



Improving Tolerance of Tomato Plants to NaCl Toxicity for Agricultural Sustainability

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Abstract

Plant growth and yield are affected by salinity. Symbiotic interactions between plants and endophytic fungi are a promising approach to promoting crop growth under salt-stress conditions. Here, the tolerance of the endophytic fungus *Pleosporaceae* sp. was verified under diverse NaCl levels (0, 50, 100, 150, and 200 mM). Subsequently, *Pleosporaceae* sp. production of indole acetic acid (IAA) was assessed in vitro at various salinity levels (0, 50, 100, 150, and 200 mM). Additionally, the effect of *Pleosporaceae* sp. inoculation on germination, growth, and biochemical characteristics of tomato (*Solanum lycopersicum* L.) under five levels of salinity (0, 20, 50, 100, 150, and 200 mM NaCl) was investigated. The results indicated that *Pleosporaceae* sp. exhibited strong salt tolerance and produced approximately 138.6 ± 0.7 µg/ml of IAA under 100 mM NaCl. Moreover, the results showed that this symbiotic fungus significantly enhanced germination and growth under salinity. *Pleosporaceae* sp. also significantly improved proline and sugar accumulation under salt treatment. This study suggests that the endophytic fungus *Pleosporaceae* sp. can be employed to mitigate sodium chloride-induced stress in plants, thereby improving plant growth and productivity.

Keywords: *Solanum lycopersicum* , *Pleosporaceae* sp., NaCl stress, Germination.

Kouadria R., S. Soualem, A. S. Ouldkaddour, M. Bouzouina. 2025. Improving Tolerance of Tomato Plants to NaCl Toxicity for Agricultural Sustainability. Iranian Journal of Plant Physiology 15(1), 5433- 5441.

Introduction

One of the most important environmental issues facing arid and semi-arid regions today is the increasing accumulation of mineral salts in soils, reducing plant growth and yield through various physiological stresses (Ignatova et al., 2022). Based on the study by Otlewska et al. (2020), more than 20% of agricultural land across the globe is

impacted by high salt levels, and this percentage is expected to reach 50% by the year 2050. The stages in which plants are most sensitive to salt conditions are germination, emergence, and early seedling growth; salinity reduces germination rates (Uçarlı, 2021). Extreme absorption of ions can lead to toxicity and decrease the amount of water available to seeds, thereby inhibiting the formation of primary roots (Lu and Fricke, 2023). To combat salt stress, desalination can be used. In addition, salt-tolerant plants can be developed by conventional or innovative

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Received: November, 2024

Accepted: January, 2025

molecular techniques; nevertheless, these procedures are expensive and take a long time. Recent research focuses on identifying alternative approaches to improve plant productivity under stressful conditions (Morales-Vargas et al., 2024). Soil microorganisms can colonize roots, create populations in plants as endophytes, and stimulate plant growth during stressful conditions (Chauhan et al., 2023).

Pleiosporaceae sp. is known as an endophytic fungus residing in plant root cortical cells in saline areas (Furtado et al., 2019). Byregowda et al. (2022) revealed that salt stress could be countered by colonization with endophytic fungi in host plants.

Tomato (*Solanum lycopersicum* L.) is an important crop with high economic value and is commonly cultivated in areas where salt stress is particularly severe (Ghorbani et al., 2023).

This study aims to confirm the possibility of using *Pleiosporaceae* sp. to promote tomato growth under saline conditions to improve sustainable agriculture. The isolation of *Pleiosporaceae* sp. was done from *Anabasis prostrata* Pomel. roots. The aptitude of *Pleiosporaceae* sp. to improve salt tolerance in tomato plants was evaluated by measuring growth and osmotic regulation under saline and non-saline conditions.

Materials and Methods

Fungal Material

In this study, the fungal endophyte strain was previously isolated from roots of *Anabasis prostrata* Pomel. growing in a semi-arid environment. The endophyte *Pleiosporaceae* sp. was added to a gene bank with KJ443089 accession number (Kouadria et al., 2023).

Pleiosporaceae sp. Screening based on Salt Tolerance

Different concentrations of sodium chloride (50, 100, 150 and 200 mM) were amended with a Potato Dextrose Agar medium (PDA; Difco, Detroit, MI: 20 g Dextrose, 4 g Potato Extract, and 15 g Agar with pH: 5.6) in order to assess the salt

tolerance of *Pleiosporaceae* sp. Next, *Pleiosporaceae* sp. was inoculated at each concentration separately onto the surface medium, and it was incubated at 30 °C for 14 days.

IAA (Indole Acetic Acid) Production

The ability of *Pleiosporaceae* sp. to produce IAA was examined. In order to achieve this, *Pleiosporaceae* sp. was cultured on Potato Dextrose Broth (PDB) at various NaCl concentrations (0, 50, 100, 150, and 200 mM) accompanied with 0.1g/L of tryptophan. Next that, the culture was incubated at 30°C for 7 days. Following the incubation time, cultures were centrifuged for 20 minutes at 8000 rpm. 1 mL of the supernatant was combined with 4 mL of Salkowski reagent (consisting of 125 ml of distilled water, 3.75 ml of 0.5 M FeCl₃.6H₂O, and 75 ml of concentrated H₂SO₄), and the mixture was incubated for 20 minutes at room temperature. The development of a pink color signifies the production of IAA. Using a spectrophotometer Jenway 67155 UV/Vis (Stone, UK), the absorbance was measured at 520 nm, and the IAA standard graph (Gordon and Weber, 1951) was used to calculate the amount of IAA.

Spore Suspension Preparation

On PDA medium, *Pleiosporaceae* sp. was permitted to develop and sporulate. The culture was incubated at 28–30 °C for 7 days. After using distilled water to scrape the spores off the agar surface, they were suspended in a 0.05% Tween 80 solution. After that, the spore suspension was gathered and shaken for two minutes in a sterile test tube. Hemocytometer was used to measure the suspension's concentration microscopically after it was filtered through a double-layered mesh filter that had been serially diluted (Akagi et al., 2015).

Plant Material, Salt Treatments and *Pleiosporaceae* sp. Inoculation

Tomato seeds (*Solanum lycopersicum* L. var. Rudolph) were blotted dry onto sterile filter paper after being surface sterilized for five minutes using a sodium hypochlorite solution (NaClO, 5%) and rinsed three times, for one minute each time, in

sterile distilled water. After sterilization, tomato seeds were immersed in *Pleiosporaceae* sp. spores' suspension (10^7 spores/mL) or distilled water and then allowed to germinate on Petri dishes within a Phytotron (BINDER) at 25 °C for 7 days under non-saline (0 mM) and saline conditions (20, 50, 100, 150 and 200 mM of NaCl). Pre-germinated seedlings were transferred to pots (19 cm in diameter and 50 cm in length), filled with autoclaved soil. In each pot, ten seedlings were planted with three replicates (10 seedlings/pot and 3 pots/treatment). The experiment was carried out under greenhouse conditions with 12 h light, relative humidity of 55–65% and 25/18 °C (day/night).

Four (4) sets of treatments were included in the randomized complete block design experiment. The treatments included controls and endophyte-inoculated tomato plants under non-saline conditions (0 mM), controls for salt stress (20, 50, 100, 150, and 200 mM) and combinations of fungal inoculation \times salt conditions (20, 50, 100, 150, and 200 mM).

Growth Measurements

Germination percentage, root and shoot lengths were measured.

Analyses of Proline Accumulation in Tomato Seeds

Proline accumulation was determined using Troll and Lindsley's (1955) methodology. One gram of fresh plant material was homogenized in 2 mL of 40% methanol. Then, 1 mL extract was mixed with 2 mL glacial acetic acid and 2 mL of ninhydrin reagent (1.25 g ninhydrin dissolved in 20 mL phosphoric acid 6 mol L⁻¹ and 30 mL glacial acetic acid). After 60 minutes of boiling at 100 °C in a water bath, 5 mL of toluene was added to the mixture. Utilizing a spectrophotometer Jenway 67155 UV/Vis (Stone, UK), the absorbance measurement was done at 528 nm. The content of proline was calculated as mg g⁻¹ of fresh weight (FW) by using a calibration curve.

Determination of Total Soluble Sugar Content

Tomato plants' soluble sugar content was measured according to Shields and Burnett (1960) method. One gram of fresh plant material was extracted in 5.25 mL of 80% ethanol for a period of 24 h. Dilution of the resulting extract was carried out ten times with 80% ethanol. Next, 2 mL extract were added to 4 mL anthrone reagent (2 g anthrone dissolved in 1000 mL sulfuric acid). By a spectrophotometer Jenway 67155 UV/Vis (Stone, UK), the developed blue-green color was measured at 585 nm. Since glucose was used to create a standard curve, the results are expressed in mg g⁻¹ of fresh weight (FW).

Statistical Analyses

Two-way ANOVA has been used for the analysis of the results with STATBOX v6.4 software, and means were compared with the LSD test ($P < 0.05$).

Results

Screening of *Pleiosporaceae* sp. Salt Tolerance

The analysis demonstrated that the *Pleiosporaceae* sp. mycelial growth was significantly affected by salinity (Fig. I). At 100 mM NaCl concentration, *Pleiosporaceae* sp. showed the highest mycelial growth, reaching 6.1 \pm 1 cm compared with the control (without NaCl), demonstrating its ability to alleviate NaCl stress. In contrast, *Pleiosporaceae* sp. mycelial growth decreased when NaCl concentration exceeded 100 mM.

Indole Acetic Acid (IAA) Production

The synthesis of indole acetic acid by *Pleiosporaceae* sp. under different NaCl concentrations is shown in (Fig. II). Data indicated that the highest IAA level of 138.6 \pm 0.7 μ g/mL was achieved at 100 mM NaCl. This indicates that the 100 mM NaCl concentration was optimal for IAA production by *Pleiosporaceae* sp. at 0.1 g/L tryptophan.

Germination Rate

NaCl treatments significantly decreased the germination rate of tomato seeds compared to the control. Moreover, germination was totally

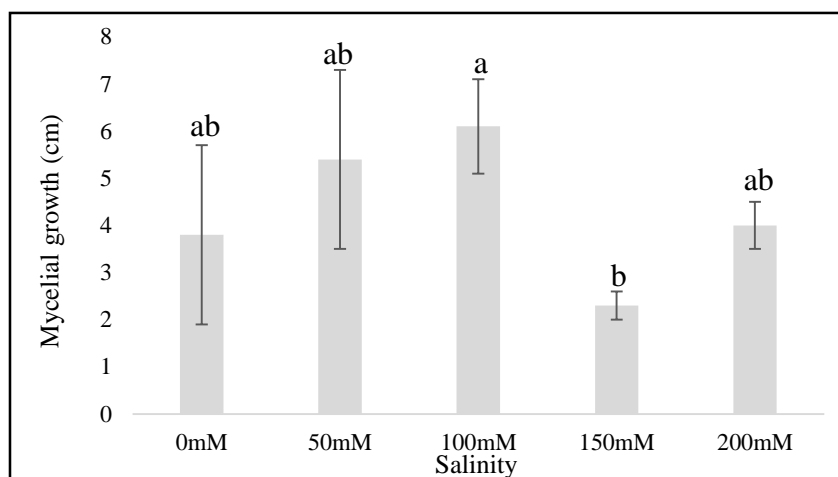


Fig. I. Effect of NaCl levels (50, 100, 150 and 200 mM) on *Pleosporaceae* sp. mycelial growth (cm). Means followed by the same letter are not significantly different ($P < 0.05$) according to LSD test

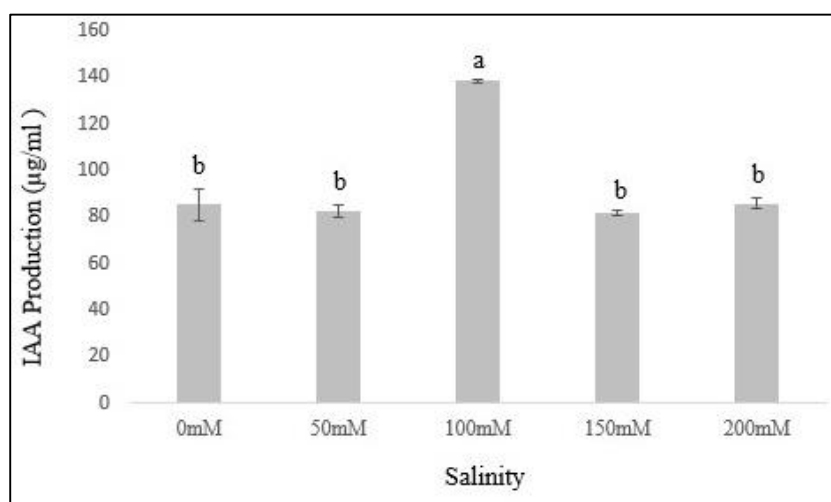


Fig. II. Indole acetic acid production by *Pleosporaceae* sp. under salt stress (µg/ml). Means followed by the same letter are not significantly different ($P < 0.05$) according to LSD test.

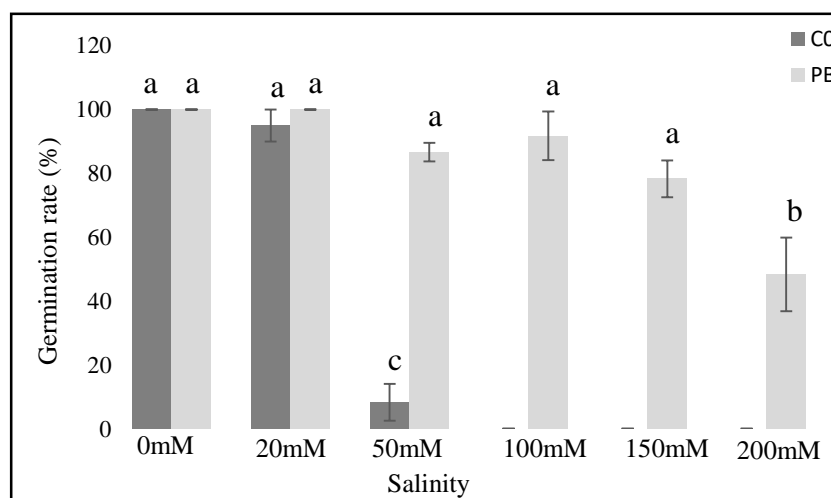


Fig. III. Effect of NaCl, *Pleosporaceae* sp. application, and their interactions on germination rate of tomato seeds (%). Means followed by the same letter are not significantly different ($P < 0.05$) according to LSD test.

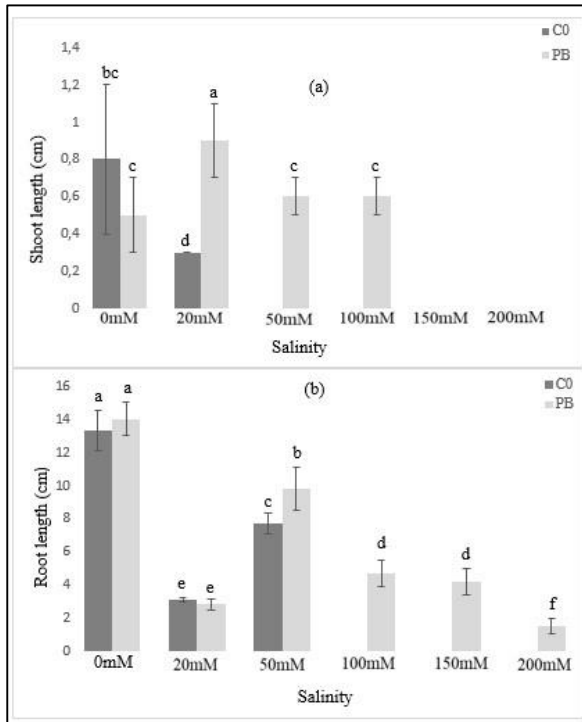


Fig. IV. Effect of NaCl, *Pleosporaceae* sp. application, and their interactions on shoot length (a) and root length (b) of tomato seeds (cm). Means followed by the same letter are not significantly different ($P < 0.05$) according to LSD test.

inhibited under high saline stress (100, 150, and 200 mM) in non-*Pleosporaceae* sp. treated seeds (Fig. III). Data showed a total inhibition of germination in tomato plants subjected to high concentrations of NaCl (100, 150, and 200 mM) conducted in the absence of *Pleosporaceae* sp. In the present study, it was found that *Pleosporaceae* sp. stimulated tomato plant germination even at high salinity levels (100, 150, and 200 mM).

Shoot and Root Lengths

The obtained results showed that the shoot (Fig. IV a) and root lengths (Fig. IV b) of tomato plants inoculated with *Pleosporaceae* sp. increased significantly ($P < 0.05$) compared to non-inoculated ones. Indeed, a growth reduction was observed. Moreover, these characteristics were significant in the inoculated tomatoes under different salinities. The highest shoot length (0.9 ± 0.1 cm) was measured in the inoculated plants treated with 20 mM NaCl. The longest root (14 ± 1 cm) was recorded in inoculated plants without salt treatment.

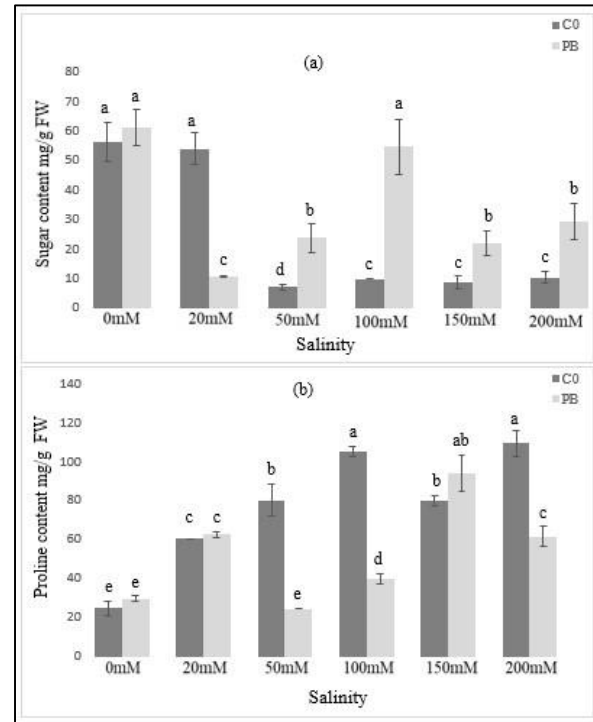


Fig. V. Effect of NaCl, *Pleosporaceae* sp. application, and their interactions on sugar content (a) and proline content (b) of tomato seeds (mg/g FW). Means followed by the same letter are not significantly different ($P < 0.05$) according to LSD test.

Total Soluble Sugar and Proline Accumulation

A significant decrease in soluble sugar content was noted in tomato plants under saline conditions. Under control conditions, the sugar content of *Pleosporaceae* sp.-inoculated tomato leaves was higher (61.1 ± 6.1 mg/g FW) than non-inoculated plants (56.2 ± 6 mg/g FW). Except for the 20 mM NaCl treatment, increased salinity significantly improved the sugar content in the inoculated plants compared to the treatments without *Pleosporaceae* sp. However, the recorded sugar levels remained lower than those observed in the control plants (both *Pleosporaceae* sp. associated and non-associated tomato plants). Sodium chloride treatment induced higher sugar accumulation in inoculated tomato plants under 100 mM of salinity (Fig. V a).

The obtained results demonstrated that proline levels in non-*Pleosporaceae* sp.-inoculated tomato plants exposed to saline conditions of 50, 100, and 200 mM exceeded the values recorded in tomato plants grown under favorable conditions (Fig. V b).

Discussion

This research displays tolerance improvement in *Pleiosporaceae sp.*-inoculated tomatoes under NaCl stress. To our knowledge, this study presents the first *in vitro* and *in vivo* experimental evidence of the ability of *Pleiosporaceae sp.* fungi to promote plant salt stress tolerance. *Pleiosporaceae sp.* is a pigmented endophytic fungus from the *Ascomycetes* phylum that may play a role in host tolerance to stressful conditions (Furtado et al., 2019). Pigmented fungi that live inside plants are frequently found in salty environments and could be crucial for plants to survive and resist high salt levels, as stated by Sun et al. (2012). These fungi produce high levels of pigments that can protect plants growing in saline environments (Venkatachalam et al., 2019). In recent years, the evaluation of fungal strains tolerance to saline conditions has received considerable attention. In fact, numerous studies have described the tolerance of endophytic fungi to different sodium chloride concentrations (Ghorbani et al., 2023; Jalili et al., 2020). The obtained results indicated that *Pleiosporaceae sp.* was halotolerant.

Endophytic fungi tolerance to salt stress can be explained by several mechanisms. According to Kondrasheva et al. (2022), endophytes produce Indole Acetic Acid (IAA) *in vitro*, and this production increases under salt stress conditions. The current study's findings support the ability of *Pleiosporaceae sp.* to produce this plant hormone (IAA); this suggests that *Pleiosporaceae sp.* may play an effective role in promoting plant tolerance to salt stress. Improved plant growth in abiotic stress conditions can be attributed to the production of plant growth-promoting substances (IAA and GAs) by endophytic fungi (Ghorbani et al., 2023). Shahzad et al. (2022) showed that plants can overcome the negative effects of salt stress by application of exogenous IAA.

According to the study's findings, the germination percentage of tomato plants decreased significantly with increasing salinity. Additionally, several studies have reported that salinity reduces the germination percentage of tomato plant (Nasrin and Mannan, 2019) and prolongs the germination time (Adilu and Gebre, 2021). Zhang et al. (2023) attributed this decrease to an osmotic dormancy mechanism that plants develop under

stressful conditions, which represents an adaptive strategy to environmental constraints. Wei et al. (2008) reported that glycophytes and halophytes plants respond to salinity in the same way, by reducing the total number of germinated seeds and delaying the germination process initiation. The negative effects of salt stress on seed germination can be the consequence of ionic imbalance or salinity-induced toxicity (de la Reguera et al., 2020). In addition, the reduction in the final germination rate corresponds to an increase in external osmotic pressure and/or an accumulation of Na^+ and Cl^- in the embryo, which affects the water uptake of plants (Tebini et al., 2022).

A total inhibition of germination in tomato plants subjected to high concentrations of NaCl and conducted in the absence of *Pleiosporaceae sp.* was observed. The obtained results are consistent with those of de la Reguera et al. (2020), signaling that high salt concentrations led to germination blockage. Hadjadj et al. (2022) revealed that toxic and osmotic combined salt effects are responsible for this inhibition. However, germination of tomato plants was improved by *Pleiosporaceae sp.* According to Ghorbani et al. (2018), the endophyte *Piriformospora indica* improved tomato growth under salt stress compared to non-inoculated plants. Endophytic fungi have a significant impact on plant adaptation to environmental stress conditions, including drought, heat, salinity and nutrient stress (Ameen et al., 2024). On the other hand, Verma et al. (2022) showed that some plants couldn't survive stressful conditions in the absence of their associated fungi.

The results showed that treatment of tomato with sodium chloride resulted a growth reduction, corroborating the results reported by Ghorbani et al. (2023). Moreover, shoot lengths decreased as the NaCl concentration rises. Despite the negative effects of salt stress on shoots and roots, the obtained results revealed that root lengths seem to be less impacted than shoot lengths, which are significantly affected. Singh et al. (2012) signaled similar findings. Moreover, these characteristics were significant in the inoculated tomatoes under different salinities. The highest shoot length (0.9 ± 0.1 cm) was measured in the inoculated plants

treated with 20 mM NaCl. The longest root ($14\pm 1\text{cm}$) was recorded in inoculated plants without salt treatment. The results of this study indicated that tomato plants exposed to salt stress and inoculated with *Pleosporaceae* sp. exhibited improvements in shoot and root growth. According to Otlewska et al. (2020), endophytes employ direct or indirect strategies to enhance plant salt stress tolerance, such as improving nutrient uptake, accumulating osmolytes, and producing certain phytohormones. The endophytes, *Phoma glomerata* and *Penicillium* sp. secreted gibberellic acid and indole acetic acid to promote rice growth under salt stress conditions (Manjunatha et al., 2022; Waqas et al., 2012).

Accumulation of osmolytes such as proline, glycine betaine and sugars is the most common strategy for plants to tolerate stress conditions (Liu et al., 2022). Under salinity stress, raising the concentration of these osmolytes can maintain a favorable water potential gradient for soil water absorption and plant damage reduce (Zhao et al., 2021). In this study, tomato plants decrease their sugar content under salt stress. Laksana et al. (2023) indicated that sugar amounts decreased substantially in plants exposed to salty conditions compared to non-subjected ones.

Inoculation of *Pleosporaceae* sp. increases total soluble sugar content in tomato seeds compared with untreated ones under normal or stress conditions. According to Ismail et al. (2018), both under stressful and non-stressful condition, *Aspergillus japonicus* increases the amount of soluble sugar in sunflower and soybean plants when compared to non-*Aspergillus japonicus*-associated plants. According to Li et al. (2017), endophytic fungi have the ability to reduce the negative impacts of environmental stresses and promote plant growth via synthesis, degradation and storage of sugars. Several reports have shown that endophytic fungi protect plants from environmental stresses by enhancing their antioxidant activity; this change promotes the accumulation of sugars, which may lead to scavenge ROS or avoid oxidative cell damage (Badawy et al., 2021).

In addition to its osmotic effect, proline is also involved in the detoxification of reactive oxygen

species and protein stabilization (Atta et al., 2024). Plants often increase their proline levels as one of their typical reactions to different types of stress, such as salty conditions. This is an initial step in how plants adapt to challenging environments (Kumar et al., 2015).

Compared to non-colonized tomato plants, the inoculated ones showed lower proline levels. However, Li et al. (2017) reported different findings; demonstrating that proline content was increased by inoculating *Chlorophytum borivillianum* plants with the endophyte *Brachybacterium paraconglomeratum*.

Conclusion

we introduce this desert-adapted halotolerant fungal endophyte, *Pleosporaceae* sp., isolated from halophyte plant, as a novel environmentally friendly way to help tomato (*Solanum lycopersicum* L.) cope with salinity stress. Future studies on the epigenetic, cellular and molecular levels are needed *in vitro* and *in planta* to understand the mechanisms by which these endophytes enhance plant growth and yield under salt stress; and will help to understand how endophytes interact with their hosts.

References

- Adilu, G. S. and Y. G. Gebre. 2021. Effect of salinity on seed germination of some tomato (*Lycopersicon esculentum* Mill.) varieties. *Journal of Aridland Agriculture*, 7, 76-82.
- Akagi, A., C.-J. Jiang and H. Takatsuji. 2015. Magnaporthe oryzae inoculation of rice seedlings by spraying with a spore suspension. *Bio-protocol*, 5, (11) e1486-e1486.
- Ameen, M., A. Mahmood, A. Sahkoo, M. A. Zia and M. S. Ullah. 2024. The role of endophytes to combat abiotic stress in plants. *Plant Stress*, 100435.
- Atta, N., M. Shahbaz, F. Farhat, M. F. Maqsood, U. Zulfiqar, N. Naz, M. M. Ahmed, N. U. Hassan, N. Mujahid and A. E.-Z. M. Mustafa. 2024. Proline-mediated redox regulation in wheat for mitigating nickel-induced stress and soil decontamination. *Scientific Reports*, 14, (1) 456.

- Badawy, A. A., M. O. Alotaibi, A. M. Abdelaziz, M. S. Osman, A. M. Khalil, A. M. Saleh, A. E. Mohammed and A. H. Hashem. 2021. Enhancement of seawater stress tolerance in barley by the endophytic fungus *Aspergillus ochraceus*. *Metabolites*, 11, (7) 428.
- Byregowda, R., S. R. Prasad, R. Oelmüller, K. N. Nataraja and M. Prasanna Kumar. 2022. Is endophytic colonization of host plants a method of alleviating drought stress? Conceptualizing the hidden world of endophytes. *International journal of molecular sciences*, 23, (16) 9194.
- Chauhan, P., N. Sharma, A. Tapwal, A. Kumar, G. S. Verma, M. Meena, C. S. Seth and P. Swapnil. 2023. Soil microbiome: Diversity, benefits and interactions with plants. *Sustainability*, 15, (19) 14643.
- De La Reguera, E., J. Veatch, K. Gedam and K. L. Tully. 2020. The effects of saltwater intrusion on germination success of standard and alternative crops. *Environmental and Experimental Botany*, 180, 104254.
- Furtado, B. U., M. Gołębiewski, M. Skorupa, P. Hulisz and K. Hryniewicz. 2019. Bacterial and fungal endophytic microbiomes of *Salicornia europaea*. *Applied and Environmental Microbiology*, 85, (13) e00305-00319.
- Ghorbani, A., L. Pishkar, K. V. Saravi and M. Chen. 2023. Melatonin-mediated endogenous nitric oxide coordinately boosts stability through proline and nitrogen metabolism, antioxidant capacity, and Na⁺/K⁺ transporters in tomato under NaCl stress. *Frontiers in Plant Science*, 14, 1135943.
- Ghorbani, A., S. Razavi, V. G. Omran and H. Pirdashti. 2018. Piriformospora indica alleviates salinity by boosting redox poise and antioxidative potential of tomato. *Russian Journal of Plant Physiology*, 65, 898-907.
- Gordon, S. A. and R. P. Weber. 1951. Colorimetric estimation of indoleacetic acid. *Plant physiology*, 26, (1) 192.
- Hadjadj, S., B. B. Sekerifa, H. Khellafi, K. Krama, S. Rahmani and A. O. El Hadj-Khelil. 2022. Salinity and type of salt effects on seed germination characteristics of medicinal plant *Zygophyllum album* L. (Zygophyllaceae) native to the Algerian Sahara. *Journal of Applied Research on Medicinal and Aromatic Plants*, 31, 100412.
- Ignatova, L., A. Usmanova, Y. Brazhnikova, A. Omirbekova, D. Egamberdieva, T. Mukasheva, A. Kistabayeva, I. Savitskaya, T. Karpenyuk and A. Goncharova. 2022. Plant probiotic endophytic *Pseudomonas fluorescens* D5 strain for protection of barley plants from salt stress. *Sustainability*, 14, (23) 15881.
- Ismail, M. Hamayun, A. Hussain, A. Iqbal, S. A. Khan and I.-J. Lee. 2018. Endophytic fungus *Aspergillus japonicus* mediates host plant growth under normal and heat stress conditions. *BioMed Research International*, 2018, (1) 7696831.
- Jalili, B., H. Bagheri, S. Azadi and J. Soltani. 2020. Identification and salt tolerance evaluation of endophyte fungi isolates from halophyte plants. *International journal of environmental science and technology*, 17, 3459-3466.
- Kondrasheva, K., F. Egamberdiev, R. Suyarova, D. Ruzieva, S. Nasmetova, L. Abdulmyanova, G. Rasulova and T. Gulyamova. 2022. Production of indole-3-acetic acid by endophytic fungi of halophyte plants under salt stress. *Proc. IOP Conference Series: Earth and Environmental science*, 2022, 1068:012040: IOP Publishing.
- Kouadria, R., M. Bouzouina, B. Lotmani and S. Soualem. 2023. Unraveling the role of endophytic fungi in barley salt-stress tolerance. *Hellenic Plant Protection Journal*, 16, 12-22.
- Kumar, V., V. Shriram, M. A. Hossain and P. Kishor. 2015. Engineering proline metabolism for enhanced plant salt stress tolerance. *Managing salt tolerance in plants: molecular and genomic perspectives*, 1,
- Laksana, C., O. Sophephun and S. Chanprame. 2023. In vitro and in vivo screening for the identification of salt-tolerant sugarcane (*Saccharum officinarum* L.) clones: molecular, biochemical, and physiological responses to salt stress. *Saudi Journal of Biological Sciences*, 30, (6) 103655.
- Li, X., S. Han, G. Wang, X. Liu, E. Amombo, Y. Xie and J. Fu. 2017. The fungus *Aspergillus aculeatus* enhances salt-stress tolerance, metabolite accumulation, and improves forage quality in perennial ryegrass. *Frontiers in microbiology*, 8, 1664.
- Liu, C., B. Mao, D. Yuan, C. Chu and M. Duan. 2022. Salt tolerance in rice: Physiological

- responses and molecular mechanisms. *The Crop Journal*, 10, (1) 13-25.
- Lu, Y. and W. Fricke.** 2023. Salt Stress—Regulation of root water uptake in a whole-plant and diurnal context. *International Journal of Molecular Sciences*, 24, (9) 8070.
- Manjunatha, N., N. Manjunatha, H. Li, K. Sivasithamparam, M. G. Jones, I. Edwards, S. J. Wylie and R. Aggarwal.** 2022. Fungal endophytes from salt-adapted plants confer salt tolerance and promote growth in wheat (*Triticum aestivum* L.) at early seedling stage. *Microbiology*, 168, (8) 001225.
- Morales-Vargas, A. T., V. López-Ramírez, C. Álvarez-Mejía and J. Vázquez-Martínez.** 2024. Endophytic fungi for crops adaptation to abiotic stresses. *Microorganisms*, 12, (7) 1357.
- Nasrin, S. and M. A. Mannan.** 2019. Impact of salinity on seed germination and seedling growth of tomato. *J Biosci Agric Res*, 21, 1737-1748.
- Otlewska, A., M. Migliore, K. Dybka-Stępień, A. Manfredini, K. Struszyk-Świta, R. Napoli, A. Białkowska, L. Canfora and F. Pinzari.** 2020. When salt meddles between plant, soil, and microorganisms. *Frontiers in plant science*, 11, 553087.
- Shahzad, K., E. H. Siddiqi, S. Ahmad, U. Zeb, I. Muhammad, H. Khan, G.-F. Zhao and Z.-H. Li.** 2022. Exogenous application of indole-3-acetic acid to ameliorate salt induced harmful effects on four eggplants (*Solanum melongena* L.) varieties. *Scientia Horticulturae*, 292, 110662.
- Shields, R. and W. Burnett.** 1960. Determination of protein-bound carbohydrate in serum by modified anthrone method. *Analytical Chemistry*, 32, (7) 885-886.
- Singh, J., E. D. Sastry and V. Singh.** 2012. Effect of salinity on tomato (*Lycopersicon esculentum* Mill.) during seed germination stage. *Physiology and Molecular Biology of Plants*, 18, 45-50.
- Sun, Y., Q. Wang, X. Lu, I. Okane and M. Kakishima.** 2012. Endophytic fungi associated with plants collected from desert areas in China. *Mycol Prog*, 11, 781-790.
- Tebini, M., G. Rabaoui, S. M'rah, D.-T. Luu, H. Ben Ahmed and A. Chalh.** 2022. Effects of salinity on germination dynamics and seedling development in two amaranth genotypes. *Physiology and Molecular Biology of Plants*, 28, (7) 1489-1500.
- Troll, W. and J. Lindsley.** 1955. A photometric method for the determination of proline. *Journal of biological chemistry*, 215, (2) 655-660.
- Venkatachalam, M., L. Gérard, C. Milhau, F. Vinale, L. Dufossé and M. Fouillaud.** 2019. Salinity and temperature influence growth and pigment production in the marine-derived fungal strain *Talaromyces albobiverticillius* 30548. *Microorganisms*, 7, (1) 10.
- Verma, A., N. Shameem, H. S. Jatav, E. Sathyanarayana, J. A. Parray, P. Pocza and R. Sayyed.** 2022. Fungal endophytes to combat biotic and abiotic stresses for climate-smart and sustainable agriculture. *Frontiers in plant science*, 13, 953836.
- Waqas, M., A. L. Khan, M. Kamran, M. Hamayun, S.-M. Kang, Y.-H. Kim and I.-J. Lee.** 2012. Endophytic fungi produce gibberellins and indoleacetic acid and promotes host-plant growth during stress. *Molecules*, 17, (9) 10754-10773.
- Wei, Y., M. Dong, Z.-Y. Huang and D.-Y. Tan.** 2008. Factors influencing seed germination of *Salsola affinis* (Chenopodiaceae), a dominant annual halophyte inhabiting the deserts of Xinjiang, China. *Flora-Morphology, Distribution, Functional Ecology of Plants*, 203, (2) 134-140.
- Zhang, Y., J. Xu, R. Li, Y. Ge, Y. Li and R. Li.** 2023. Plants' response to abiotic stress: Mechanisms and strategies. *International Journal of Molecular Sciences*, 24, (13) 10915.
- Zhao, S., Q. Zhang, M. Liu, H. Zhou, C. Ma and P. Wang.** 2021. Regulation of plant responses to salt stress. *International Journal of Molecular Sciences*, 22, (9) 4609.