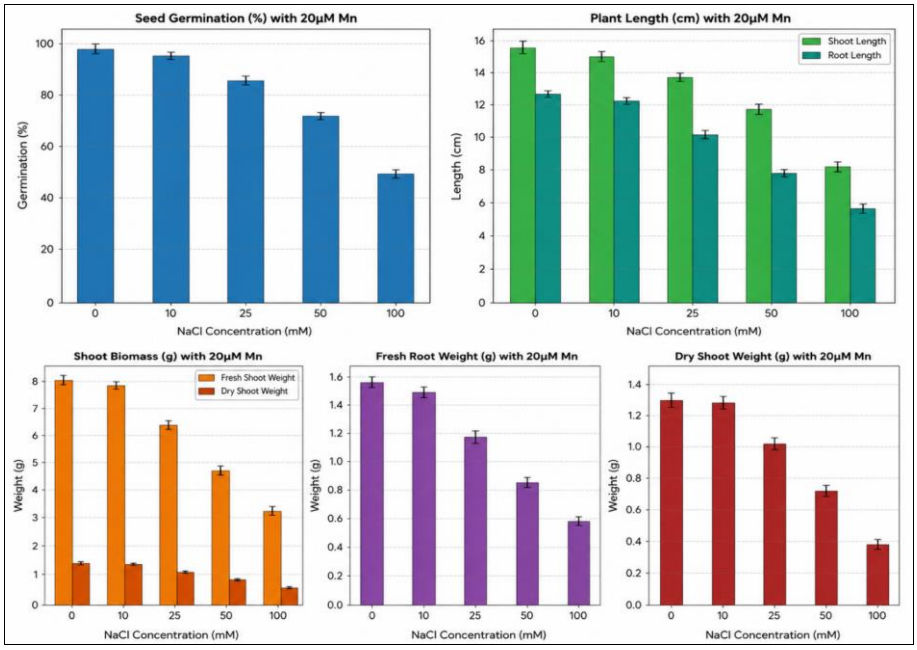
Salinity stress significantly affected seed germination and vegetative growth of tomato plants. A gradual decline in germination percentage was observed with increasing NaCl concentration. Seed germination decreased from 96.0% under control conditions to 47.7% at 100 mM NaCl,

indicating severe inhibition of seed viability and early seedling establishment under salt stress. Similarly, shoot and root growth were markedly reduced by salinity. Shoot length declined from 15.63 cm in control plants to 7.77 cm at 100 mM NaCl, while root length decreased from 12.00 cm to 5.00 cm. Fresh and dry biomass accumulation was also significantly reduced under saline conditions. Fresh shoot weight decreased from 7.47 g in the control treatment to 2.90 g at 100 mM NaCl, whereas dry shoot weight declined from 1.25 g to 0.46 g (Graph 1). Fresh root weight and dry root weight exhibited similar reductions, demonstrating the detrimental effects of salinity on plant growth and biomass production. Exogenous manganese supplementation alleviated the adverse effects of salinity stress. Among the tested concentrations, 20 µM Mn produced the most pronounced improvement in germination and growth parameters.

Under severe salinity (100 mM NaCl), seed germination increased from 47.7% in salt-stressed plants to 50.5% in plants receiving 20 µM Mn. Likewise, shoot length increased from 7.77 cm to 8.20 cm, and root length improved from 5.00 cm to 5.60 cm. Fresh shoot biomass under 100 mM NaCl increased from 2.90 g to 3.20 g following application of 20 µM Mn, while fresh root biomass increased from 0.48 g to 0.58 g. Dry shoot weight and dry root weight also showed notable improvement under Mn supplementation (Graph 2). In contrast, 50 µM Mn was less effective and resulted in lower growth performance compared with 20 µM Mn, suggesting that excessive manganese may negatively influence plant growth. Overall, manganese application improved germination, growth, and biomass accumulation under saline conditions, with 20 µM Mn being the optimum concentration for enhancing salinity tolerance in tomato.



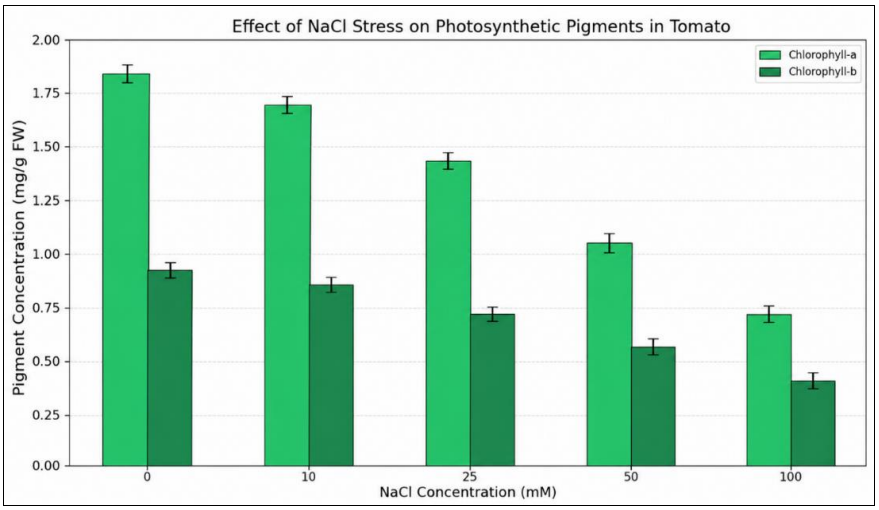
Graph 1: Effect of NaCl Concentrations on Growth Parameters of Tomato



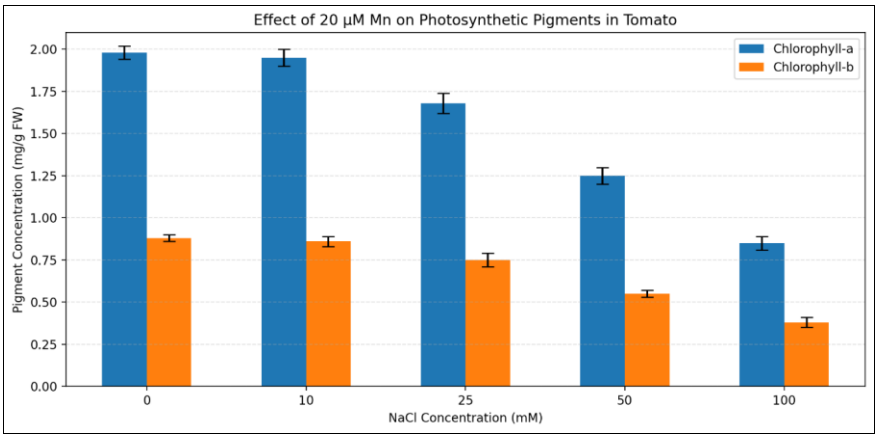
Graph 2: Effect of NaCl + 20 µM Mn on Growth Parameters of Tomato

2. Effect of Salinity Stress and Manganese Application on Photosynthetic Pigments

Salinity stress significantly reduced chlorophyll content in tomato leaves. Chlorophyll-a content declined progressively from 1.83 mg g^{-1} FW in control plants to 0.72 mg g^{-1} FW at 100 mM NaCl. Similarly, chlorophyll-b decreased from 0.93 mg g^{-1} FW under control conditions to 0.39 mg g^{-1} FW at the highest salinity level. Application of manganese improved chlorophyll retention under saline conditions (Graph 3). The most substantial improvement was observed at 20 µM Mn. At 100 mM NaCl, chlorophyll-a increased from 0.72 mg g^{-1} FW in salt-stressed plants to 0.85 mg g^{-1} FW in Mn-treated plants. Chlorophyll-b content also showed improvement under manganese supplementation. The beneficial effect of Mn was evident across all salinity levels; however, the magnitude of improvement varied with Mn concentration. While 10 µM Mn produced moderate enhancement, 20 µM Mn consistently maintained higher chlorophyll levels. Conversely, 50 µM Mn resulted in lower chlorophyll contents than 20 µM Mn, indicating that higher Mn concentrations may adversely affect photosynthetic pigment stability (Graph 4). The results clearly demonstrate that manganese supplementation mitigates salinity-induced chlorophyll degradation and contributes to the maintenance of photosynthetic capacity under saline conditions.



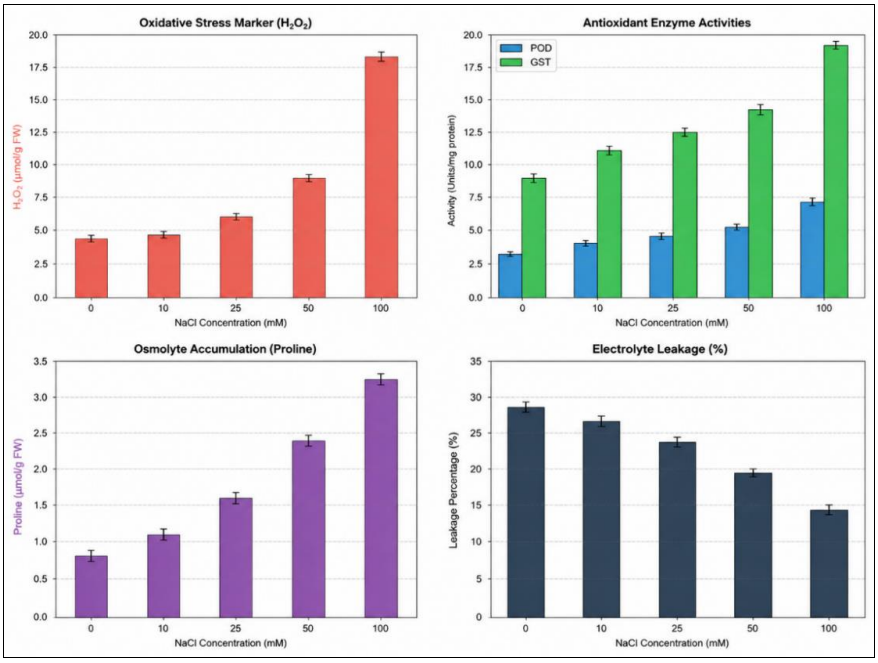
Graph 3: Effect of NaCl concentrations on photosynthetic parameters of tomato



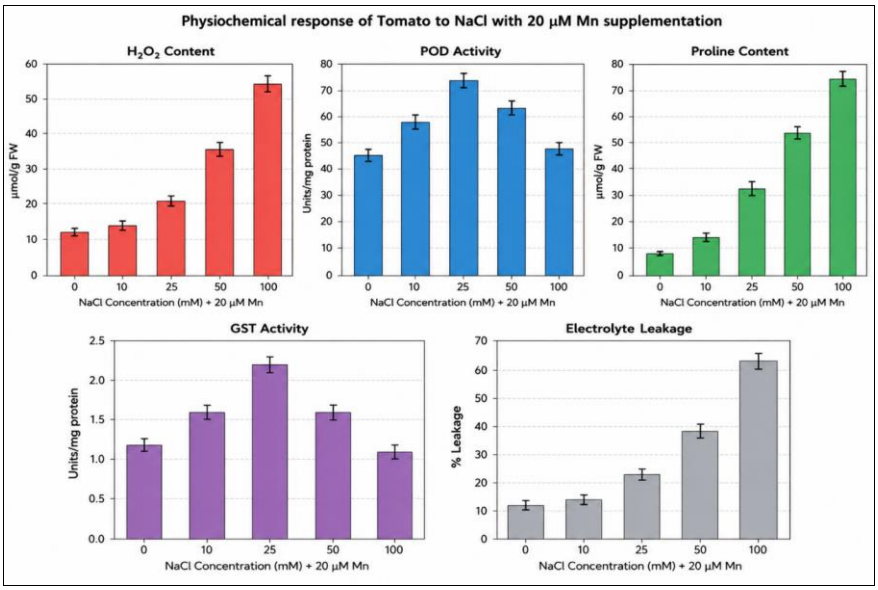
Graph 4: Effect of NaCl + 20 µM Mn on photosynthetic parameters of Tomato

3. Effect of Manganese on Electrolyte Leakage Under Salinity Stress and Hydrogen peroxide (H_2O_2)

Increasing NaCl concentrations induced substantial membrane injury, resulting in enhanced electrolyte leakage in tomato plants. Under salinity stress, EL increased progressively with increasing salt concentration, indicating deterioration of membrane integrity due to oxidative stress and ionic imbalance (Graph 5). Application of manganese significantly influenced membrane stability under saline conditions. Among the tested concentrations, 20 µM Mn proved most effective in reducing electrolyte leakage compared with untreated salt-stressed plants. Under 100 mM NaCl, plants treated with 20 µM Mn exhibited lower membrane damage than those receiving 50 µM Mn, suggesting that an optimum Mn concentration enhanced membrane protection mechanism. In contrast, application of 50 µM Mn resulted in higher electrolyte leakage at elevated salinity levels, indicating that excessive Mn concentration may exert toxic effects and aggravate membrane injury. Therefore, moderate Mn supplementation was more beneficial than higher Mn doses for maintaining cellular membrane stability under saline environments. Salinity stress induced substantial biochemical alterations in tomato plants. Hydrogen peroxide (H_2O_2), a key indicator of oxidative stress, increased progressively with increasing NaCl concentration. H_2O_2 content increased from 4.51 µmol g^{-1} FW under control conditions to 18.62 µmol g^{-1} FW at 100 mM NaCl, indicating enhanced production of reactive oxygen species (ROS) under salt stress (Graph 6).



Graph 5: Effect of NaCl Concentrations on various physiochemical parameters of Tomato



Graph 6: Effect of NaCl + 20 µM Mn on various physiochemical parameters of Tomato

4. Effect of Salinity Stress on Proline and Antioxidant Enzyme Activities

Proline accumulation was also significantly stimulated by salinity stress. Proline content increased from 0.81 µmol g^{-1} FW in control plants to 3.28 µmol g^{-1} FW at 100 mM NaCl. This increase suggests activation of osmotic adjustment mechanisms in response to saline conditions. Activities of antioxidant enzymes, including peroxidase (POD) and glutathione-S-transferase (GST), increased with increasing salinity levels. POD activity increased from 3.36 to 7.24 units mg^{-1} protein, while GST activity increased from 9.10 to 19.65 units mg^{-1} protein between control and 100 mM NaCl treatments. These increases indicate activation of the antioxidant defence system in response to oxidative stress generated by salinity.

Conclusion

Salinity stress is one of the major abiotic constraints limiting plant growth and productivity worldwide. In the present study, increasing NaCl concentrations significantly reduced seed germination, growth, biomass accumulation, and photosynthetic pigment content in tomato plants. These findings indicate that salinity adversely affects physiological and biochemical processes essential for normal plant development. The reduction in seed germination observed under saline conditions may be attributed to osmotic stress and ion toxicity caused by excessive accumulation of Na+ and Cl− ions. High salt concentrations reduce water uptake by seeds and interfere with metabolic processes required for successful germination. Similar inhibitory effects of salinity on germination have been reported in tomato and other crop species. A significant reduction in shoot length, root length, and biomass production was also observed with increasing salinity levels. Salinity-induced growth inhibition is generally associated with reduced cell division, impaired cell elongation, nutrient imbalance, and decreased water availability. Roots are often more severely affected because

they are directly exposed to saline conditions, resulting in restricted nutrient and water absorption.

Photosynthetic pigments were markedly reduced under salt stress. The decline in chlorophyll-a and chlorophyll-b contents may be attributed to chloroplast damage, inhibition of chlorophyll biosynthesis, and accelerated pigment degradation under oxidative stress conditions. Reduced chlorophyll content directly affects photosynthetic efficiency and consequently limits biomass production. Hydrogen peroxide accumulation increased significantly under salinity stress, indicating enhanced oxidative damage. Excessive generation of reactive oxygen species (ROS) is a common consequence of salinity stress and can lead to lipid peroxidation, membrane disruption, protein oxidation, and nucleic acid damage. To counteract oxidative stress, plants activate antioxidant defence systems.

The increased activities of POD and GST observed in the present study suggest activation of antioxidant mechanisms in response to salinity-induced oxidative stress. These enzymes play important roles in detoxifying ROS and protecting cellular components from oxidative injury. Similarly, the progressive accumulation of proline under increasing salinity levels reflects an adaptive response that contributes to osmotic adjustment, membrane stabilization, and ROS scavenging. Exogenous manganese application effectively mitigated the adverse effects of salinity stress. Manganese-treated plants exhibited improved germination, greater shoot and root growth, enhanced biomass accumulation, and higher chlorophyll contents compared with plants exposed to salinity alone. These improvements indicate that Mn plays a protective role under saline conditions. The beneficial effects of manganese may be attributed to its involvement in photosynthesis, enzyme activation, and antioxidant defence. Manganese is a structural component of the oxygen-evolving complex of Photosystem II and is therefore essential for efficient photosynthetic activity. Improved chlorophyll retention in Mn-treated plants suggests enhanced protection of the photosynthetic apparatus against salt-induced damage.

Among the tested concentrations, 20 µM Mn was found to be the most effective in alleviating salinity stress. Plants receiving 20 µM Mn consistently showed better growth, pigment content, and biochemical performance than those receiving either 10 µM or 50 µM Mn. The reduced effectiveness of 50 µM Mn may be associated with excessive Mn accumulation, which can disturb nutrient homeostasis and interfere with normal metabolic processes. Overall, the results demonstrate that manganese supplementation enhances salinity tolerance in tomato by improving growth, maintaining photosynthetic pigments, and strengthening antioxidant defence mechanisms.

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