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RESEARCH ARTICLES

Fungal endophytes contribute to enhancing salinity stress tolerance in eggplant (*Solanum melongena* L.)

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Abstract

Endophytes benefit the host by enhancing its ability to withstand abiotic and biotic stresses by producing plant-specific hormones and secondary metabolites. The generation of plant hormones like indole acetic acid and gibberellins is one advantage of the mutualistic relationship between the host plant and the endophytes. Thus, the present study was designed to isolate the endophytic fungi from brinjal var. Mattu Gulla under salinity stress conditions. The endophytes were isolated from leaves and roots using the standard protocol and identified based on the morphology of the spores. The effect of salinity on germination of the spores and growth of the endophytes under salinity conditions and its effect on seed germination, root architecture, and gas exchange parameters were studied. *Colletotrichum* sp. and *Curvularia* sp. dominated the roots of salt-stressed plants, but *Phomopsis* sp. dominated the endophyte community in the leaves. *Curvularia* sp. and *Phomopsis* sp. are salinity tolerant, based on in vitro investigations of spore germination from isolated endophytes and growth in NaCl mixed media. Additionally, different NaCl concentrations were used to allow the spores of *Phomopsis* sp. and *Curvularia* sp. to germinate, and the germ tube length was longer in the 100 mM NaCl treatment group than in the control group. In contrast to the control group, *Phomopsis* sp. germ tubes decrease in length when exposed to salinity stress. Our research showed that endophyte-conditioned media, for the first time, modifies root architecture and promotes seed germination. The present study describes the endophytic communities of brinjal grown under salinity stress and their plant growth- promoting activity.

Keywords Brinjal · Salinity · Endophytes · Seed germination · Root architecture · Gas exchange

Introduction

Eggplant (*Solanum melongena* L.) is an economically significant crop cultivated worldwide for its nutritional, medicinal and culinary value. However, its productivity is often challenged by various biotic and abiotic stresses (Kaniyassery et al. 2023; 2024), including salinity stress, which adversely affects growth, development, and yield (Abideen 2021). Salinity stress arises from elevated levels of specific salt ions within the soil (Numan et al. 2018). Salinity stress disrupts plant physiological processes by inducing osmotic and ionic imbalances, leading to reduced water uptake and nutrient absorption, oxidative stress, and ultimately, decreased productivity (Soni et al. 2023). The regulation of ethylene-responsive genes, including those encoding biosynthesis enzymes, receptors, and signalling proteins, along with their interactions with other hormonal pathways such as ABA, IAA, and cytokinin, mediates plant adaptation to salinity stress through mechanisms involving ion homeostasis and crosstalk with MAPK and CDPK signalling cascades (Godara and Ramakrishna 2023).

Endophytes are microbes (fungi or bacteria) that live within the host plant without causing any signs or symptoms, and in turn provide beneficial effects to the host by producing plant hormones and secondary metabolites and helping to increase abiotic and biotic stress tolerance (Ogbe et al. 2020). The beneficial effect of the endophyte on the host plant in mitigating stress is either due to endophyte-induced activation of the stress response by the host plant or the direct production of anti-stress metabolites by the endophytes (Lata et al. 2018). The endophyte *Piriformospora*

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indica provides tolerance to salinity stress by activating the enzymatic antioxidant machinery in barley (Baltruschat et al. 2008). *Exophiala pisciphila*, an endophytic fungus, reduces Cd stress in *Zea mays* by modulating genes involved in Cd absorption, translocation, and chelation (Wang et al. 2016). Although there are few studies available on the characterization of endophytes from eggplant, no systematic studies are available for this unique and geographic Indication status-tagged variety, Mattu Gulla. As a result, the current study sought to screen and identify the endophytic communities isolated from the leaves and roots of the unique variety of brinjal, Mattu Gulla, under salinity conditions. The effects of salinity on endophyte growth and spore germination were investigated. Additionally, the impact of the endophytic extract on gas exchange parameters, root architecture, and seed germination was ascertained.

Materials and methods

Plant treatment

The seeds of Mattu Gulla were surface sterilised, as mentioned by Thorat et al. (2022). The sterilised seeds were then planted in pots containing a sterile mix of soil, coir, and sand (1:1:1 ratio) under greenhouse conditions. Two-week-old Mattu Gulla seedlings were distributed randomly into three groups of five pots each with the same soil mix. Every day, the seedlings were treated with 100 mL of half-strength MS (Murashige and Skoog 1962) media supplemented with NaCl (75 or 150 mM), while the control group received 100 mL of MS media (half-strength) without NaCl and was maintained under greenhouse conditions with 35 ± 2 ℃ and 70% moisture. The plants were treated with NaCl-amended MS medium for 21 days, and fresh weight was recorded.

Isolation of endophytes

Roots and leaves were collected from both control and NaCl-treated plants. The tissues were thoroughly washed with tap water to remove any adhering dust particles, followed by rinsing with sterile distilled water. The cleaned tissues were then cut into small segments (~ 0.5 cm^2) and surface sterilised following the protocol described by Sawmya et al. (2013). In summary, surface sterilization was carried out using 70% ethanol for 30 s, followed by 4% sodium hypochlorite for 90 s, and finally rinsed with sterile distilled water to remove any residual disinfectants. The sterilized tissue segments were then placed on Potato Dextrose Agar (PDA) supplemented with chloramphenicol (150 mg/L) to inhibit bacterial contamination. The plates were incubated at 26 ℃, for 7–14 days depending on the growth rate of the fungi and fungal growth was monitored daily. Upon sufficient growth, the fungal endophytes were sub-cultured onto fresh PDA plates and classified into different morphotypes based on their cultural and morphological characteristics. The colonization frequency (CF%), density percentage (DP%), and contribution of the dominant endophyte (DE%) was calculated.

Identification of endophytes

The endophytes were identified based on the morphology of the spores as described (Ellis 1971). Agar blocks containing the mycelial growth of the fungi were kept on a clean glass slide. This sample was covered with a sterile coverslip. The glass slides were then placed in a sterile Petri plate with sterile Whatman filter paper moistened with 2 mL of autoclaved distilled water and incubated at 28℃ for 4–5 days. After sporulation, the coverslip was placed on a new, clean glass slide and examined with a Nikon Eclipse Ci microscope at 40X magnification (Riddell 1950).

Effect of NaCl on the growth of endophytes and spore germination

The effect of salinity on the growth of endophytes was assessed by growing the endophytes on media supplemented with various concentrations of NaCl. Two-week-old endophytes grown on Sabouraud dextrose agar (SDA) media were inoculated on Czapek Dox Agar (CDA) media supplemented with 50, 100, or 200 mM NaCl. CDA medium without NaCl was used as a control. The plates were incubated for 3–4 days at 28 ℃. The plates were observed every day for growth, and the diameter of the fungal colonies was measured. The growth rate of the fungi on the NaCl-amended media was calculated. The germination of endophyte spores was studied by allowing them to germinate on CDA media supplemented with various amounts of NaCl. The glass slides were sterilised , and blocks of CDA medium supplemented with NaCl (0, 50, 100, and 200 mM) were placed on them. The endophyte spores were harvested with sterile distilled water and counted in a Neubauer chamber. The CDA blocks were placed on clean, sterile glass slides, and 10,000 spores were seeded on them. They were then incubated at 28℃ for two hours in the dark. The spores were examined for germination with a Nikon Eclipse Ci microscope at 40X, and photos were captured. When the length of the germ tube is more than the width of the spores, then the spores were considered germinated. Images of different

areas were captured, 100 spores were observed for germination, and the length of the germ tube was measured using Fiji ImageJ software.

Effect of endophyte extract on seed germination and root architecture

The endophytes were inoculated on Czapek Dox broth supplemented with or without 50 mM NaCl and incubated at 28℃ in a shaker incubator at 120 rpm for two weeks. Then, the cultures were filtered using Whatman filter paper, and an endophyte-conditioned medium was used to investigate the effect of the extracellular secretome of the endophytes on the germination of the seeds. The endophyte-conditioned medium was concentrated using an IKA RV10 rotary evaporator at 100 rpm under 72 mm pressure at 60℃ and then lyophilized using a Heto Powerdry LL1500 freeze dryer (Thermo Scientific). The powder was reconstituted in sterile distilled water. The MS medium was supplemented with 0.1 mg mL^{-1} reconstituted endophyte-conditioned medium. The Mattu Gulla seeds were surface sterilised and inoculated on MS media supplemented with endophyte-conditioned media. The bottles were incubated at 25℃ with a photoperiod of 16 h of light and 8 h of dark as described by Muthusamy and Jayabalan (2014). The seeds were observed, and the percentage of germination was recorded. The seeds were surface sterilized before being inoculated onto MS media containing 0.1 mg mL^{-1} of endophyte-conditioned media. The 21-day-treated plants were carefully removed, and the roots and shoots were separated. The roots were spread out on a transparent sheet and imaged with an HP Scanjet G3110 scanner. The number of secondary roots was counted, and the primary and secondary root lengths were measured using the Fiji ImageJ software.

Effects of endophyte-conditioned media on the photosynthetic rate, stomatal conductance and transpiration

A LI-6400XT portable photosynthesis system (Licor Inc., Lincoln, Nebraska, USA) was used to analyse the stomatal conductance, transpiration rate, and net photosynthetic rate. The readings were recorded on three consecutive days under greenhouse conditions from 10 to 11.30 am. The reference was retained at 400 ppm for the CO_2 level in the leaf cuvette, 500 ppm for the flow rate, 500 ppm for the density of photon flux from the LED lamp, 25 ± 2 ℃ for the leaf block temperature, and 1 for STOMRT. The data was measured as five readings per plant, and 5 plants per treatment were measured for stomatal conductance (mol H_2O m^{-2} s^{-1}), transpiration rate (mmol m^{-2} s^{-1}), and net photosynthetic rate (µmol CO_2 m^{-2} s^{-1}) as described by Evans and Santiago (2014).

Statistical analysis

All the experiments described in the study were performed in triplicates and the data were represented as mean ± SEM (n = 3). One-way ANOVA and Dunnet's multiple comparison tests (*p < 0.05, **p < 0.01, ***p < 0.001) were performed. Experimental data were analyzed for significance and plotted using GraphPad Prism version 8.

Results and discussion

Endophytic fungi were recovered from the roots and leaves of Mattu Gulla that had been treated with various NaCl concentrations. A total of 60 distinct endophyte isolates were identified from the roots of control plants, with a 62.5% colonization rate. The roots of plants treated with 75 mM and 150 mM NaCl yielded 48 and 68 isolates, respectively, with colonization frequencies of 50 (75 mM NaCl) and 70.83 (150 mM NaCl). Similarly, 44 isolates were identified from control plant leaves, with a 45.83% colonization rate. A total of 36 and 38 isolates were obtained from the leaves of *S. melongena* treated with 75 mM and 150 mM NaCl, respectively, with colonization frequencies of 37.5 and 39.58, respectively (Fig. 1). The difference in the colonization frequency of endophytic fungi in NaCl-treated and control plants was found to be statistically insignificant in both roots and leaves. The higher colonization rates in roots compared to leaves align with findings from previous studies. For instance, research has shown that endophytic fungi are more prevalent in root tissues due to direct soil contact, which exposes roots to a

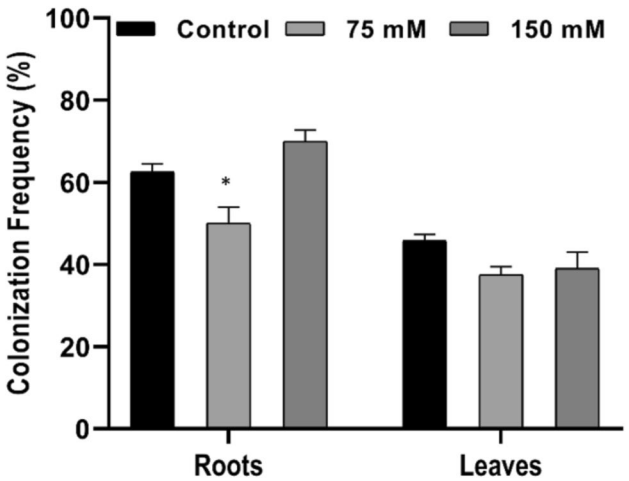

Fig. 1 The colonization frequency (CF%) of endophytes in the roots and leaves of *S. melongena* L. var Mattu Gulla treated with different concentrations of NaCl. Data were represented as mean ± SEM (n = 3) and Dunnet's multiple comparison tests (*p < 0.05)

diverse microbial community (Nurrahma et al. 2024). The predominance of *Curvularia* sp. in root tissues under high salinity conditions is consistent with other studies. For example, an endophytic *Curvularia* sp. isolated from the halophytic plant *Suaeda salsa* was able to establish beneficial symbiosis with poplar (*Populus tomentosa*), enhancing the host's tolerance to saline environments (Henson 2011). Endophytic fungi are known to improve nutrient uptake, maintain ionic homeostasis by modulating ion accumulation, and enhance the plant's antioxidant system to scavenge reactive oxygen species generated under stress conditions (Gupta et al. 2021). These mechanisms collectively aid in alleviating the detrimental effects of salinity on plant growth and development.

Identification of isolated endophytes

The endophytic fungal isolates were identified based on their culture and spore morphology. A total of 12 sporulating morphotypes were identified in the root endophytes *Penicillium* sp. and *Curvularia* sp. were abundant in the roots of control plants, with a %CF of 9.6. *Curvularia* sp. was abundant in the roots of the 75 and 150-mM groups, with DP% values of 13.44 and 15.36, respectively (Table S1). A total of 10 morphotypes were identified in the leaves of the control and treated plants. *Phomopsis* sp. was abundant in leaves, with DP% values of 9.38 and 10.42 in the control and 150 mM NaCl-treated plants, respectively (Figs. S1 and S2). However, *Curvularia* sp. was found to be abundant, with a DP% of 7.29 in the leaves of the 75 mM NaCl treatment group (Table S2). In the present study, endophytic fungi were exposed to salt stress by growing in NaCl-enriched growth media. *Curvularia* sp. and *Phomopsis* sp. could grow in vitro at moderate and high NaCl concentrations, respectively. *Colletotrichum* sp. and *Penicillium* sp. were tolerant to mild salinity stress, whereas *Nigrospora* sp. and *Fusarium* sp. were found to be sensitive to salinity stress, as their growth was inhibited even at low concentrations of NaCl.

Effect of NaCl on the growth of endophytes

The endophyte cultures were grown in the presence of different concentrations of NaCl. The growth of *Colletotrichum* sp. was similar at 0 and 50 mM NaCl (100 and 98.83%, respectively), whereas the growth was decreased to 84.88 at 100 and 200 mM NaCl, respectively. The growth of *Nigrospora* sp. decreased with increasing NaCl concentration. Compared with that of the control, the growth of *Curvularia* sp. plants that were tolerant to mild NaCl stress increased to 116 at 50 mM NaCl, whereas the growth of these plants was similar to that of the control at 100 mM NaCl (104.16). However, the growth was slightly reduced at 200 mM NaCl (91.66). *Penicillium* sp. growth slightly increased in the 50 mM NaCl treatment group (103.26) compared to that in the control group, but the growth decreased with increasing concentrations of NaCl. *Phomopsis* sp. was tolerant to a high concentration of NaCl, where maximum growth was observed at 100 mM NaCl (125.64), followed by 200 mM NaCl (115.38), while the growth was similar to that of the control at 50 mM (101.28). *Fusarium* sp. was not tolerant to NaCl, as growth decreased with increasing concentrations of NaCl (Fig. 2 and S3).

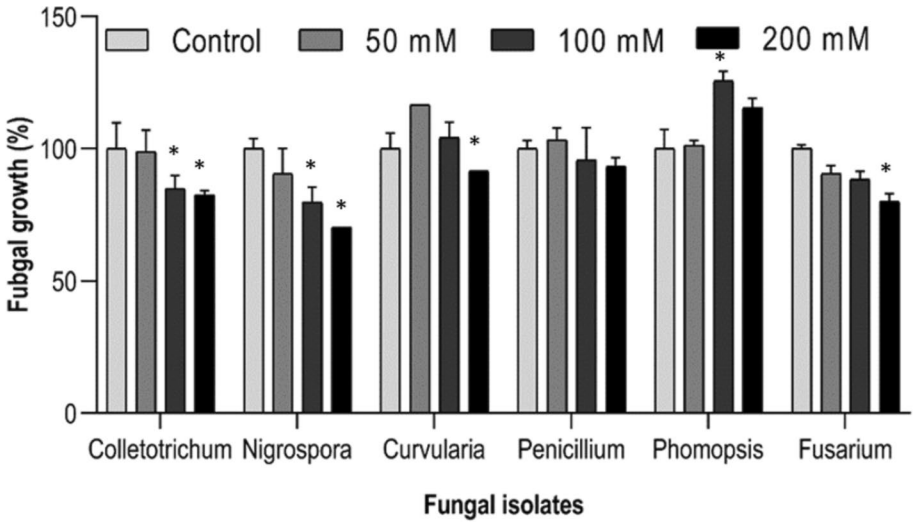

Fig. 2 Growth of different endophytes on growth media supplemented with different concentrations of NaCl. The growth rate was calculated as 100% for control and the other values were calculated as a percentage compared to control. Data were represented as mean ± SEM (n = 3) and Dunnet's multiple comparison tests (*p < 0.05)

Effect of NaCl on the germination of spores of endophytes

The effects of NaCl on the germination of spores of *Curvularia* sp. and *Phomopsis* sp. were evaluated by allowing the spores to germinate on media supplemented with different concentrations of NaCl (0, 50, 100, and 200 mM). Representative images of germinating spores of *Curvularia* sp. and *Phomopsis* sp. under different concentrations of NaCl are shown in Figures S5-S7. A significant increase in the germination tube length of *Curvularia* sp. was observed in the 50, 100, and 200 mM NaCl treatment groups compared to the control group (Figs. 3 and 4a–d). The germ tube (GT) length increased with increasing NaCl concentration. However, in *Phomopsis* sp., the length of GTs was not affected by 50 or 200 mM NaCl compared to that of the control. However, the length of the GT slightly increased in the 100 mM NaCl treatment group (Fig. S5a-d).

Effect of endophyte extract on seed germination

The effect of the culture extract of *Curvularia* sp. on seed germination was tested by inoculating the brinjal seeds on MS media supplemented with 0.1 mg mL^{-1} culture extract. The seeds showed a significant increase ($p < 0.001$) in germination in media supplemented with 0.1 mg mL^{-1} *Curvularia* sp. extract (Figs. 4 and 5). The germination percentage was 56.66% when the media was supplemented with the extract of *Curvularia* sp., whereas the germination percentage was 36.66% in the control. In our study, the spores of *Curvularia* sp. and *Phomopsis* sp. were able to germinate when treated with a relatively high concentration of NaCl, which was correlated with their ability to grow under salinity stress.

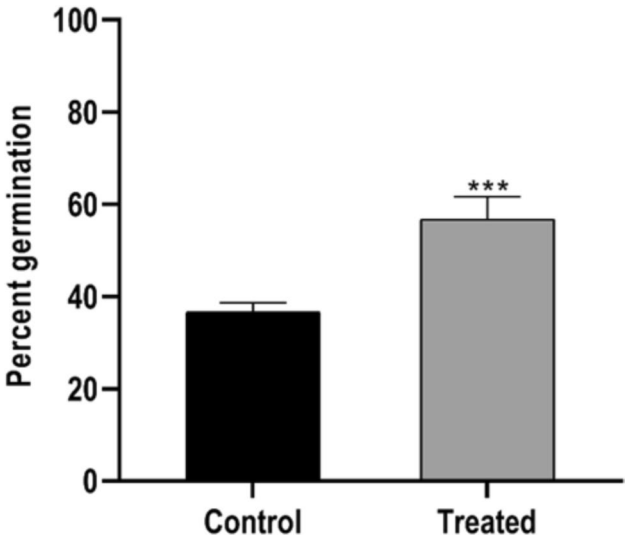

Fig. 4 Germination percentage of seeds of *S. melongena* L. var Mattu Gulla in control and seeds treated with culture extract of *Curvularia* sp. Data were represented as mean ± SEM (n = 3) and Dunnet's multiple comparison tests (***p < 0.001)

Endophyte-conditioned media is a rich source of metabolites that might play a key role in the growth and development of plants. The adenine derivatives secreted by the endophytic fungus *Rhodotorula minuta* act as precursors for the synthesis of cytokinin (Pirttilä et al. 2004). Hubbard et al. (2012) reported increased germination of wheat seeds in the presence of endophytic fungi.

Effect of the endophyte culture filtrate on the root architecture of *S. melongena*

The effect of the culture extract of endophytes on the root architecture of plants grown on media supplemented with 0.1 mg mL^{-1} *Curvularia* sp. extract was examined.

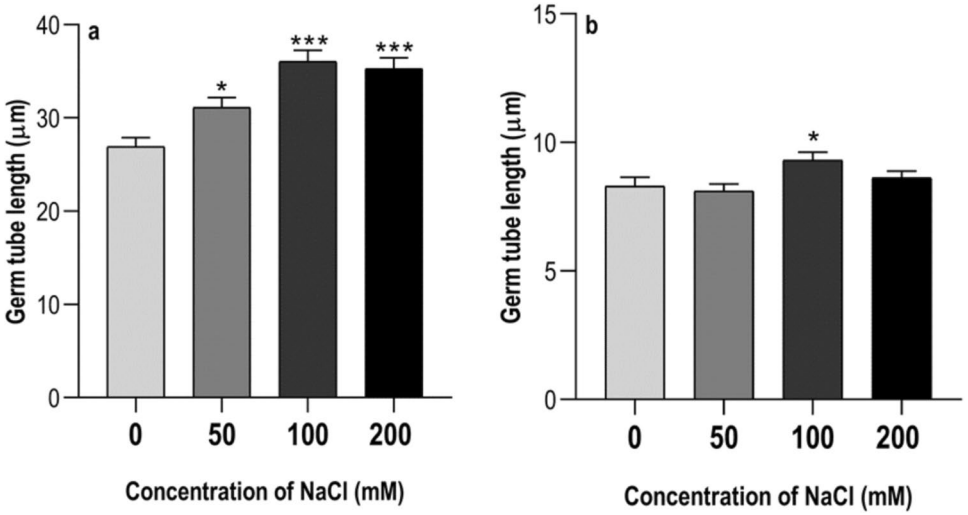

Fig. 3 Length of the germination tube when spores of a) *Curvularia* sp. and b) *Phomopsis* sp. inoculated on medium containing different concentrations of NaCl. Data were represented as mean ± SEM (n = 3) and Dunnet's multiple comparison tests (*p < 0.05, ***p < 0.001)

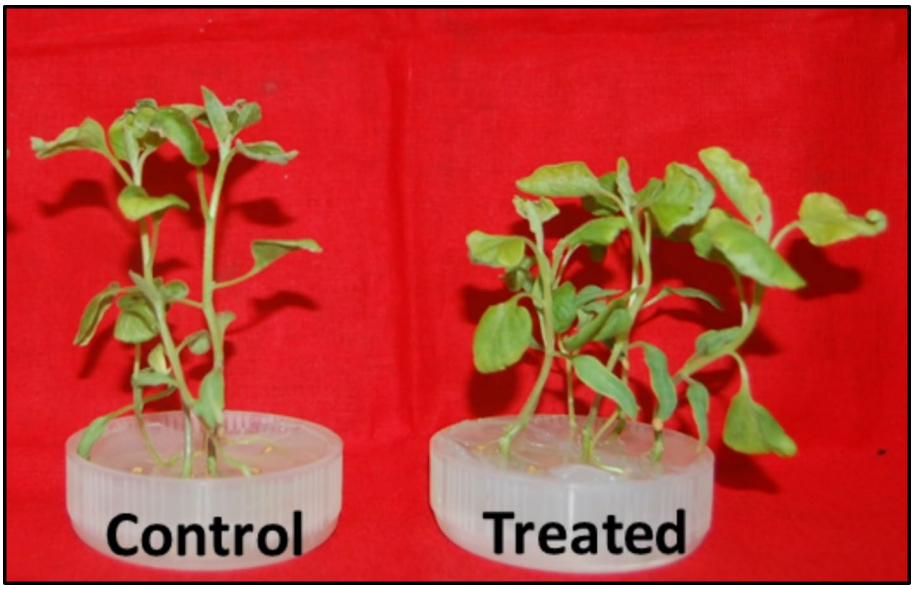

Fig. 5 Difference in growth characteristics in control (MS medium) and endophyte conditioned media. The treated group was grown in MS media supplemented with 0.1 mg mL^{-1} of endophyte conditioned media and the control group was grown in the MS media

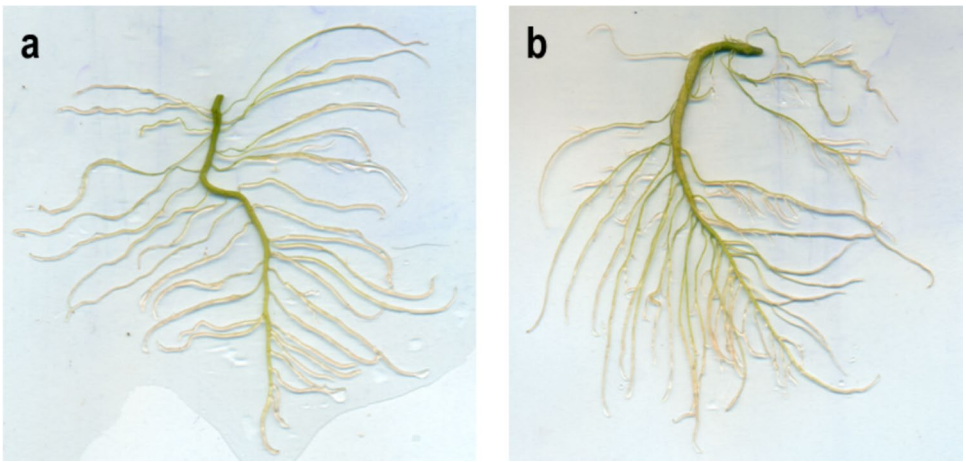

Fig. 6 Representative images of root architecture of **a** control plants and **b** plants grown on media supplemented with 0.1 mg mL^{-1} of *Curvularia* sp. extract

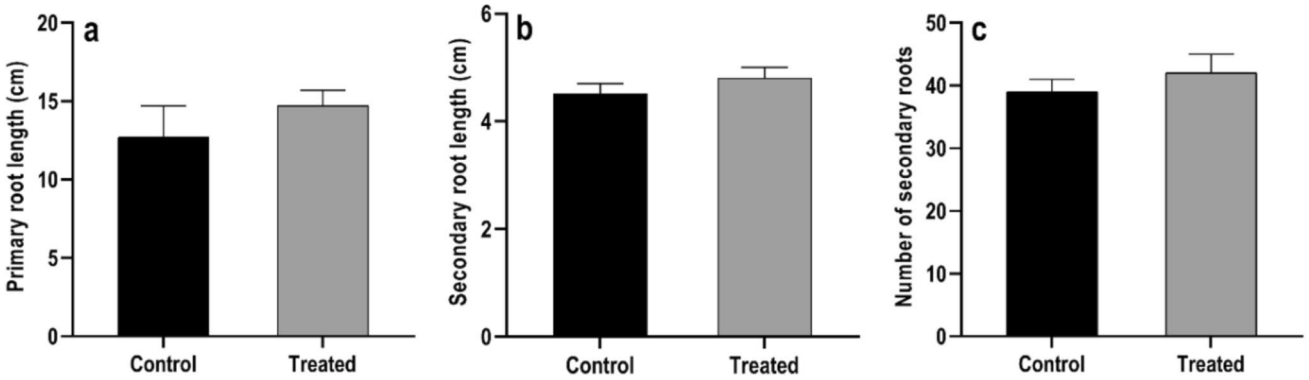

Fig. 7 Effect of fungal culture filtrate on the root architecture of *S. melongena* L.

The extract positively affected the primary and secondary roots of the plants (Fig. 6). The length of the primary root was slightly more significant in the plants treated with the fungal extract than in the control plants (13.97 and 12.7 cm, respectively). Furthermore, the number of secondary roots was greater in the fungal metabolite-treated

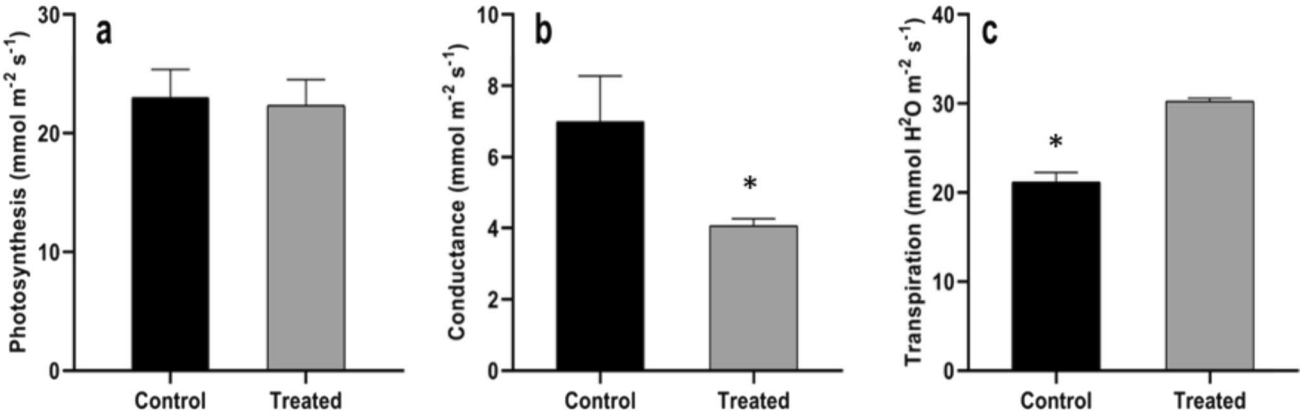

Fig. 8 Photosynthetic parameters of the plants in control and treated groups **a** Rate of photosynthesis **b** conductance and **c** Transpiration rate of seedlings. Data were represented as mean ± SEM (n = 3) and Dunnet's multiple comparison tests (*p < 0.05)

group than in the control group, whereas the length of the secondary roots was similar in both groups (Fig. 7a, b, c). The secondary metabolites of endophytes have a greater impact on root architecture in several plants (Verma et al. 2021). The volatile organic compounds of *Fusarium* sp. improved the root length of *Arabidopsis*, and fungi were able to alter the root architecture through volatile organic compounds without physical interaction with the plant (Schenkel et al. 2018). Our study also showed that the extracellular metabolites of *Curvularia* sp. can moderately modulate root architecture, with slight increases in primary root length and the number of secondary roots. Fungal metabolites act as elicitors that promote root development by activating receptor-mediated signalling pathways (Salope-Sondi et al. 2015).

Effect of the metabolites of endophytes on the fitness of *S. melongena* seedlings

The fitness of the seedlings grown in the presence of the endophyte culture filtrate was tested with respect to photosynthesis, conductance, and transpiration rate. The variation in the rate of photosynthesis was negligible in the plants grown in MS media supplemented with endophyte culture filtrate (Fig. 8a). The conductance slightly decreased in the treatment group (4.06 mmol m^{-2} s^{-1}) compared to that in the control group (6.9 mmol m^{-2} s^{-1}) (Fig. 8b). In contrast, transpiration increased significantly in the endophyte treatment group (30.25 mmol H_2O m^{-2} s^{-1}) compared to that in the control group (21.17 mmol H_2O m^{-2} s^{-1}) (Fig. 8c). The extract of *Curvularia* sp. improved the fitness of *S. melongena* L. var. Mattu Gulla. The extract of *Penicillium* sp. significantly increased the photosynthetic rate, transpiration, and stomatal conductance in *Carex kobomugi* (Hwang et al. 2011). Similarly, increased photosynthetic parameters were observed in endophyte-treated *Withania somnifera* (Pandey et al. 2018). In our study, there was no marked difference in the photosynthetic rate between the treated and control groups. However, we observed an increased transpiration rate and decreased stomatal conductance in plants grown on endophyte-conditioned media.

Conclusion

Endophytes provide assisted machinery to combat abiotic and biotic stress in the natural environment. Endophytes play a role in alleviating salinity stress in many crop plants and changes in fungal diversity have been seen under salinity stress. Salt-stressed plants' roots were dominated by *Colletotrichum* sp. and *Curvularia* sp., while *Phomopsis* sp. was the dominating endophyte in their leaves. An in vitro study of spore germination from isolated endophytes and growth in NaCl mixed media revealed that *Curvularia* sp. and *Phomopsis* sp. are salinity tolerant. Furthermore, the spores of *Phomopsis* sp. and *Curvularia* sp. were allowed to germinate under different concentrations of NaCl, and the length of the germ tube was greater in the 100 mM NaCl treatment group than in the control group. However, the germ tube length decreased in *Phomopsis* sp. under salinity stress compared to that in the control group. Endophytes have a rich repository of secondary metabolites, which aids in increasing plant fitness and alters germination parameters. Our study revealed that endophyte-conditioned media aids in the germination of seeds and alters root architecture for the first time. However, the photosynthetic features were not altered significantly in the plants treated with endophyte-conditioned media compared to those in the control plants.

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Author contributions AM, KKR and TSM conceived the idea; KKR and AM performed the experiment; KKR, AM and TSM analyzed the data; KKR, AK and AM wrote the manuscript; KKR, AK, TSM and AM edited the manuscript, and all authors gave approval for the manuscript.

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Data availability All data related to this study are available within the manuscript or its supplementary materials.

Declarations

Conflict of interest The authors have none to declare.

Consent for publication Not applicable.

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