

Fungal Endophyte *Fusarium equiseti* (SF-5) Alleviates Oxidative Stress Induced by Salinity in Tomato

G. AISHWARYA AND K. N. NATARAJA

Department of Crop Physiology, College of Agriculture, UAS, GKVK, Bengaluru - 560 065

e-Mail : nnkaraba@uasbangalore.edu.in

AUTHORS CONTRIBUTION

G. AISHWARYA :
Conceptualization, design,
curation, manuscript writing
and data analysis

K. N. NATARAJA :
Conceptualization, design,
supervision and manuscript
editing

Corresponding Author :

G. AISHWARYA

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ABSTRACT

Endophytes are the beneficial microorganisms that live inside the plant tissues and are known to enhance host resilience under stress conditions. The present study investigates the role of endophytes in mitigating oxidative stress in tomato seedlings induced by salinity. Previously characterized six fungal endophytes (SF-5, K-23, PJ-9, P-10, LAS-6 and N-14) isolated from harsh environments were analyzed for their ability to improve seedling growth and impart stress tolerance in the tomato variety, *Arka Vikas*. Among the selected endophytes, under salt stress (100 mM NaCl), the endophyte *Fusarium equiseti* (SF-5) colonized plants showed the highest percentage increase in seedling length (34%) over the untreated plants. The colonization and association of SF-5 with the host plant resulted in a significant reduction in ROS accumulation and cell death, which was confirmed by histochemical analysis and Evans blue staining, respectively. A substantial increase in activity of antioxidant enzymes (catalase and superoxide dismutase) over the control was observed in the SF-5 colonized plants. This study revealed that the enhanced salinity stress resilience in tomato colonized by endophytic fungi is primarily due to the alleviation of oxidative stress, highlighting the potential of habitat-adapted endophytes to activate stress-tolerant traits in a new host plant.

Keywords : Fungal endophytes, Oxidative stress, ROS, Antioxidants, Salt stress

SALINITY is one of the major abiotic stress factors limiting crop productivity worldwide, with significant adverse effects on plant growth, metabolism and yield (Loreto and Atzori, 2024). One of the most profound consequences of salinity stress is the generation of reactive oxygen species (ROS), which leads to oxidative stress and cellular damage in plants (Azeem *et al.*, 2023). This oxidative stress disrupts essential physiological processes, including membrane integrity, enzyme activity and photosynthesis (Farooq *et al.*, 2025). To counteract the detrimental effects of oxidative stress, plants have evolved various defense mechanisms, such as the synthesis and activation of antioxidant enzyme systems (Zhu, 2016 and Parvathi & Nataraja, 2016). However, under extreme conditions,

the intrinsic mechanisms may not be sufficient for mitigation and additional strategies are required to effectively manage the oxidative stress and improve the plant's resilience (Rahman *et al.*, 2024).

In recent years, endophytes, the beneficial microorganisms that live inside plant tissues without causing harm, often profiting from shelter and nutrients provided by the plants (Stone *et al.*, 2000 and Hyde *et al.*, 2019), have garnered significant attention due to their potential role in promoting plant growth and enhancing stress tolerance. Endophytes can produce various bioactive compounds that mitigate oxidative damage by enhancing antioxidant defense systems (Poveda *et al.*, 2020). Endophytes isolated from

stress-adapted plants can be introduced into sensitive plants, enhancing their resilience (Manasa *et al.*, 2020 and Becerril-Espinosa *et al.*, 2022). This symbiotic relationship between endophytes and plants may provide an effective strategy for alleviating the adverse effects of salinity stress.

Fungal endophytes can alleviate oxidative stress by enhancing both enzymatic and non-enzymatic systems, thereby neutralizing excess ROS (Sadeghi *et al.*, 2020). Chauhan *et al.* (2024) also reported that inoculating the halotolerant endophytic fungus *Aspergillus terreus* strain CR7 into mung beans under salt stress resulted in a significant increase of 42.52 and 49.48 per cent in superoxide dismutase (SOD) and catalase (CAT) activities, respectively, compared to the control. In addition, the colonization improved membrane integrity and decreased electrolyte leakage by enhancing the levels of non-enzymatic antioxidants, such as phenolic and proline compounds. This combined effect on the antioxidant system plays a crucial role in maintaining ROS balance and in protecting cellular structures from oxidative damage. Additionally, endophytes enhance stress resilience by facilitating osmotic adjustment, modulating phytohormone levels and promoting root growth (Ali *et al.*, 2022), as well as activating stress-responsive genes (Sampangi-Ramaiah *et al.*, 2020).

In a previous study, Pallavi and Nataraja (2022) demonstrated that a few fungal endophytes could effectively colonize the tomato variety (*Arka Saurabh*) and significantly improve seedling growth under NaCl stress, emphasizing their role in stress resilience. Building on this, the fungal endophytes used in the present study were specifically isolated from plants thriving in extreme habitats, including the cold and high-altitude regions of Kargil and Namika La mountains, the Thar Desert, the drylands of Karnataka and the brackish waters of Tamil Nadu. Endophytes from such habitats are naturally adapted to severe abiotic stresses like salinity, drought and high temperature and therefore possess inherent resilience traits. We hypothesized that introducing these habitat-adapted endophytes into a

stress-sensitive tomato variety could manipulate the plant's hologenome, thereby enhancing cellular-level tolerance, reducing oxidative stress and ultimately improving growth and stress resilience. The hologenome, comprising the genomes of the host and its associated microbiota, functions as a single integrated unit in which modifications to the microbiota can influence host traits and modulate stress responses.

MATERIAL AND METHODS

Fungal Endophytes and the Host

Six fungal endophytes designated as SF-5 (*Fusarium equiseti*), K-23 (*Fusarium incarnatum*), PJ-9 (*Fusarium* sp.), P-10 (*Fusarium* sp.), LAS-6 (*Chaetomium globosum*) and N-14 (*Fusarium* sp.) isolated from plants that were adapted to harsh environmental conditions were used in this study (Pallavi, 2022 and Pawar & Nataraja, 2024). The selected fungal endophytes were subcultured on Potato Dextrose Agar (PDA) media to obtain pure cultures, processed according to the standardized protocol (Sangamesh *et al.*, 2018) and then stored at 4°C as slants for future use. The tomato (*Solanum lycopersicum*) variety *Arka Vikas*, obtained from the Indian Council of Agricultural Research (ICAR)-Indian Institute of Horticultural Research (IIHR), Hesaraghatta, Bengaluru, was used in the present study.

Standardization of the LC₅₀ Value

The seeds were surface sterilized with 70 per cent (v/v) ethanol for 50 seconds, followed by immersion in 4 per cent (v/v) sodium hypochlorite (NaOCl) for three minutes and several washes in autoclaved water (Arnold *et al.*, 2000). These surface-sterilized seeds were soaked overnight in sterile water and germinated for 72 hours in petri plates containing sterile, moistened blotting papers and transferred to paper towels. The experiment was performed with three replications. One set of seedlings was exposed to different concentrations of NaCl (25, 50, 100, 150 and 200 mM) and another set of seedlings was treated with distilled water, which served as the control. After

ten days of growth, seedlings were harvested, seedling length (root length and shoot length) was recorded using a measuring scale and LC_{50} values were calculated using probit analysis (Sangamesh *et al.*, 2018).

Endophyte Colonization and Salinity Stress Experiment

The seeds were surface sterilized according to Arnold *et al.* (2000) and germinated for 72 hours. Five-day-old cultures were used for inoculum preparation by washing the mycelial mat with sterile distilled water. Germinated seeds were treated with the mycelia suspension (2×10^6 spores/mL) for three hours. Endophyte-enriched seeds were subjected to NaCl at their determined LC_{50} concentrations. One set of seeds was soaked in sterile distilled water and used as a control. These seedlings were incubated at room temperature in a growth room with 65 per cent relative humidity and on the tenth day, the seedling length was recorded.

Confirmation of Colonization

Endophytes were re-isolated from the tomato seedlings ten days post-inoculation (dpi). The roots and shoots of the seedlings were separated and cut into small segments, surface-sterilized, blotted dry and inoculated onto PDA media plates (enriched with streptomycin sulphate at 150 mg/L to suppress bacterial growth). These plates were then incubated for five days. To ensure the efficacy of surface sterilization, imprints of the sterilized segments were taken on PDA plates (Schulz *et al.*, 1993). Fungal growth from the cut ends of the segments was transferred to fresh PDA plates using a sterile needle to obtain pure cultures. The pure cultures were compared with their respective mother cultures based on morphology, including colony appearance, conidia and hyphae, using a light microscope.

Histochemical Assay and Antioxidant Enzyme Analysis

Germinated seeds were treated with selected endophytes as mentioned above, while distilled

water was treated as a control. The seedlings were grown in small plastic pots containing soil rite under controlled conditions for four weeks. Subsequently, salinity stress (100 mM) was imposed 21 days after sowing and maintained for a week. At the end of the stress period, leaf tissues were taken for histochemical and antioxidant enzyme activity analysis (Shalata and Neumann, 2001).

Quantification of Reactive Oxygen Species and Membrane Damage

Superoxide radical (O_2^-) reacts with pale yellow nitroblue tetrazolium (NBT) and forms a dark blue formazan, which indicates the extent of O_2^- generation (Thordal-Christensen *et al.*, 1997). The O_2^- levels were estimated using the NBT assay as described by Kumar *et al.* (2014). Leaf tissues were incubated in 0.2 per cent NBT solution (pH 7.5), bleached and visualized microscopically. For quantification, tissues were homogenized in 0.1 per cent acetic acid and absorbance was recorded at 560 nm. Data were expressed as absorbance \times 1000.

The reaction of diaminobenzidine (DAB) as substrate with hydrogen peroxide (H_2O_2) forms a distinct brown polymerization product (Thordal-Christensen *et al.*, 1997). H_2O_2 levels were quantified using DAB staining (Kumar *et al.*, 2014 and Kaur *et al.*, 2016). Vacuum-infiltrated leaves were bleached for visualization. For quantification, tissues were extracted in 0.2 M perchloric acid and absorbance was measured at 450 nm. Values were expressed as absorbance \times 1000.

Membrane damage was assessed using the Evans blue technique (Baker and Mock, 1994). Leaves were stained with Evans blue, washed and the bound dye was extracted using 1 per cent SDS. Absorbance was measured at 600 nm and results were expressed as microgram dye bound per gram fresh weight (μg Evans blue g FW^{-1}).

Estimation of Antioxidant Enzyme Activities

Fresh tomato leaf tissue (0.5 g) was homogenized in 5 mL of ice-cold extraction buffer specific to each

enzyme, using a pre-chilled mortar and pestle. The homogenate was centrifuged at 10000 rpm for 15 minutes at 4°C and the clear supernatant was used as the crude enzyme extract. All assays were carried out in triplicate (Giannopolitis and Ries, 1977), and the absorbance was measured using a UV-VIS spectrophotometer (SPECTRA max PLUS 384, Molecular Devices).

Catalase (CAT) activity was determined by measuring the decrease in absorbance at 240 nm due to the decomposition of H₂O₂ (Masia, 1998). The reaction mixture contained 50 mM sodium phosphate buffer (pH 7.0) and 15 mM H₂O₂. The activity was calculated using the extinction coefficient 187.528 and expressed as units per gram fresh weight (U g⁻¹ FW).

Superoxide dismutase (SOD) activity was assayed based on the inhibition of NBT photoreduction at 560 nm (Du and Bramlage, 1994). The reaction mixture contained 50 mM phosphate buffer (pH 7.8), 39 mM methionine, 12 μM riboflavin, 10 mM EDTA and 450 μM NBT. One unit of SOD activity was defined as the amount of enzyme required to inhibit 50 per cent of NBT reduction, expressed as U g⁻¹ FW.

Statistical Analysis

The experiments were carried out in a completely randomized design. Data were represented as mean ± standard deviation (SD). Each sample had a minimum of three biological replicates. The statistical differences among treatments were determined by one-way analysis of variance (ANOVA). The data were analyzed using OPSTAT and means were compared by Duncan Multiple Range Test (DMRT, $p < 0.01, 0.05$). The graphs were plotted through Graph Pad Prism 10.4.1. software.

RESULTS AND DISCUSSION

Fungal endophytes isolated from saline-adapted shrubs and other plants grown under harsh environmental conditions demonstrated the ability to alleviate salinity stress, improving tolerance in inoculated crop plants (Manasa *et al.*, 2020 and

Ayesha *et al.*, 2022). Following these insights, the present study investigated whether habitat-adapted fungal endophytes could enhance salt tolerance in tomato seedlings.

Effect of Fungal Endophyte Colonization on Tomato Seedlings under Salt Stress

Probit analysis indicated that the lethal concentration of NaCl causing 50 per cent mortality (LC₅₀) in the tomato variety *Arka Vikas* was 104.46 mM. The LC₅₀ value was determined to identify a sub-lethal concentration that could inhibit growth without causing mortality, thereby providing a reliable stress level for evaluating endophyte-mediated tolerance. Accordingly, 100 mM NaCl was used for stress induction in all subsequent salinity experiments. To assess the impact of fungal endophytes on seedling vigour, tomato seedlings were colonized with six different endophytes and grown under both non-stress and salt stress conditions. Under both conditions, the endophytes promoted seedling growth to varying extents compared to the uninoculated controls (Fig. 1). The differential performance of endophyte-colonized seedlings highlights the specificity of microbes.

Among the selected isolates, SF-5 consistently performed better than the other fungal isolates tested, showing a significant increase in seedling length (25% in non-stressed plants and 34 % under NaCl stress; Table 1). This indicates its strong ability to alleviate the inhibitory effects of salt on early growth. On the other hand, N-14 did not promote growth (0 and 1%, respectively), indicating that not all endophytes confer stress tolerance. The percentage increase in seedling length over uninoculated control without and with NaCl stress is depicted in Fig. 1. Other isolates like K-23 (15 and 27%) and PJ-9 (13 and 22%) also significantly promoted the growth under both conditions, though less effectively than SF-5. Similar trends of enhanced seedling growth under salinity have been reported in tomato and soybean upon fungal endophyte colonization, often linked to improved ionic balance and hormonal regulation (Mutungi *et al.*, 2024 and Hamayun *et al.*, 2017).

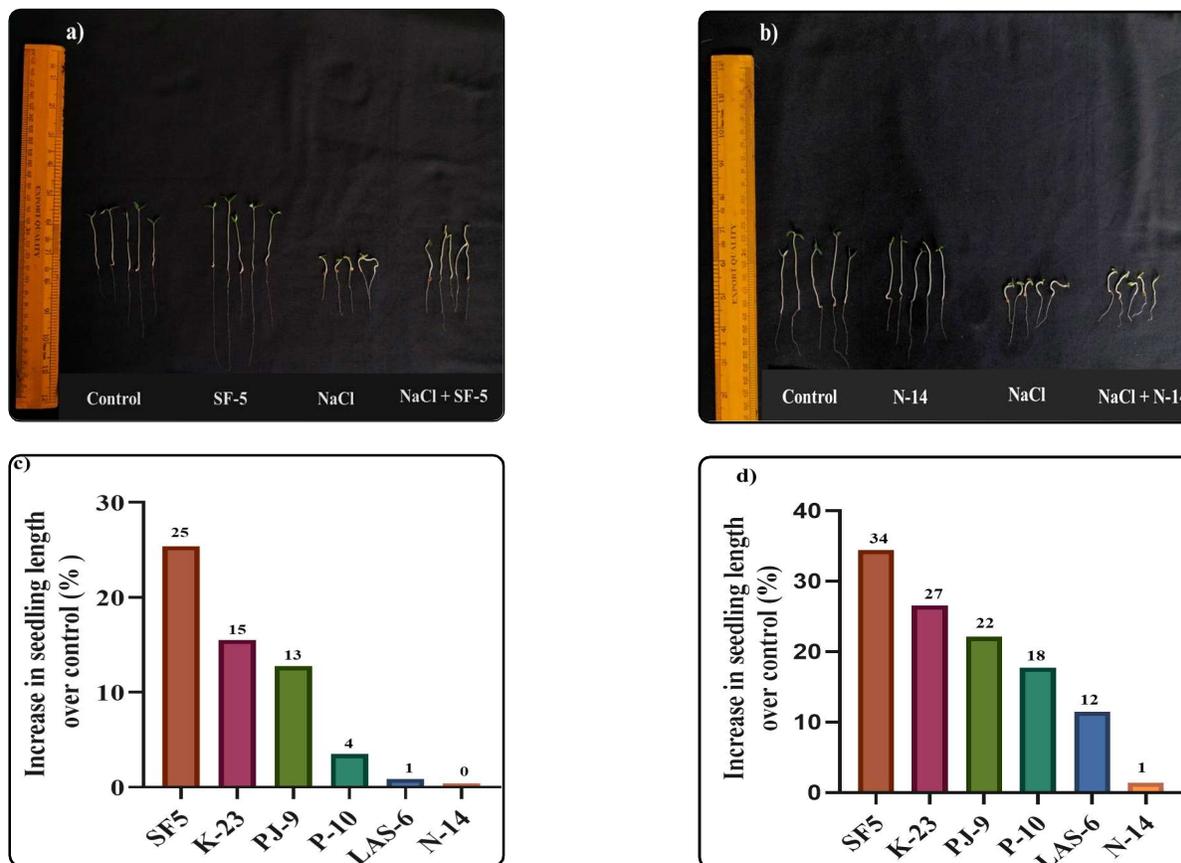


Fig. 1 : Effect of Endophyte Colonization on Seedling Growth of Tomato Without and With 100 mM NaCl Stress. A) SF-5; B) N-14; C) Without Stress; D) With NaCl Stress

TABLE 1

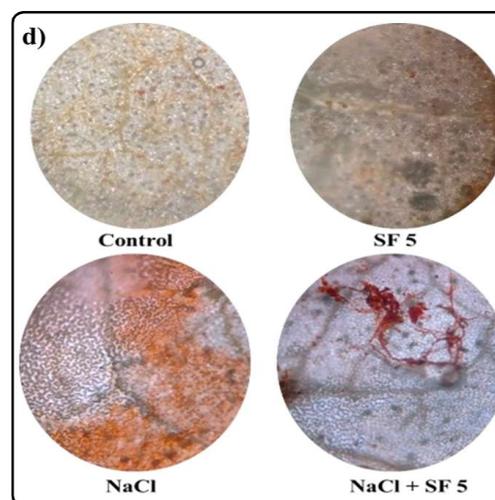
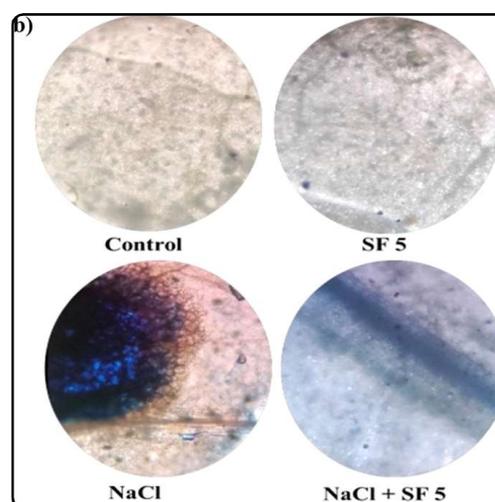
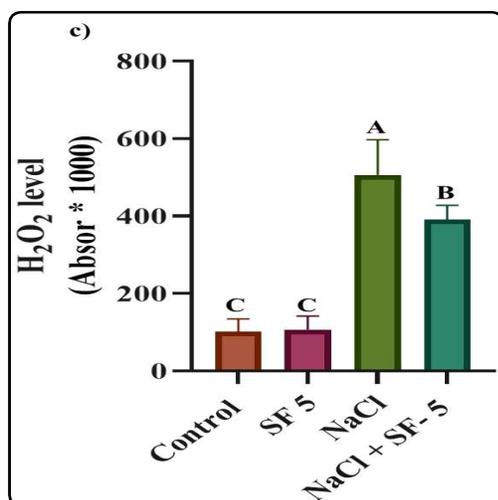
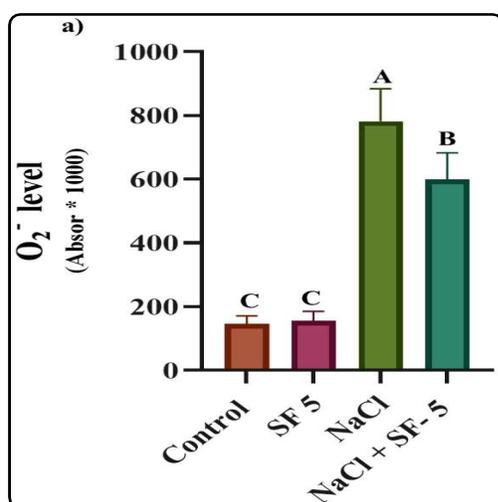
Effect of different endophyte colonization on seedling length of tomato without (NaCl -) and with salinity stress (NaCl +) conditions. Values represented were mean ± SD. (Data represents an average of n = 30 seedlings) SF-5 (*Fusarium equiseti*), K-23 (*Fusarium incarnatum*), PJ-9 (*Fusarium sp.*), P-10 (*Fusarium sp.*), LAS-6 (*Chaetomium globosum*) and N-14 (*Fusarium sp.*)

Fungal endophytes/ treatments	Seedling length (cm)	
	NaCl (-)	NaCl (+)
Control (without endophyte)	11.51 ± 1.27 ^c	5.91 ± 0.31 ^d
SF-5	15.4 ± 0.29 ^a	9.02 ± 0.4 ^a
K-23	13.6 ± 0.42 ^b	8.08 ± 0.61 ^{ab}
PJ-9	13.2 ± 0.51 ^{bc}	7.61 ± 0.5 ^{bc}
P-10	12.05 ± 0.78 ^{bc}	7.21 ± 0.52 ^{bc}
LAS-6	11.72 ± 0.85 ^c	6.71 ± 0.53 ^{cd}
N-14	11.55 ± 0.73 ^c	6.01 ± 0.38 ^d
SEM±	0.44	0.27
C.V%	7.28	8.04

Biochemical Basis of Endophyte-Mediated Stress Tolerance

Based on the preliminary screening, SF-5, which showed significant improvement in growth under both stress and non-stress conditions, was selected for further investigation to examine possible mechanisms of salinity tolerance in tomato. Since SF-5 colonized seedlings exhibited less reduction in growth under salt stress, we hypothesized that the symbiotic association is helping in managing major secondary stress, the oxidative stress, through modulation of the host antioxidant defense system (Sahu *et al.*, 2025). To assess major ROS generated under salinity, NBT and DAB assays were used to visualize O_2^- and H_2O_2 levels, respectively. Leaf samples of non-stressed conditions, such as control and SF-5 colonized plants,

showed little or no blue or brownish-red pigmentation, representing low levels of O_2^- and H_2O_2 . Under salt stress, intense staining was observed due to increased levels of ROS accumulation. In contrast, plants inoculated with SF-5 under stress conditions showed significantly lower ROS accumulation compared to non-enriched plants under stress (Fig. 2). Membrane integrity was further evaluated using Evans blue staining, which serves as an indicator of cell death and membrane damage. Reduced dye uptake in colonized plants indicated better membrane integrity compared to uninoculated seedlings under salinity. Collectively, these assays confirm that SF-5 alleviates oxidative stress by lowering ROS accumulation and maintaining membrane stability, consistent with the earlier reports on endophyte-mediated stress mitigation (Sahu *et al.*, 2021 and 2023).



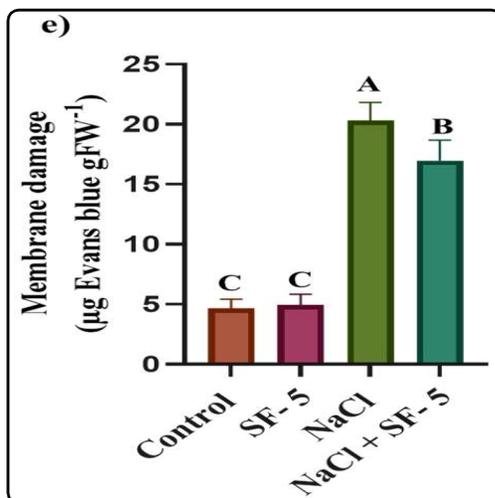


Fig. 2 : ROS accumulation and membrane integrity in NaCl-stressed tomato leaves colonized with endophyte SF-5. a) Levels of O_2^- expressed as absorbance *1000; b) *In vivo* localization of O_2^- by NBT staining; c) Levels of H_2O_2 expressed as absorbance *1000; d) *In vivo* localization of H_2O_2 by DAB staining (All images were captured at 4×magnification under a light microscope); e) Cell membrane integrity expressed as $\mu\text{g Evans blue g FW}^{-1}$

To further validate the phenotype observed, antioxidant enzyme activities were quantified. CAT and SOD were chosen as the primary enzymatic defenses against ROS. SOD converts O_2^- to H_2O_2 and CAT detoxifies H_2O_2 into water and oxygen. Compared to uninoculated stressed plants, SF-5 colonization significantly increased CAT and SOD activity (Fig.3), correlating with the reduced histochemical ROS signals and improved membrane stability. Enhancing the activities of these anti

oxidants is a key strategy for improving salt tolerance in plants (Sahu *et al.*, 2025).

Our findings align with the previous reports where fungal endophytes improved salt tolerance through modulation of antioxidant responses (Irshad *et al.*, 2023; Damankeshan *et al.*, 2024 and Khalid *et al.*, 2018). Additional studies have shown that endophytes may also activate Mitogen-activated protein kinase (MAPK) cascades, influence hormonal

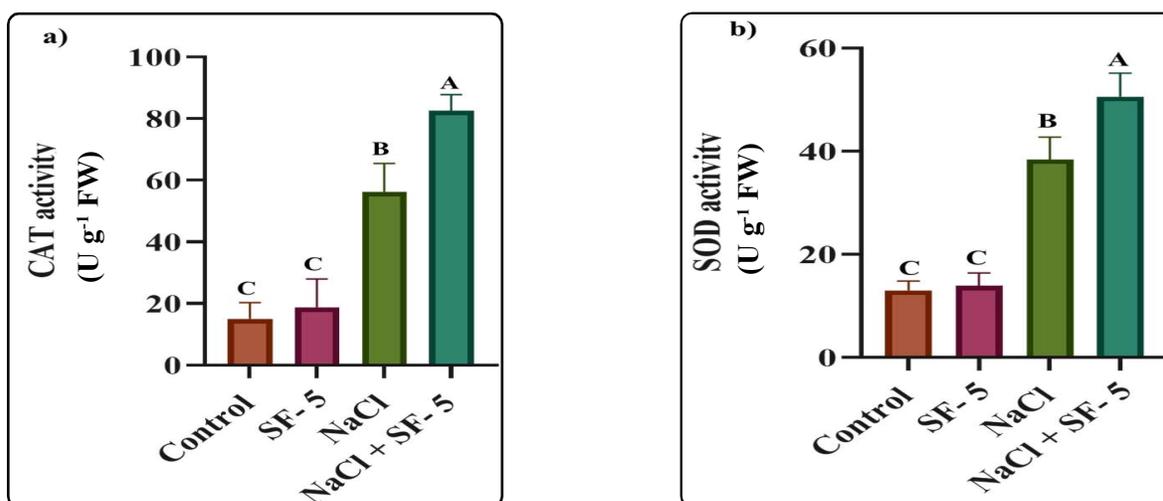


Fig. 3 : Effect of fungal endophyte (SF-5) colonization on antioxidant enzyme activity in tomato seedlings exposed to salt stress. a) Catalase (CAT) activity; b) Superoxide dismutase (SOD) activity

signaling and regulate redox-sensitive transcription factors such as HSFs, NAC and WRKY (Javed *et al.*, 2022 and Roy *et al.*, 2021). While these mechanisms were not examined in this study, the observed reduction in ROS accumulation and enhanced antioxidant activity strongly suggest that SF-5 confers oxidative stress tolerance by strengthening the host's antioxidant defense machinery.

In this study, we demonstrated that habitat-adapted fungal endophytes enhanced cellular-level tolerance in non-host tomato seedlings under salinity stress. Among the isolates, SF-5 exhibited the most consistent growth-promoting effect and was selected for further analyses. SF-5 colonization enhanced antioxidant enzyme activity, reduced ROS accumulation, improved membrane stability and promoted better growth under salt stress. The findings highlight the potential of habitat-adapted endophytes as bio-inoculants for sustainable agriculture. This study encourages the integration of endophyte-based approaches with existing methods, which can accelerate the development of stress-resilient crops for agriculture.

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