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Research Article

ACC-Deaminase producing *Pseudomonas putida* RT12 inoculation: A promising strategy for improving *Brassica juncea* tolerance to salinity stress

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Abstract

An important abiotic stressor that hinders plant growth, nutrient uptake, and global agricultural productivity is soil salinity. Among the different strategies to overcome the issue of salinity in agriculture sector, plant growth-promoting rhizobacteria (PGPR) have gained recognition as promising beneficial microbes that can improve plants' response to biotic and abiotic stressors. The salinity tolerance and traits that promote plant growth of eight PGPR strains (RT1, RT2, RT3, RT4, RT5, RT7, and RT12) were evaluated in this study. During screening, one strain, RT12, had the highest plant growth-promoting activity and salt tolerance in the group. The strain when subjected to NaCl stress showed quantitative ACC-deaminase activity, in the presence of NaCl at various concentrations, demonstrating extraordinary tolerance to salt stress by withstanding doses of up to 3M NaCl. In order to further investigate the effects of salt stress on *Brassica juncea* (mustard), RT12, which was identified as *Pseudomonas putida* using 16s RNA sequencing, was inoculated. Two salt treatments (100 and 150 mM) were applied to the mustard variety 'Mingora' in a greenhouse. The results revealed that through ACC utilization, PGPR directly induced plant growth in salt-stressed mustard plants by lowering excess ethylene production. All plant parameters were negatively impacted by an increase in NaCl concentration in uninoculated plants. However, *P. putida* RT12 inoculation enhanced all growth parameters, antioxidant production, total soluble sugar (TSS), total protein (TP), proline, relative water content (RWC), chlorophyll contents, and nutrient uptake in salt-treated plants. The inoculation with *P. putida* also caused a marked decline in Na$^+$ uptake and an increase in K$^+$ uptake in the shoot. By maintaining a greater K$^+$/Na$^+$ ratio in the tissues of RT12-inoculated plants compared to controls, this change in ion uptake helped to maintain nutritional balance of the plants. The findings suggest that inoculating plants with ACC deaminase-producing PGPR, such as *P. putida* RT12, may boost growth and stress resistance.

Keywords: ACC-deaminase; antioxidants; *Brassica juncea*; *Pseudomonas putida* RT12; PGPR; salinity stress

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Introduction

Globally, industrialization and other anthropogenic activities have declined the production of crops by disturbing the composition of fertile soil, which have alternately disturbed the production. In many agroecosystems, increased agricultural productivity is extremely influenced by climatic factors, edaphic elements, agricultural practices, and management strategies (Du *et al*., 2024; Shah and Wu, 2019). Crop productivity is hampered by a number of abiotic factors, including temperature, salinity, drought, pH of the soil, heavy metals and the use of fertilizers and pesticides (Khan *et al*., 2022; Wei *et al*., 2020). Among all of these stress factors, salinity is seen as posing a serious danger to agricultural output (Khan *et al*., 2021; Li *et al*., 2023). In the last few decades increase in food insecurity due to soil salinity in the world's arid and semiarid regions have been found which is being affected by climate change at a rate of 1-2% annually (Khan *et al*., 2023; Zaman *et al*., 2018). Some sources claim that due to the faster pace of salinization, over a third of land under irrigation may eventually become arid and eventually barren (Sunita *et al*., 2020). Soil salinity has recently been recognised as a growing danger to agricultural sustainability, per the information made public using the most recent FAO main report (Li *et al*., 2023; Panagos *et al*., 2020). According to various recent studies, 33% of irrigated agricultural area and 20% of the land under cultivation worldwide are affected by high levels of salinity, totalling approximately 1,128 million hectares globally (Mandal *et al.*, 2018).

Hyperosmotic conditions are the major mechanism through which salinity affects the development of plants; when stress worsens, the plant experiences toxicity from ions. The morpho-physiological, and chemical aspects of plants are adversely affected by this ionic and osmotic imbalance. which hinders plant development and growth (Singh e*t al.*, 2018; Wani *et al*., 2019). Once crops are subjected to saline conditions, morphological alterations such as chlorosis, wilting, necrosis, stunted root and shoot development, and ultimately patchy and stunted plant growth take place (Zeeshan *et al*., 2020). Some of the major physiological and biochemical effects on plants under saline regime include a reduction in the photosynthetic process, variations in transpiration and gaseous exchange via decreasing chlorophyll and carotenoids con-centration, modification of chloroplast ultrastructure and PSII system, lowering stomatal conductance, increased Na+ transport and decreased K^+ transport leading to ion toxicity (Mehmood *et al*., 2021). One of the major drawbacks of salinity stress is production of Reactive oxygen species (ROS) (Kerchev and Van Breusegem, 2022). Plants need an efficient antioxidant defences system (enzymatic and non-enzymatic antioxidants) to increase plant tolerance to cytosolic ROS toxicity (Du *et al*., 2024; Falcinelli *et al*., 2017).

In order to combat the issue of soil salinity, a number of techniques have been suggested thus far, including the use of growth regulators for plants (PGRs), the administration of exogenous chemicals like IAA, ABA, and other chemicals, enhancing the effectiveness of mineral fertilization, and alteration of the expression of genes for plant salt tolerance. The most eco-friendly and sustainable approach is to include helpful microbes, such as arbuscular mycorrhizal fungi or plant growth-promoting rhizobacteria (PGPR), to boost stress resistance (Hayat *et al*., 2020; Khan *et al*., 2023; Zainab *et al*., 2021). Rhizobacteria that promote plant growth (PGPR) have been widely employed to boost plant development and develop plant tolerance to biotic and abiotic challenges. By their stress tolerance mechanism, these PGPR has been proved to have a great potential to improve crop sustainability under biotic and abiotic stress conditions (Egamberdieva *et al*., 2019). The PGPR develops systemic resistance to environmental factors such salt, drought, and heavy metals via changing plant physiology (Li *et al*., 2023; Wang *et al*., 2022). A few PGPR strains that invade plant roots can also lead to an ISR (Induced systematic resistance), which functions systemically across the entire plant and is frequently effective against a variety of plant diseases. Therefor PGPR are advantageous rhizobacterial strains which might be a great option for enhancing crop plant salinity and disease resistance (Tiwari *et al.*, 2019).

Due to its significant commercial and nutritive significance, mustard (*Brassica juncea*), an annual herb, currently ranks third within the numerous oilseed species. Several bioactive substances, including ascorbic acid, glucosinolates, anthocyanins, flavonoids, and ß-carotene, help to increase the food's nutritional value (Khan *et* *al.*, 2015; Lim *et al.*, 2000). Its seeds, in addition to the leaves, are abundant in carbohydrates, protein, vitamins, dietary fibre, lipids, a number of trace minerals (Mg, Zn, Ca, Cu, Fe, Se, Cu, Mn), and minerals. The bulk of soil and groundwater sources in the North-West agroclimatic zone where oilseed plants are grown, are very salty (16-17%) and have acidity issues, which limit plant development and grain yield (Mandal *et al.*, 2010; Mo *et al.*, 2023).

A fresh perspective on the mechanistic approach could be gained by including PGPR for salt tolerance and investigating the probable mechanism through the investigation of various physiological and biochemical indicators. In this study, 100 and 200 mM NaCl stress was applied to mustard cultivars. Additionally, a PGPR strains with maximum PGP potential was applied to these salt-stressed plants, either separately or together. Among the eight strains RT12 strain which was later confirmed by sequencing confirmed to be *P. putida*, showed maximum growth attributes qualitatively as well as IAA, EPS and ACC-deaminase activities were confirmed quantitatively. RT12 also showed maximum tolerance to salinity stress which is also confirmed in several PGPR that are frequently re-ported for growth (Ahmad *et al.*, 2018).

Materials and Methods

Acquirement and salt tolerance analysis of bacterial strains

Bacterial strains i-e RT1, RT2, RT3, RT4, RT5, RT7, RT8, and RT12 were previously isolated from *Gossypium hisutum* (cotton) plants (Akbar *et al.*, 2022). To find the most salt tolerant strain we subjected all strains to three different concentrations of salt i-e Control, 1M, 2M and 3M by following the protocol of Hina *et al.* (2020). Using the population density under salt stress in a tryptic soy broth (TSB) medium, the salinity tolerance of the bacterial strains was ascertained. The bacteria were examined in sterile flasks filled with 100 cc of TSB medium and various salt concentrations. 10 l of freshly made bacterial broth was used to inoculate the TSB medium, which was subsequently incubated at 26 °C and 150 rpm in a shaking incubator. As an uninoculated control, 10 ml of sterile broth with both salt concentrations was incubated. A spectrophotometer (Agilent 8453 UV-visible Spectroscopy System) was used to assess the optical density of the culture after 24 hours of incubation, and the growth was compared to uninoculated treatments(Gontia-Mishra *et al.*, 2017).

Analysis of plant growth promoting traits of the acquired strains

In the start of our experiment, we screened eight bacterial strains for plant growth promoting traits. All the strains were inoculated in N-free media to evaluate their potential of fixing atmospheric N. For N fixation Alexandrov agar medium was used as early de-scribed (Khedher *et al.*, 2021). Solubilization of potassium was also evaluated by growing single colony of each strain on Alexandrove agar plates adjusted at pH 7.5. Formation of halo zones around the colony post 7 days of streaking confirms potassium solubilization potential (Parmar and Sindhu, 2013). For analysing zinc solubilization potential of the strains, all the strains were inoculated on the proper Zn medium supplemented with zinc carbonate for 7 days at 32 °C. To analyse Indole acetic acid (IAA) production by the strains. LB broth medium was supplemented with 1g.L^{-1} of L-tryptophan. The inoculated medium was kept on shaker for 3-4 days at 128 rpm and 28 °C temperature. After 4 days the medium was supplemented with five drops of Kovac's reagents. Formation of red colour circular ring confirm the pro-duction of IAA by the strains (Tahir *et al.*, 2019). For siderophore production the strains were grown in Chrome Azurol medium by following the protocol of Mehmood *et al.* (2021). Formation of yellow and orange colour zones around the colony on CA medium confirms the production of siderophore (Ahmad *et al.*, 2018). Finally all the strains were inoculated into a medium of peptone water for ammonia production by following the protocol of Dinesh *et al.* (2015). After 3 days of incubation at 28 °C, addition of 0.5 mL of Nessler's reagent to test tube developed a dark brown colour which confirmed the production of ammonia by the bacterial strain.

ACC deaminase, exopolysaccharides and extracellular enzymes assays

The ACC deaminase activity of the bacterial strains both under normal condition and saline environment was analysed by the given protocol (Maqbool *et al*., 2021). The ability of the strains to produce extracellular enzymes such as amylase, protease, catalase, and pectinase were assayed by the previous protocol (Ahmad *et al*., 2018). While chitinase and cellulose enzymes were assayed by following the previous protocol (Hjort *et al*., 2014). For exopolysaccharide production assay, the strains were inoculated on ATCC medium for 3 days at 32 °C. A slimy appearance of the strain was an indication of EPS production(Mehmood *et al*., 2021).

Quantitative analysis of ACC deaminase, EPS and IAA production by the strains with maximum PGP potential

After it was established that the isolates could use ACC as a source of nitrogen, a quantification assay was carried out. In this test, late log phase bacterial cultures were employed. Briefly, the pellet of five strains with maximum potential of PGP (Supplementary Table 1) were further suspended in a DF medium enhanced with 3 mM ACC with or without salt stress after being washed in 0.1M Tris HCl. Salt stress for quantitative analysis was applied in 10 and 15 mM NaCl concentration. Next, samples were cultured for 72 hours. By quantifying the alpha ketobutyric acid created by the ACC deaminase's cleavage of ACC, these induced bacterial cultures were also utilised to quantify ACC (Penrose and Glick, 2003). After performing a qualitative analysis, late log phase culture was used to determine the quantitative level of induce ACCD activity. After cleaning the cell pellet with 0.1M Tris-HCl at pH 7.5, DF minimum medium was added, along with 3mM ACC under both normal and heavy metal stress conditions, and the incubation process was carried out for 72 hours while being shaken at 120 rpm. The extracted cell pellet was labialized with toluene (5%) and supplemented with 0.3M ACC to measure the concentration of -KB. The 50 l of toluinized cells were utilised as a negative control without ACC. A 500 ml solution of 0.56 N HCl was blended and vortexed in each sample. Centrifuging the bacterial suspension at 12000 rpm for 5 minutes. Each sample's supernatant was changed by adding DNF and 0.56 N HCl solution to 500 ml of it. A measurement of the absorbance at 540 nm was made following 30 minutes of incubation. Each sample then received 1 mL of 2N NaOH before to the absorbance test. By using the known concentrations of KB, a standard curve for -ketobutyrate was created. In toluinized cells, the amount of protein was measured, according to Bradford (1976). In order to measure the production of EPS by the chosen bacterial isolates, a batch culture was grown at different salt concentrations (0, 200, 400 and 600 mM NaCl). In a nutshell, freshly grown bacterial culture (108 CFU/ml) was inoculated into 250 ml flasks containing 100 ml of a medium and incubated for 48 hours on a shaker at 160 rpm at 30 °C. After centrifugation, the supernatant was collected, combined with three volumes of 100% ethanol that had already been refrigerated, and kept at 4 °C for 24 hours to precipitate the EPS fraction. The pellet containing bacterial EPS was isolated after centrifugation at 15,000 rpm for 20 min. It was then dried at 58 °C for 24 h.

Molecular profiling of RT12

The RT12 strain's DNA was extracted by following the protocol (Khan and Bano, 2016). The reaction mixture was composed of 1.25 U of Top Taq DNA polymerase, 200 M dNTPs, 100 µM per primer, and 50 L of volume including 2 L of genomic DNA. PCR products for 16S rDNA were sent to Origen, Hebei China, for sequencing. The sequence's homology was identified using BLAST analysis on the NCBI database. Similar sequences were retrieved, and MEGA 11 software was used to build a phylogenetic tree.

Analysis of soil and inoculation of RT12 to mustard seeds

Soil was collected from the green house at University of Swat, KPK Pakistan (34.8548oN, 72.4512oE). The soil was first kept until drying. Then it was crushed, and sieved by 2 mm sieve, mixed with dry sand in 3:1 and finally sterilized to remove any microbial contaminants (Khan *et al*., 2021). The physiochemical characteristics of soil such as pH (7.9), Electrical conductivity (0.21 dSm^{-1}), and SOM (0.49%) were analysed. The available concentration of sodium, phosphorus, and potassium were 44.2, 17 and 2.4 mm/kg respectively. Pots were filled with 1 kg soil and were kept for later seed sowing. By repeatedly rinsing the seeds for five minutes in 70% ethyl alcohol, following by washing in 0.1% $HgCl_2$ for one minute, the seeds were sterilised. All seeds underwent three rinses with double distilled water following disinfection. LB broth was used to cultivate the *P. putida* RT12 strain in 250-ml flasks. The culture was taken after 48 hours and the culture was centrifuged at ten thousand rpm for ten minutes. The pellet was cleaned with 0.85% sodium chloride, suspended in deionized water to keep the absorbance at 0.5, and a uniform bacterial population was obtained [108 colony-forming units (CFU) ml^{-1}. Mustard seeds were immersed in bacterial solution for 2-4 hours, whereas uninoculated seeds served as the control and were steeped in sterilised water. Pots were classified into five different treatments (Table 1). 10 seeds were sown in each pot which was later thinned and only three uniform seedlings were left for experiment. The pots were kept in green house under semi control conditions (temperature ranging from 20 to 35 °C, photoperiod of 10 hrs light and 14 hrs dark and humidity of 60±10%). NaCl was applied in aliquots of 25 ml/day to pots until the final concentration of 100 and 200 mM was attained (Noreen and Ashraf, 2008). 50 days post germination mustard plants were harvested and their roots were surface washed from debris and soil particles.

Estimation of morphological parameters

After harvesting the morphological parameters of the plants were investigated for root length (RL), shoot length (SL), plant length (PL), fresh weight (FW), and dry weight (DW) of the plants.

Estimation of plants chlorophyll contents, and relative water contents (RWC)

After plants were subjected to salt stress for fifty days, the amount of chlorophyll in the leaves was calculated using the Khan *et al.* (2021) methodology. In short, DMSO was used to create a homogeneous mixture of the mustard leaves, and readings were calculated using a spectrophotometer at several wavelengths, including 480, 649, and 665 nm, respectively. Applying the recommended formulas helped us to calculate the amount of chlorophyll content.

$\text{Chl (a)} = 12.47A665.1 - 3.62A649.1$

$\text{Chl (b)} = 25.06A649.1 - 6.5A665.1$

$\text{Chl (c)} = (1000A480 - 1.29Ca - 53.78Cb)/220$

$\text{Carotenoids} = OD470X4$

After leaf harvesting, relative water content was calculated. We measured the fresh weight (FW) of the leaves. After that, the leaves spent 24 hours submerged in distilled water. Then, the weight of fully turgid leaves was measured by reweighing them. After 72 hours of oven drying at 70 °C, the leaves' constant dry weight (DW) was observed. Based on Khan *et al.* (2021) calculations the relative water content was determined. RWC was calculated using the formula below:

$\text{RWC (\%)} = [FW - DW/TW - DW] \times 100$

Where FW= fresh weight of the leaf sample, TW=turgid weight of the leaf sample and DW=dry weight

Antioxidants enzymatic assays in mustard

Fresh mustard plant leaves were examined for antioxidant activities such as catalase (CAT), superoxide dismutase (SOD), peroxidase (POD), and ascorbate peroxidase (APX) in accordance with the methods of Khan *et al.* (2016) and Hossain *et al.* (1984). To assess the APX content, freshly cut leaf samples (0.2 g) were crushed in 2 ml of extraction buffer (potassium phosphate, pH 7.5) and ascorbic acid (1 mM). The crushed materials were centrifuged at 4 °C and 13,000 rpm for 20 minutes. To assess APX, the OD was measured at 290 nm.

Total soluble proteins and sugars

Total soluble sugars (TSS) were calculated using the Grad method (Grad *et al.*, 2021). Briefly, fresh leaves of 0.1 g weight were centrifuged for 10 minutes at 10,000 rpm after being homogenised with 3-5 ml of 80% ethanol to remove any residues of soluble carbohydrates. To determine TSS, the supernatant was gathered and processed. In test tubes, a freshly made anthrone solution (3 ml) was combined with 0.1 mL of an alcoholic extract. All test tubes were heated for 12 minutes in boiling water, cooled for 10 minutes, and then incubated for 20 minutes at 25 degrees Celsius. A spectrophotometer (752N UV-VIS, Beijing, China) was used to measure the optical density of the solution at 625 nm. The glucose standard curve was used to measure the total soluble sugars in fresh weight in terms of g/mL. According to (Mendez and Kwon, 2021), the protein content of fresh mustard leaves was assessed using Bovine Serum Albumin (BSA) as a reference. Crushed fresh leaves (0.1 g) were centrifuged for 10 minutes at 3,000 rpm after being combined with 1 cc of phosphate buffer (pH 7.5) in a mortar and pestle.

Determination of Hydrogen peroxide and MDA contents

By using the thiobarbituric method previously reported by (A. A. Khan et al., 2022)the MDA level was measured to determine the extent of lipid peroxidation, and the H_2O_2 assessed as previously stated by Singh *et al.* (2019).

Analysis of mineral uptake by mustard shoots

The technique used by Khan *et al.* (2021; 2022) was followed to assess the presence of minerals in the mustard shoot, including Na, K, Ca, and Mg. In short, a 3:1 v/v digestion mixture of HNO_3 and $HCLO_4$ was produced. In an 8 mL digestion solution, one gram of dried mustard plant shoots was digested overnight. The digesting combination was then placed in flasks and heated on a heat plate until brown fumes turned white. The mixture was filtered through Whatman 42 filter paper after being cooled down and diluted to 40 mL.

Statistical analysis

To analyse the data the mean values and standard error were calculated in excel. Analysis of variance (Anova) of the data was analysed by using Statistix software version 8.1 following by LSD pairwise comparison of all mean values. Principal component analysis and Pearson's correlation analysis were performed by R software.

Results

Growth curve of bacterial strain

Salt stress causes high osmotic potential and lower potential which affects the biological activities of an organism, and is also attributed to negative growth of bacterial strains except those which are halotolerant. To investigate the salt tolerance ability of *Pseudomonas putida* Rt12, it was grown in salt of different molar concentrations i-e 1,2 and 3M NaCl. The results revealed that it can tolerate up to 3M concentration of salt and also from the log phase on the seventh day of incubation in Lb medium as shown in Figure 2.

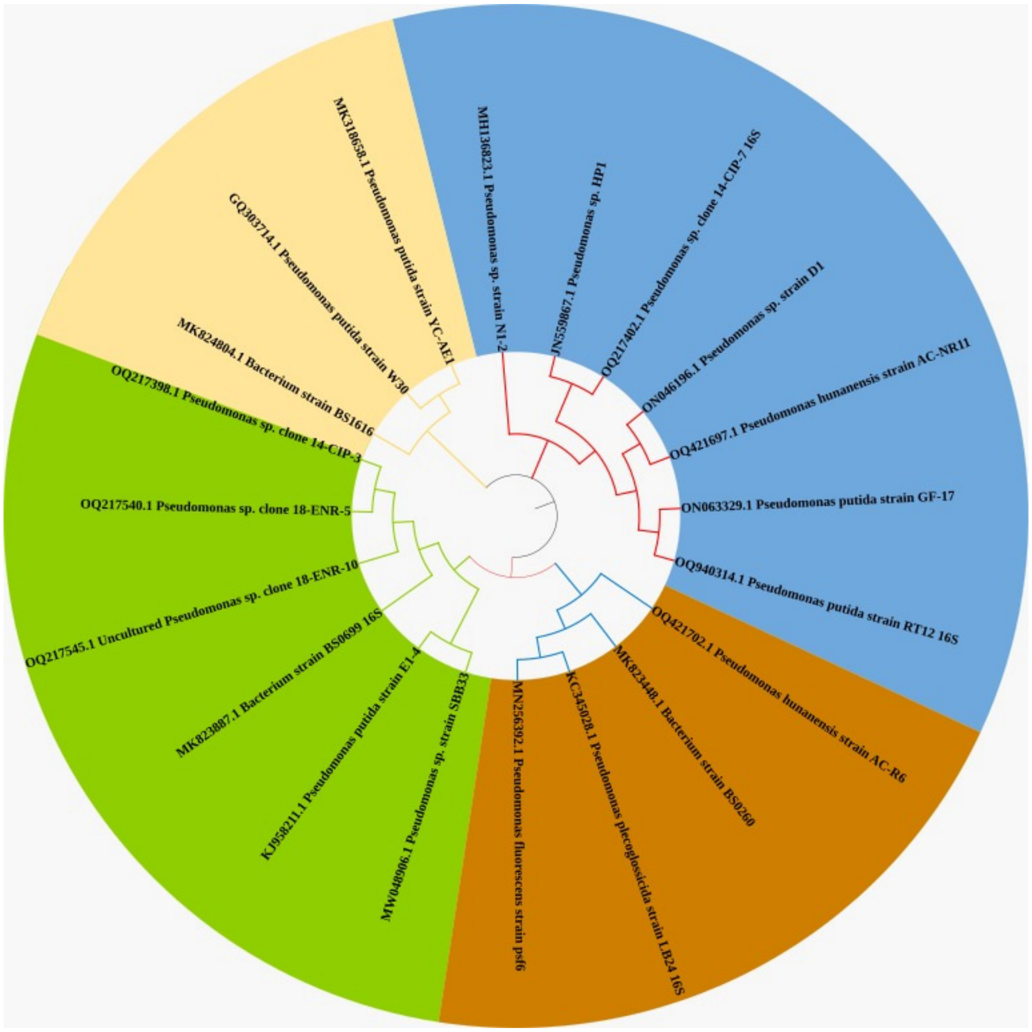

Figure 1. Phylogenetic tree of the *Pseudomonas putida* Rt12 constructed by Neighbor-joining method. Bootstrap-1000 replicated applied by using MEGA 11

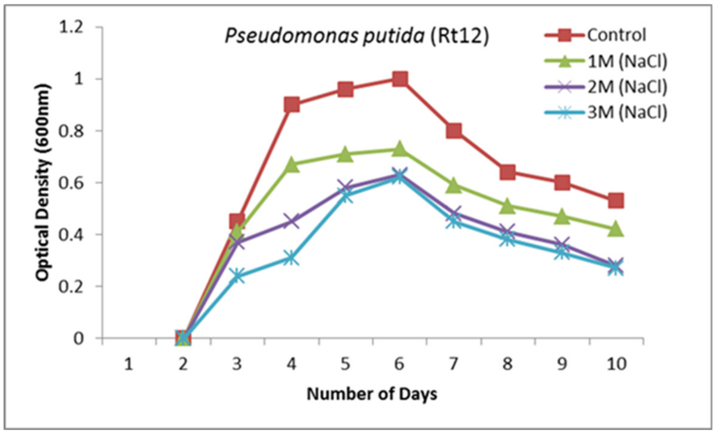

Figure 2. *Pseudomonas putida* Rt12 growth curve analysis under control, and different molar concentration of NaCl

Bacterial plant growth promoting traits analysis

Application of PGPR strains demonstrates advantageous characteristics in reducing the harmful effects of high salt concentrations on structural, functional, and biochemical processes in plants, leading to the notable recovery of morphophysiological parameters. PGPR shows different mechanisms of rescuing plants under stress from the detrimental effects such as production of 1-aminocyclopropane-1-carboxylate (ACC) deaminase, exopolysaccharides (EPS), better ion stability, and the synthesis of phytohormones are all approaches through which PGPR decreases the adverse effects of salinity stress. The strain when analysed for PGP traits it showed positive PGP activities for nitrogen fixation, phosphate solubilization, zinc solubilization, indole acetic acid (IAA) production, siderophore production, and ammonia production. The strain also exhibited positive extracellular enzymatic activities for protease, catalase, cellulase, pectinase, and exopolysaccharide production (Table 1). After confirmation of the ACC deaminase activity, as described in Figure 3 the ACC deaminase activity of the bacterial strain *Pseudomonas putida* Rt12 showed a net quantitative in-crease with increasing NaCl concentration as compared to the control.

Table 1. Shows the plant growth promoting biochemical attributes of RT12 *Pseudomonas putida* RT12

<table>
<tr><th colspan="2"></th><th>N Fixation</th><th>K solubilization</th><th>Zn solubilization</th><th>IAA production</th><th>Siderophore</th><th>NH3</th><th>Acc deaminase</th></tr>
<tr><td colspan="2"></td><td>+</td><td>+</td><td>+</td><td>+</td><td>+</td><td>+</td><td>+</td></tr>
<tr><td colspan="9">Extracellular Enzyme Analysis</td></tr>
<tr><td>Amylase</td><td colspan="2">Protease</td><td>Catalase</td><td>Cellulase</td><td>Chitinase</td><td colspan="2">Pectinase</td><td>EPS</td></tr>
<tr><td>-</td><td colspan="2">+</td><td>+</td><td>+</td><td>-</td><td colspan="2">+</td><td>+</td></tr>
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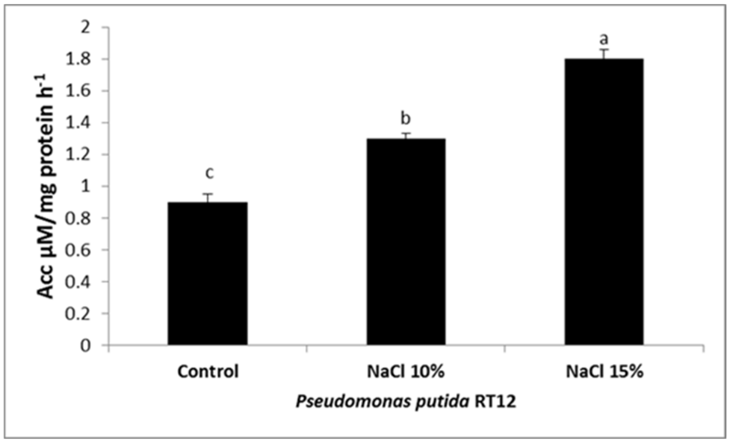

Figure 3. ACC-deaminase quantitative analysis of *Pseudomonas putida* under 0, 10 and 15% of NaCl

Mustard plant growth attributes

High salinity levels in the soil induce plants to go through a number of morphological, biochemical, and physiological modifications that show up as changed phenotypic characteristics. Osmotic stress is brought on by elevated salt levels, which causes a water shortage in plant tissues. As a result, plants may show reduction in growth parameters such as root length, shoot length, fresh weight, and dry weight. When mustard plants were exposed to salinity stress, they exhibited negative growth parameters (Figure 4). However, inoculation of bacteria to mustard plants improved all the growth parameters both under stress and normal conditions. The results reveal that inoculation of *P. putida* Rt12 to *B. juncea* under salinity stress of 100 and 150 mM shows a net increase of RL (21.38 and 17.11%), SL (23 and 18%), FW (30 and 21%) and DW (80 and 78%) respectively as compared to uninoculated control plants (Figure 4). As the strain showed positive growth at-tributes during biochemical analysis. When plants without stress were inoculated with bacteria showed an increase of 27.71%

in RL, 11.32 in SL, 15.16% in FW and 66.67% in DW as compared to the control plants under normal conditions.

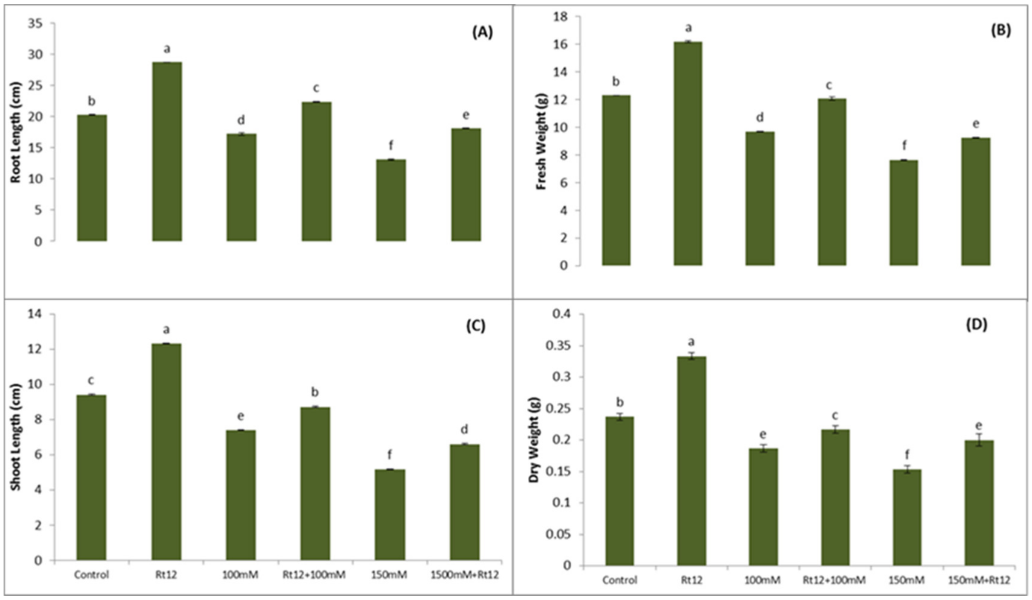

Figure 4. Mustard growth, and biomass under salinity stress inoculated or uninoculated with *Pseudomonas putida* Rt12

Estimation of photosynthetic pigments and RWC of mustard plants

The relative water content, carotenoid concentrations and chlorophyll content of a plant all suffer from the stress brought on by salt. As a result of the disruption of photo-synthetic processes brought on by the combined effects of oxidative stress and water restriction, growth and production are reduced. To examine the beneficial impact of *P. putida* Rt12 on photosynthetic pigments and relative water levels, five alternative treatments were created (Table 2). This experiment demonstrated that all photosynthetic pigments are negatively impacted by salinity stress. Under salinity stress, the pigmented content quantity decreased (Table 2). Compared to their non-inoculated counterparts, the *P. putida* Rt12-inoculated plants showed a beneficial influence on pigments. Chl a (44 and 35%), Chl b (66 and 55%), total chlorophyll (53 and 35%), and carotenoids (83 and 39%) showed the most promising increases after *P. putida* Rt12 was inoculated under salinity stress of 100 and 150 mM, respectively (Table 2). While the RWC at 100 mM NaCl showed a net increase of 15% as compared to uninoculated plants at 100mM NaCl.

Table 2. Shows the chlorophyll a, b, total chlorophyll, carotenoids and relative water contents in mustard leaves inoculated with RT12 under saline regime

	Chl a	**Chl b**	**Total chl**	**Carotenoids**	**RWC**
Control	0.31±0.03f	0.23±0.03d	0.54±0.04f	0.62±0.01c	24.23±0.03b
Rt12	0.36±0.02e	0.31±0.02c	0.68±0.03d	0.71±0.03b	28.64±0.04a
100 mM	0.42±0.01d	0.19±0.04f	0.61±0.01e	0.52±0.03e	7.60±0.01e
Rt12+ 100 mM	0.55±0.04c	0.33±0.03b	0.89±0.07b	0.91±0.05a	16.22±0.05d
150 mM	0.61±0.05b	0.21±0.03e	0.82±0.03c	0.46±0.02f	22.72±0.04b
150 mM+ Rt12	0.64±0.03a	0.44±0.02a	1.09±0.01a	0.60±0.03d	20.14±0.03c

Estimation of osmolytes contents and oxidative burst

Reactive oxygen species (ROS), which have the potential to harm cellular components, are produced as a result of oxidative stress, which is indicated by elevated levels of MDA and H_2O_2. Photosynthesis, minerals uptake and absorption, and hormone control are among the critical physiological processes that are impacted by this imbalance be-tween ROS and antioxidant defences. By strengthening the plant's antioxidant defences mechanisms, lowering ROS production through ion immobilization, and promoting nutrient absorption efficiency, PGPR play a critical role in balancing MDA and H_2O_2 levels in plants under salinity stress and also by enhancing the level of osmolytes such as pro-line, soluble sugar and total protein contents in plants under stressful condition. As it is obvious from our findings that when mustard plants were exposed to salinity stress of 100 and 150 mM NaCl a net increase of 17.48 and 79% in MDA content and 41 and 98% of H_2O_2 contents were observed respectively as compared to control (Figure 5A and B). However, when plants were inoculated with *P. putida* Rt12 strain the MDA content de-creased by 13 and 30% respectively under 100- and 150-mM stress. Same reduction of 28 and 66% in H_2O_2 level was observed as compared to the uninoculated stressed plants (Figure 5). Similarly, the level of osmolytes such as proline increased by 112 and 72% in uninoculated plants as compared to the uninoculated control ones (Table 3). Inoculation of bacteria also enhanced the total soluble sugar contents by 14 and 11% and total protein con-tents by 15 and 13% under 100 and 150 mM NaCl as compared to uninoculated ones.

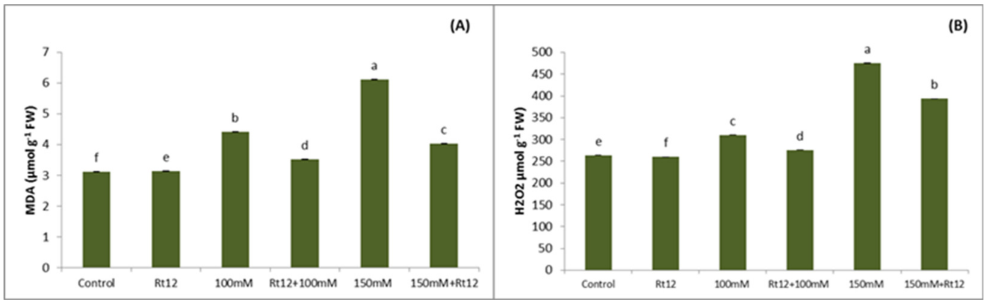

Figure 5. MDA and H_2O_2 contents in mustard leaves under saline condition inoculated with *P. putida* Rt12 strain

Table 3. Shows the total sugar, total protein and proline contents in the leaves of mustard plants under saline condition inoculated with *P. putida* Rt12 strain

	TSS (mg.g^{-1} FW)	**TP(mg.g^{-1} FW)**	**Proline contents (µmol g^{-1} FW min^{-1})**
Control	42.08±0.03e	8.22±0.05c	4.13±0.02e
Rt12	47.3±0.04b	12.22±0.01a	4.1±0.01e
100mM	44.12±0.07c	6.31±0.05e	6.31±0.1d
Rt12+100mM	48.12±0.01a	9.33±0.02b	8.8±0.03c
150mM	38.12±0.02f	5.17±0.05f	13.12±0.09b
150mM+Rt12	43.58±0.03e	7.31±0.10d	16.1±0.07a

Antioxidants enzyme analysis

To combat the damaging effects of ROS produced as a result of salt stress, plants have evolved a sophisticated antioxidant defence system. Scavenging ROS requires the action of antioxidant enzymes such Superoxide Dismutase (SOD), Peroxidase (POD), Cata-lase (CAT), and Ascorbate Peroxidase (APX). Superoxide radicals are changed by SOD in-to H_2O_2, which is then broken down by CAT and APX into water and oxygen. On the other hand, POD is responsible for the detoxification of peroxides like H_2O_2 and others. Under saline condition the antioxidants enzymes were analysed in *B. juncea* (Figure 6). There was an increase in the level of antioxidants with increasing salt concentration. However as compared to uninoculated plants, mustard plants with *P. putida* Rt12 accumulated more enzymes such as SOD (87 and 74%), POD (24 and 10%), CAT (55 and 33%) and APX (38 and 26%) at 100 and 150 mM NaCl respectively (Figure 6).

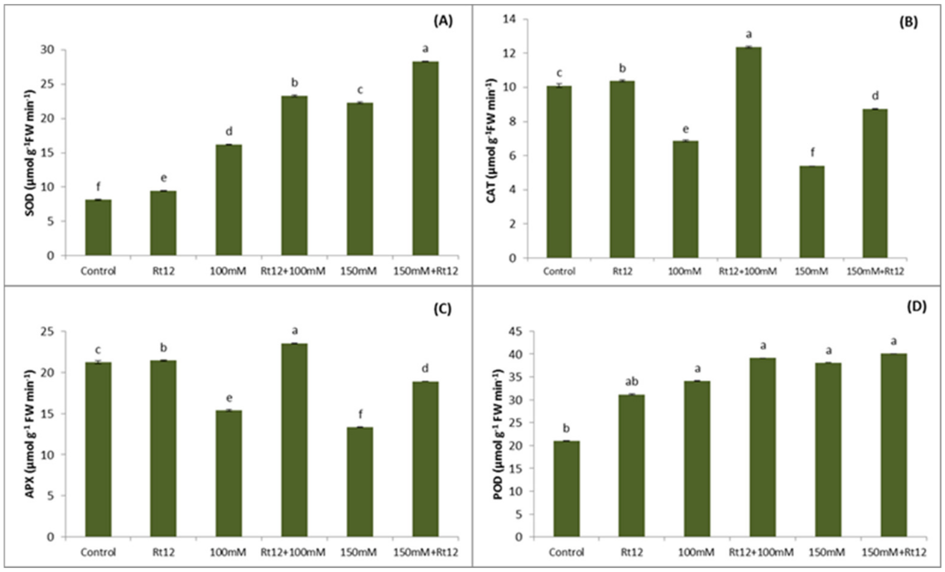

Figure 6. Shows the antioxidants A. SOD; B. CAT; C. APX and D.POD, contents in the leaves of mustard plants under saline condition inoculated with *P. putida* Rt12 strain

Plant mineral analysis

Salinity stress severely impairs a plant's ability to absorb nutrients, making it challenging for the plant to obtain the minerals required for growth and development. The environment's osmotic potential rises when plants are exposed to salty soil, which causes a water shortage within the plant cells. Furthermore, too much salt in the soil can disrupt the equilibrium of ions, especially by increasing the sodium (Na^+) and chloride (Cl^-) ions, which hinders the uptake of essential nutrients like potassium (K^+), calcium (Ca^{2+}), and magnesium (Mg^{2+}). In the current experiment the mineral analysis of mustard plants was analysed (Table 4). The concentration of Na^+ increased with increasing salt con-centration which was 170 and 300% at 100 and 150 mM NaCl. However, inoculation of Rt12 strain decreased the uptake of sodium ion by 80 and 20% respectively at both concentrations. The results also reveal that with increasing concentration of salt the level of inorganic osmolytes such as K^+, Ca^+, and Mg^+ also decreased, however inoculation of the strain helped plant to increase the uptake of all these minerals.

Table 4. Shows the mineral analysis i-e sodium, potassium, calcium and magnesium in the leaves of mustard plants under saline condition inoculated with *P. putida* RT12 strain

	Na^+(mg.g DW)	K^+(mg.g DW)	Ca^+(mg.g DW)	Mg^+(mg.g DW)	K^+/Na^+ ratio
Control	5.31±0.01e	32.37±0.03b	4.50±0.00a	7.16±0.05b	6.11±0.01b
Rt12	5.2±0.04f	33.59±0.04a	4.50±0.03a	7.32±0.02a	6.45±0.03a
100mM	14.29±0.04c	28.21±0.07d	3.53±0.01c	6.42±0.01c	1.97±0.01d
Rt12+100mM	10.21±0.01d	31.11±0.03c	4.25±0.01b	7.21±0.04b	3.05±0.03c
150mM	21.33±0.07a	16.23±0.01f	2.33±0.07e	5.31±0.01e	0.76±0.07f
150mM+Rt12	17.22±0.01b	18.16±0.02e	2.89±0.04d	5.69±0.05d	1.05±0.05e

Principal component and Pearson's correlation analysis

The principal component Biplot analysis revealed that many variables correlated under salinity regimes and *P. putida* Rt12 therapy. Variables that were significantly correlated were grouped in quadrates. An 87.2% variance was shown by the biplot (PC1 = 67.2%; PC2 = 20%) (Figure 7). Antioxidants, morphological characteristics, pigmented con-tent, relative water content, and suitable solutes of mustard all showed positive correlations. Plant biomass was calculated using Pearson's correlation to compare antioxidants and biochemical characteristics (Figure 8). Chlorophyll concentration was found to significantly improve SL, FW, and RL in mustard plants. The production of plant bio-mass significantly increases when these qualities are improved (Figure 8). Significant correlations were seen between SL, FW, and RL and carotenoids, RWC, total soluble sugar, and chlorophyll content. The increase in biomass (SL, RL, and FW) and chlorophyll con-tent led to elevated levels of SOD, POD, CAT, APX, TP, TSS, and proline being generated. A significant negative connection between H_2O_2 and MDA and all plant biomass indices were found (Figure 8). The association between total soluble sugars, antioxidants, total protein, MDA, antioxidant enzymes, and radical scavenging activity, on the other hand, was found to be significantly unfavourable. Under certain conditions, decreased antioxidants result in decreased plant biomass.

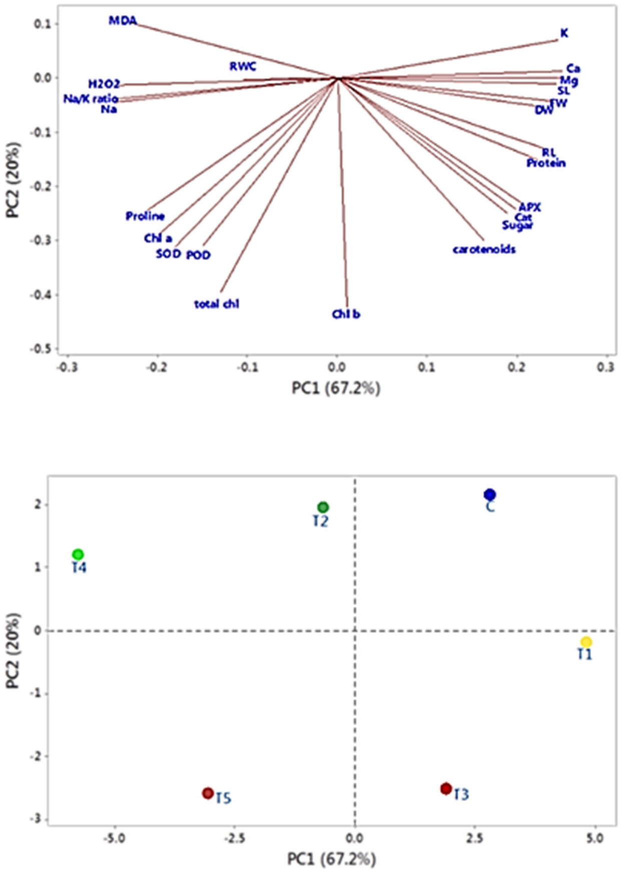

Figure 7. Shows the PCA analysis of different treatments of mustard plant inoculated with *Pseudomonas putida* Rt12 strain under salinity stress

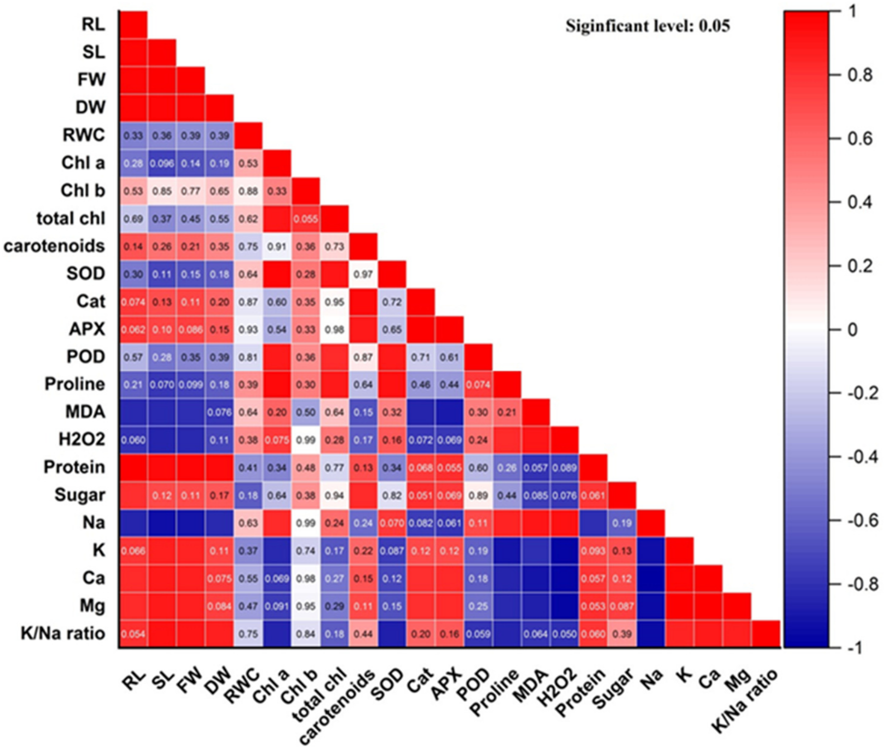

Figure 8. Shows the Pearson's correlation analysis of different treatments of mustard plant inoculated with *Pseudomonas putida* Rt12 strain under salinity stress

Discussion

Microorganisms are the most frequent inhabitants of a wide range of habitats, and they have amazing metabolic capacities that enable them to endure abiotic stresses. Microbial interactions with plants are intricate, vital, and dynamic processes that affect local and systemic defence mechanisms in plants that help them withstand adverse environmental conditions. This is so because bacteria play a crucial role in the environment of plants(Nisha *et al.*, 2023). PGPR considerably reduces abiotic stress in plants and offers a sustainable, ecologically friendly way to boost crop resilience and output. Plants' roots are colonised by PGPR in a beneficial symbiotic relationship. They assist plants in adjusting to various environmental conditions by cooperating (Arif *et al.*, 2020; Mo *et al.*, 2023). In light of this, the current study intends to examine the potential of ha-lo-tolerant Pseudomonas putida RT12 for promoting mustard growth and reducing salinity stress. Strain used in the current study ie., *Pseudomonas putida* RT12 was exposed to salinity of different levels (0-3 Molar concentration of NaCl). The strain displayed extremely high tolerance to salt stress at 3M concentration (Figure 2). The strain showed a steady growth curve till seventh day of inoculation. Which confirms that the strain is halotolerant and the finding are similar to the previous findings (Nadeem *et al.*, 2016; Ullah and Bano, 2021).

After confirming the halotolerance potential of the strain. It was further examined for other PGP traits. The *Pseudomonas putida* RT12 strain showed a variety of beneficial screening traits that are very promising for sustainable agriculture (Table 1). It can significantly in-crease the availability and uptake of nutrients for plants because of its ability to solubilize phosphates and zinc, fix ambient nitrogen into ammonia, and produce growth-regulating substances like indole-3-acetic acid (IAA), siderophores, and ammonia (Table 1). The role of mineral solubilizing bacteria have been acknowledged previously for their services under stressful conditions

(Franchi and Fusini, 2021; Mulani *et al.*, 2021; Stegelmeier *et al.*, 2022).Furthermore, the strain's ACC deaminase activity at different salt concentrations (Table 1; Figure 3) provides a mechanism to minimise the impacts of ethylene and enhance tolerance to a variety of abiotic environments like salinity and drought. These findings are also in agreement with other researchers who have inoculated PGPR and PGPE strains having Acc-deaminase producing ability for mitigating salinity stress (Naing *et al.*, 2021; Phour and Sindhu, 2022; Shahid *et al.*, 2022; Singh *et al.*, 2022). *Pseudomonas putida* RT12 can support hormone synthesis, nu-trient solubilization, and nitrogen fixation, which can enhance root growth, increase crop yield, and reduce the need for synthetic fertilisers. Additionally, by assisting in the alleviation of iron deficiency in calcareous and alkaline soils, its capacity to increase iron uptake through siderophores improves plant health and productivity and EPS also have shown to alleviate salinity stress in different plants under saline regime(Farahat *et al.*, 2020; Fatima *et al.*, 2020; Khan *et al.*, 2021; Khan *et al.*, 2021).

The PGPR strain, *P. putida* RT12, exhibits IAA, siderophore, ACC deaminase, and EPS which are all favourable growth-promoting characteristics (Table 1). Indole acetic acid (IAA) promotes seed germination and the growth of roots with longer and more numerous root hairs, both of which help with indirect nutrient absorption. P. putida when inoculated to mustard plant under saline treatment or under normal conditions it showed enhanced root length and shoot length (Figure 4). Previously the role of IAA in plant development under stress has been addressed. Additionally, it also offers a great deal of potential for the development of large-scale grain crops (Alemneh *et al.*, 2021; Hasimuna *et al.*, 2023). It is also one of the findings that, IAA generated by bacteria promotes cell elongation and/or responds to cell division, which in turn promotes root and shoot growth (Hsu *et al.*, 2021; Ravelo-Ortega *et al.*, 2023). In response to salinity stress, root development and structural changes are related to IAA production (Etesami and Noori, 2019; Kumar *et al.*, 2020; Mo *et al.*, 2023). According to earlier studies, *Kocuria rhizophila, Enterobacter species, Bacillus species, Bacillus tequilensis, Bacillus thuringiensis*, and *Bacillus mycoides* all grew plants more rapidly when PGPB synthesised IAA were administered to plants(Ali *et al.*, 2023; Ayuso-Calles *et al.*, 2021). Considering all these positive and advantageous traits, Pseudomonas putida RT12 has a high potential to assist sustainable agricultural practises and create robust crops able to flourish in challenging environmental situations.

Results of the current study shows that inoculation of halotolerant *P. putida* RT12 helps mustard plant to mitigate the negative effects of salinity stress by the production of ACC deaminase enzyme and certain osmolytes. The results also showed that inoculation of the strain enhanced morphological parameters of the plants such as root length, shoot length, fresh weight, dry weight and biochemical parameters such as chlorophyll con-tents, proline, antioxidants, RWC, total soluble sugar and protein etc. The role of ha-lo-tolerant bacterial strains has previously been reported in tomatoes, wheat, and pea, maize, and soybean plants under saline regime (Azeem *et al.*, 2022; Fatima *et al.*, 2020; Khan *et al.*, 2021; Masmoudi *et al.*, 2021; Shahid *et al.*, 2021). These findings are in agreement that application of halotolerant PGPR is a useful approach to alleviate salinity stress in plants.

When a plant is under salinity stress, ethylene builds up in its tissues, which slows down root growth and seed germination(Choudhary *et al.*, 2022). In the current study, *P. putida* RT12 demonstrated the synthesis of ACC deaminase at different concentrations of salt (Figure 3), which reduced the severe effects of ethylene on plant health when exposed to salinity stress by cleaving ACC into -ketobutyrate and ammonia. Additionally, both under control and salinity treatments, this salt-tolerant Acc deaminase-producing strain promoted growth in the mustard variety. When soybean plants were inoculated with Acc-deaminase producing halotolerant strain *Rhizobium leguminoserum* bv it showed enhanced growth parameters (Ali *et al.*, 2023; Alinia *et al.*, 2022). Similarly, when pea plant under saline environment was inoculated with two Acc-deaminase producing strains ie., *Bacillus subtilis* & *Pseudomonas aeruginosa* they showed enhanced growth parameters. Our findings are also in agreement with the findings (Singh *et al.*, 2022), they inoculated wheat plants with *Enterobacter cloaceae* ZNP-4 strain and it enhanced all the growth parameters of the plants under

150mM NaCl stress. Taking together all these findings confirms the role of Acc-deaminase producing PGPR strains in growth promotion under salinity stress.

The PGPR may also increase water intake in situations with high levels of salt, hence lowering the inhibition of photosynthesis brought on by salinity stress (Singh *et al*., 2023). Moreover, canola plant under saline environment when was inoculated with two PGPR strains *Enterobacter sp.* S16-3 and *Pseudomonas sp*. C16-2O they showed increase in chlorophyll contents (W. Khan et al., 2023; Neshat et al., 2022). Similarly, in another study when rice plants were inoculated with *B. pumilus* JIZ13 strain under salinity stress. The strain not only enhanced the water uptake of the plants but also enhanced the chlorophyll and carotenoid contents of the plants (Wang *et al*., 2023). In the current experiment inoculation of *P. putida* RT12 not only increased the RWC (Table 2) but also enhanced the chlorophyll and carotenoid contents (Table 2) in inoculated plants as compared to uninoculated plants. Tolerance to abiotic stress is correlated with the use of ACC deaminase-producing bacteria in plants (Wang *et al*., 2022). One of the main mechanisms mediated by these bacteria that allows for optimum nutrient intake by encouraging root growth may be the lowering of endogenous ethylene (Fadiji *et al*., 2022).

Salinity stress results in oxidative stress, which is the production and accumulation of re-active oxygen species (ROS). ROS accumulation is lethal to plants and severely toxic to humans. Canola yield decreases as a result of salinity stress as a result of MDA and H_2O_2 production. By lowering MDA and H_2O_2 concentrations, plant growth-promoting rhizobacteria (PGPR) can colonise plant root surfaces and lessen the effects of salt stress on plants (Hasanuzzaman *et al*., 2020). MDA and H_2O_2 are the indicators of oxidative stress caused by salinity in *Brassica napus* plant. When two PGPR strains i.e., *Pseudomonas* and *Saphylococcus* species were inoculated to *B. napus* plant it showed reduced MDA and H_2O_2 contents as compared to uninoculated plants. (Khan *et al*., 2023; Lalay *et al*., 2022). Similarly, exposure of eggplant to salinity resulted in increase in MDA and H_2O_2 production. However, inoculation of PGPR strain *Pantoea agglomerans* helped to decline the MDA and H_2O_2 level in plants and protecting it from the detrimental effects of salinity (Kul, 2022). The decrease in MDA content (66%) and H_2O_2 (30%) is confirmed in the current study under 150 mM of NaCl stress. Which shows that P. putida RT12 play its rule in decreasing the MDA and H_2O_2 contents and hence protecting plant from the oxidative stress damage (Figure 5). These results are also in agreement with the previous findings of Urooj *et al*. (2021)in wheat plants. Antioxidants are one indicator of a plant's resilience to stress. Plants produce low molecular weight antioxidants like APX, catalase, SOD, and POD and osmolytes such as proline aid in their resistance to salt stress (Dugasa *et al*., 2019). To counter the damaging effects of salt stress, the majority of plant species do not produce adequate antioxidants (Aazami *et al*., 2021). The high NaCl-induced oxidative stress in wheat plants may have been reduced as evidenced by increased POD, CAT, SOD, and proline enzyme activities due to PGPR inoculation(Desoky *et al*., 2020). Similarly, Acc-deaminase producing bacterial strain enhanced Proline, POX, SOD, POD and other defensive enzymes are produced in greater quantities by common bean plants to tolerate salt stress (Gupta and Pandey, 2020). These results are in agreement with our findings because the inoculated treatment under salinity showed significant level of antioxidants concentrations; SOD (87.29 and 74%), CAT (54.45 and 33.16%), APX (38.28 and 26.23%) and POD (23.93 and 10%) under 100 and 150 mM of NaCl respectively (Figure 6).

The mutualistic relationship between plants and PGPR has many benefits, including a rise in the quantity of total protein and sugar contents. By means of mechanisms like improved nutrient absorption, nitrogen fixation, and the activation of growth-promoting chemicals, PGPR are essential in improving the health and productivity of plants. Crop yields and nutritional quality increase as a result, advancing agriculture and ensuring food security (Bhadrecha *et al*., 2023; Borah *et al*., 2023; Zeng *et al*., 2022). *P. putida* RT12 increased the total soluble sugar and total protein contents in inoculated plants as compared to uninoculated one. This is also one of the reasons of enhanced growth attributes. Similar results were found in wheat plants inoculated with multifarious Serratia marcescens strain under salinity stress (Singh and Jha, 2016). Our results are also in agreement with (Khan *et al*., 2019) when chickpea plant was inoculated with three PGPR strains;

Bacillus subtilis, *Bacillus thuringiensis*, and *Bacillus megaterium* under drought stress they showed increase in total soluble sugar and protein contents which lead to the growth of plant under stressful condition. Similarly, increase in the up-take of essential elements such as sodium, potassium, calcium and magnesium is vital for the growth of plant (Johnson *et al.*, 2022). Higher salinity causes oxidative stress, which is lessened by the increased K+ absorption (Etesami and Glick, 2020). In our current experiment inoculation of mustard plant resulted in increased uptake of K/Na concentration as compared to uninoculated treatments (Table 4). The highest K/Na was observed in T2 plants which is followed by control. However, under NaCl the concentration of K/Na was decreased by 55% and 67% under 100 and 150 mM respectively. Plant growth under salinity stress is inversely proportional to the concentration of Na and directly proportional to the concentration of K ion (Breś *et al.*, 2022). In the current experiment similar pattern of results were studied. Inoculated treatments showed a net increase in growth parameters, increase in K+ uptake and restricted uptake of Na+. Which resulted in increase in growth parameters of mustard plant. These results confirm that inoculation of PGPR is important to increase the uptake of nutrients and maintain the growth under unfavourable conditions. The study's findings generally imply that *P. putida* RT12 has a high potential for use as a sustainable and environmentally responsible method of boosting crop resistance and yield under difficult environ-mental circumstances like salinity stress. We can create effective tactics to enhance agricultural practises and food security by comprehending and utilising microbial interactions with plants.

Conclusions

Agriculture productivity is significantly hampered by abiotic stresses, particularly salt. The amazing metabolic capabilities of microbes, particularly halotolerant *Pseudomonas putida* RT12, allow them to withstand abiotic stressors. The strain demonstrated a very high tolerance to salt stress and exhibited several features that were helpful for increasing plant growth, including the solubilization of nutrients, nitrogen fixation, and hormone synthesis. It also produced ACC deaminase, which encourages root and shoot growth and helps counteract the harmful effects of ethylene under salinity stress. The injection of *P. putida* RT12 improved a number of morphological and biochemical traits in mustard plants, such as root and shoot length, chlorophyll content, antioxidants, and osmolytes, which improved plant development and stress resistance. Additionally, the strain de-creased sodium uptake while increasing the uptake of necessary components like potassium.

Authors' Contributions

The author read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

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Conflict of Interests

The author declares that there are no conflicts of interest related to this article.

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