Plant growth-promoting bacteria and silicon fertilizer enhance plant growth and salinity tolerance in *Coriandrum sativum*

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**ABSTRACT**

Plant growth-promoting bacteria (PGPB) and silicon (Si) can augment salinity tolerance in plants. In this study, 25 potential PGPB were isolated from alfalfa rhizosphere and screened for their ability to synthesize indole-3-acetic acid, 1-aminocyclopropane-1-carboxylate deaminase, and solubilize tricalcium phosphate. Two promising strains were tentatively identified as *Pseudomonas pseudoalcaligenes* (KB-10) and *P. putida* (KB-25) based on phenotypic, biochemical and 16S rRNA gene phylogeny. Subsequently, a pot experiment was conducted to evaluate the effectiveness of KB-10 and KB-25 treatment, alone or in combination with Si fertilizer, in alleviating salinity stress in coriander. The results showed that treatment with PGPB strains and/or Si significantly increased relative water content, concentrations of photosynthetic pigments, peroxidase activity, total biomass, salt tolerance index, and reduced salt-induced total phenolic contents. Overall data suggested that the combined application of PGPB and Si fertilizer could be a feasible and effective approach to improve growth and salinity tolerance in coriander.

**KEYWORDS**

Salinity tolerance; plant growth-promoting bacteria; *Pseudomonas*; phytohormones; silicon; coriander

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**Introduction**

Salinity is one of the major abiotic factors that severely affects the soil quality of agricultural lands and limits crop productivity worldwide (Mucbate et al. 2016). Soils are classified as saline when an electrical conductivity (EC) of the saturation soil-paste is 4 dS m$^{-1}$ (about 40 mM NaCl) or more (Munns and Tester 2008; Hanin et al. 2016). Although the threshold level of salinity stress differs among plant species, the growth and yield of most of the crop plants is adversely affected at this level (Munns 2005; Jamil et al. 2011). Soil salinity triggers osmotic and ionic stresses that can lead to secondary stresses, for example, nutritional imbalances, and oxidative stress resulted due to the generation of reactive oxygen species (ROS) such as hydrogen peroxide (H$_2$O$_2$), superoxide (O$_2^-$) and hydroxyl (·OH) radicals in plants (Yang and Guo 2018). These stresses can detrimentally affect physiological, biochemical and molecular processes including water relations, transpiration, photosynthesis, cellular homeostasis, hormonal and enzymatic activities, and gene expression patterns in plants (Deinlein et al. 2014; Yang and Guo 2018). However, several mechanisms such as active Na$^+$ influx, inhibition of Na$^+$ influx, vacuolar sequestration of Na$^+$, up-regulation of antioxidative defense systems, accumulation of compatible osmolytes have evolved in plants to mitigate salinity stress (Zhang and Shi 2013; Gupta and Huang 2014; Liang et al. 2018). Unfortunately, despite these tolerance mechanisms, salinity stress remarkably reduces growth and yields of many crop plants (Parida and Das 2005; Abdi et al. 2016; Askari-Khorasagani et al. 2017).

Microorganisms play an important role in plant growth and development in diverse environmental conditions (Lugtenberg and Kamilova 2009; Qin et al. 2016). Interestingly, many studies have reported that beneficial plant-associated bacteria, known as plant growth-promoting bacteria (PGPB), can improve growth and yields of many crop plants grown under saline conditions (Radhakrishnan and Baek 2017; Numan et al. 2018). PGPB can alleviate salinity stress by reprogramming stress-induced physiological changes in plants through various mechanisms like synthesis of different phytohormones including indole-3-acetic acid (IAA), 1-aminocyclopropane-1-carboxylate (ACC) deaminase, exopolysaccharides, volatile organic compounds, fixation of atmospheric nitrogen, and solubilization of mineral phosphate (P) (Glick 2012; Ilangumaran and Smith 2017; Khan et al. 2019). Therefore, it has been suggested that harnessing the potential of PGPB is a promising approach to enhance plant performance in salt-affected soil (Glick 2014; Numan et al. 2018).

Silicon (Si), next to oxygen, is the second major element in the Earth’s crust, and the application of Si fertilizer (potassium silicate, K$_2$SiO$_3$) has been reported to ameliorate the negative effects of various biotic and abiotic stresses on plants including salinity (Alzahrani et al. 2018; Etesami 2018). Si may enhance salinity tolerance in plants by improving Na$^+$ and K$^+$ homeostasis, nutritional status, ROS-scavenging enzymes activity, and photosynthetic efficiency, among others (Garg and Bhandari 2016b; Li et al. 2016; Rios et al. 2017). On the other hand, application of K may augment plant growth and salinity tolerance by improving Na$^+$ and K$^+$ homeostasis, chlorophyl content, and decreasing malondialdehyde (MDA) concentration (Wei et al. 2016; Amjad et al. 2016). Recently, Mahmood et al. (2016) reported that application of PGPB along with foliar spray of Si fertilizer...
exhibited better tolerance to salinity stress in mung bean plants as compared to PGPB or Si fertilizer alone. Although combined application of PGPB and Si fertilizer seems a feasible and promising strategy to improve plant performance in salt-affected farmland, reports on using this strategy are still limited (Etesami 2018).

Coriander (Coriandrum sativum L.) is an important annual Apiaceae species that has nutritional and medicinal value, and is widely used as herb and spice (Neffati and Marzouk 2010). The growth and physiology of coriander plants is adversely affected by salinity (Meriem et al. 2014). Till now, no systematic research has explored the effects of using PGPB and Si fertilizer, alone or in combination, on salt-stressed coriander plants. Therefore, in the present study, we isolated and characterized potential PGPB strains and evaluated their efficacy with or without foliar application of Si fertilizer in alleviating salinity stress in coriander.

Materials and methods

Isolation of bacteria

Potential PGPB strains were isolated from the rhizosphere soil of alfalfa (Medicago sativa L.) growing at the Agricultural Research Station of King Abdulaziz University located at Hada Al-Sham (21°48′3″N, 39°43′25″E), Jeddah, Saudi Arabia in November 2017 following the method described by Sarkar et al. (2012). The soils of the area are sandy loam, alkaline (pH 7.73), and saline (EC 2.9) (Mahmood et al. 2016; Daur et al. 2018). In the present study, alfalfa plants were selected because of the availability of the plants during the period of sample collection. The rhizosphere soil samples (1 g) were added to 10 mL of sterile distilled water, and the resulting suspensions were serially diluted (up to 10^-8). Exactly, 100 μL aliquot from each dilution was spread on plates containing nutrient agar (NA) medium and incubated for 48 h at 30°C. Morphologically distinct bacterial colonies were purified by repeated streak culture on fresh NA plates. Finally, purified bacterial strains were preserved in 20% glycerol solution at −80°C for subsequent use.

Bioassays for plant growth promoting traits

IAA production

The ability of bacterial isolates to produce IAA was determined based on the colorimetric method described by Patten and Glick (2002) with some modifications. Bacterial strains were propagated overnight in 5 mL of DF salts minimal media (Dworkin and Foster 1958), and then aliquots of 20 μL were inoculated into DF salts minimal media (5 mL) supplemented with 2 mg mL^-1 L-tryptophan. After 48 h of incubation at 30°C with continuous shaking at 200 rpm, bacterial cultures were centrifuged at 6000 rpm for 10 min, and 1 mL supernatant was mixed with 2 mL Salkowski’s reagent (Gordon and Weber 1951). The mixture was allowed to stand in the darkness for 20 min at room temperature before the absorbance was recorded at 535 nm using a spectrophotometer. The IAA concentration of each sample was calculated by comparison with a standard curve.

ACC deaminase activity

The ability of the isolated strains to produce ACC deaminase was determined according to Penrose and Glick (2003) measuring the amount of α-ketobutyrate produced when ACC deaminase enzyme cleaves ACC. The concentration of μmol of α-ketobutyrate produced by the bacterial isolates was measured by comparing the absorbance of a sample to a standard plot of α-ketobutyrate (Santa Cruz Biotechnology, Inc., Heidelberg, Germany) between 0.1 and 1.0 μmol at 540 nm.

Inorganic P-solubilization

Bacterial strains were assayed for their mineral P-solubilization ability using National Botanical Research Institute’s phosphate (NBRIP) growth medium following the protocol described by Nautiyal (1999). Briefly, each bacterial strain was inoculated on the NBRIP agar plate in triplicates and incubated at 30°C. After incubation for 72 h, insoluble tricalcium phosphate (TCP) solubilizing ability of the isolate was measured in terms of phosphate solubilization index (PSI) [PSI = A/B, where A is the total diameter (colony + halo zone) and B is the colony diameter (Islam and Hossain 2012)].

Growth, IAA and ACC deaminase activities of the selected isolates under salinity stress

The growth of the two selected isolates, namely KB-10 and KB-25, was observed in nutrient broth (NB) media supplemented with 1–10% NaCl according to Sharma et al. (2016). In addition, the production of IAA and ACC deaminase by the isolates was determined in DF salts minimal media supplemented with 5% NaCl following the method described above.

Identification of selected bacterial isolates

Phenotypic and biochemical characterization

Colony morphology such as color, shape, margin, elevation and surface of the PGPB isolates was recorded after 24 h of growth on NA plates at 30°C. Gram reaction was conducted according to Vincent and Humphrey (1970), and cell shape was observed by light microscopy. The motility of the isolates was tested using the protocol described by Elbeltagy et al. (2000). The KOH lysis test was performed as described by Suslow et al. (1982). Catalase and Oxidase tests were conducted according to Hayward (1960) and Shekhawat et al. (1992), respectively. The ability of bacterial isolates to produce ammonia and hydrogen cyanide (HCN) was assessed as described by Cappuccino and Shermen (1992) and Lorcq (1948), respectively. Additionally, various biochemical features of the isolates were determined using the gram-negative identification card with VITEK 2 system version 08.01 (bio-Mérieux Inc., Hazelwood, MO) according to manufacturer’s instructions.

16S rRNA gene sequencing and phylogenetic analysis

Total genomic DNA of purified cultures of the selected isolates was extracted using a DNeasy Blood and Tissue kit (Qiagen, Germany) as described by the manufacturer. The 16S rRNA gene was amplified with the universal primers 27F (5’ AGAGTTTGATCCTGGCTCAG 3’) and 1492R (5’ GGTTACCTTGTGAGGCTCAG 3’) (Lane 1991). The purified PCR products were Sanger sequenced at Macrogen, Korea and the 16S rDNA sequences obtained (about 700 base pairs) were compared with the GenBank database of NCBI (http://www.ncbi.nlm.nih.gov) using BLAST. Multiple
sequence alignment was performed using the CLUSTALW Multiple Alignment program in BioEdit version 7.0.5.3 (Hall 1999) and gaps were edited manually. A phylogenetic tree was inferred using the neighbor-joining (NJ) method (Saitou and Nei 1987) with MEGA version 7.0.26 (Kumar et al. 2016). The pairwise evolutionary distances were computed using the Kimura 2-parameter model (Kimura 1980).

Hemolytic activity
The selected bacterial isolates were grown on human blood agar media at 37°C for 48 h to observe their hemolytic activity according to standard protocols.

Pot experiment
In order to evaluate the potential of two selected isolates, namely KB-10 and KB-25, along with/without foliar application of Si fertilizer in alleviating salinity stress in coriander, a pot experiment was conducted in a growth room at the Department of Biological Sciences, King Abdulaziz University, Jeddah, Saudi Arabia in July 2018. Coriander seeds were surface sterilized by soaking in 70% ethanol for 1 min followed by soaking in 0.1% HgCl₂ for 3 min, and subsequently rinsing with sterile distilled water (5 times) (Vaishnav et al. 2015). Sterilized seeds were then soaked in sterile distilled water for 24 h inside closed petri dishes at room temperature before sowing in seedling trays containing sterilized FloraStar potting soil (Asdoco fert, Riyadh, Saudi Arabia), and incubated in a growth room at 22 ± 2°C with 14/10 h day/night photoperiod. Soil sterilization was done by autoclaving at 15 lbs/121°C for 3 h (Bharti et al. 2016). After one week of germination, healthy and uniform-sized seedlings were inoculated with bacteria by roots dipping into the NB media containing overnight grown bacterial culture for 6 h at room temperature. Untreated plants were dipped into sterile NB for the same period. The seedlings were then transplanted in pots (5 seedlings/pot) filled with sterilized soil and transferred to the growth room. The plants were irrigated every 48 h with sterile deionized water. Ten mL of bacterial suspension (as mentioned above) was applied to the rhizosphere zones of each plants at 7 days after transplantation (DAT). Same amount of sterile NB was applied to the untreated plants. In the early morning, about 150 mL Si solution (0.1% potassium silicate w/v) per pot were sprayed at 14 DAT. One week after the second inoculation, the plants were subjected to salinity stress by watering with sterile NaCl solution (75 mM). To prevent the plants from undergoing osmotic shock, the NaCl concentration in the solution was increased incrementally by 25 mM and applied to the plants at 48 h interval until the final NaCl concentration (75 mM) was reached in the solution and maintained till plant harvesting (28 DAT). Non-stressed plants were irrigated with sterile deionized water only. The experiment was conducted in a completely randomized design with 12 treatments (20 plants per treatment) defined as follows: uninoculated, Si fertilizer non-treated, non-stressed plants (negative control) (i), KB-10 inoculated, Si fertilizer non-treated, non-stressed plants (ii), KB-25 inoculated, Si fertilizer non-treated, non-stressed plants (iii), uninoculated, Si fertilizer treated, non-stressed plants (iv), KB-10 inoculated, Si fertilizer treated, non-stressed plants (v), KB-25 inoculated, Si fertilizer treated, non-stressed plants (vi), uninoculated, Si fertilizer non-treated, salt-stressed plants (positive control) (vii), KB-10 inoculated, Si fertilizer non-treated, salt-stressed plants (viii), KB-25 inoculated, Si fertilizer non-treated, salt-stressed plants (ix), uninoculated, Si fertilizer treated, salt-stressed plants (x), KB-10 inoculated, Si fertilizer treated, salt-stressed plants (xi), and KB-25 inoculated, Si fertilizer treated, salt-stressed plants (xii).

Relative water content
Leaf relative water content (RWC) was measured using fresh and completely developed plant leaves from the top of randomly selected plants according to Mahmood et al. (2016). After measuring the fresh weights (FW), leaves were soaked in distilled water inside a closed petri dish at 4°C for 24 h. After blotting the leaf samples with tissue paper, the fully turgid weights (TW) were measured. Leaf samples were then oven-dried at 72°C for 24 h to measure the dry weights (DW). Finally, RWC was calculated according to Teulat et al. (2003), using the following equation:

\[
RWC (\%) = \left[ \frac{FW – DW}{TW – DW} \right] \times 100
\]

Photosynthetic pigments
Fresh leaves were used for chlorophyl measurements according to Arnon (1949) with some modifications. Briefly, 100 mg leaves were homogenized in a tissue homogenizer with 10 mL of 80% acetone. The homogenized sample mixture was centrifuged at 6000 rpm for 15 min at 4°C, and the supernatant was used to measure chlorophyll a (Chl a), chlorophyl b (Chl b), and carotenoids at 663, 645, and 470 nm, respectively, using a spectrophotometer. The concentrations of total chlorophyl, Chl a, Chl b, and carotenoids were determined using the following equations:

\[
\text{Total chlorophyll (}\mu\text{g mL}^{-1}\text{)} = (20.20 \times A_{665}) + (8.02 \times A_{663})
\]

\[
\text{Chl a (}\mu\text{g mL}^{-1}\text{)} = (12.25 \times A_{663}) - (2.79 \times A_{645})
\]

\[
\text{Chl b (}\mu\text{g mL}^{-1}\text{)} = (21.50 \times A_{665}) - (5.10 \times A_{663})
\]

\[
\text{Carotenoids (}\mu\text{g mL}^{-1}\text{)} = (1000 \times A_{470}) - (1.82 \times \text{Chl a}) - (85.02 \times \text{Chl b}) / 198
\]

Total polyphenol content
Total polyphenol contents (TPC) were measured by the Folin-Ciocalteau colorimetric method according to Hoff and Singleton (1977) with some modifications. Aerial parts (1 g) were extracted with 250 mL methanol (80%) by continuous shaking at 150 rpm for 12 h and filtered with Whatman filter paper no. 1. The extract (50 µL) was then mixed with Folin-Ciocalteau reagent (100 µL) and methanol (850 µL), allowed to settle for 5 min at room temperature. Five hundred µL of 20% sodium carbonate was added to the reaction mixture. After 30 min incubation, the absorbance was taken at 750 nm using a spectrophotometer. Finally, TPC was determined from a standard curve obtained by measuring the absorbance of known concentrations of gallic acid and expressed as mg g⁻¹ FW gallic acid equivalent.

Peroxidase activity
Peroxidase (POD) (EC 1.11.1.7) activity was determined following the protocol described by Miranda et al. (1995). The aerial tissues (1 g) were homogenized with Tris-HCl buffer
(20 mM, pH 7.2), and centrifuged at 10,000 rpm for 10 min at 4℃. The clear supernatant was used for the enzyme assay. The assay mixture for the POD activity comprised in 1 mL: 0.008 mL of 0.97 M H₂O₂, 0.08 mL of 0.5 M guaiacol, 0.25 mL of 0.2 M sodium acetate buffer (pH 5.5), and least amount of enzyme extract. The amount of guaiacol oxidation was determined by calculating the change in absorbance at 470 nm for 1 min using a spectrophotometer. One unit of POD activity was defined as an increase of optical density (OD) 1.0 per min.

**Plant growth and salt tolerance index**
At harvest, plant growth parameters (e.g. fresh and dry weights of shoots and roots) were measured. Dry weights were determined by drying the plants at 70℃ for 72 h in an oven (Kang et al. 2014a). The salt tolerance index (STI) was determined using the following equation as described by Shetty et al. (1995):

\[
\text{STI} = \frac{\text{DWS or DWT}}{\text{DWC}}
\]

(where, DWS indicates dry weight of uninoculated, Si non-treated, unstressed plants).

**Statistical analysis**
The data were statistically analyzed by SPSS version 17.0 software. Significant differences among different treatments were carried out via analysis of variance (ANOVA) using Duncan’s Multiple Range test at the 5% significance level (P < 0.05).

**Results**

**Isolation and characterization for plant growth-promoting traits of bacteria**
In the present study, we isolated a total of 25 potential PGPB strains (KB-1 to KB-25) from the rhizosphere of alfalfa plants growing at the salt-affected farmland in Jeddah, Saudi Arabia. All the isolates were screened in vitro for their ability to synthesize IAA, ACC deaminase, and solubilize TCP. Out of the 25 isolates, ten isolates were able to synthesize IAA in presence of L-tryptophan (Table 1). Among them, KB-10 and KB-25 produced the highest (85 µg/mL) and the lowest (59 µ± 0.1) rate mg-1 h-1 respectively (Table 1). The biochemical results obtained from the VITEK 2 system showed that the isolates KB-10 and KB-25 were *Pseudomonas pseudoalcaligenes and P. putida*, respectively (Supplementary Table S1). In addition, the 16S rRNA gene of KB-10 and KB-25 was sequenced and the sequences were deposited in the GenBank database of NCBI under the accession numbers MG554687 and MG557689, respectively (Table 2). Blasting the 16S rDNA sequences of KB-10 (701 bp) and KB-25 (790 bp) against the sequences available at the GenBank showed 100% sequence homology with *P. pseudoalcaligenes* and *P. putida*, respectively (Table 2). The taxonomic positions of both isolates are presented in the phylogenetic tree (Figure 1). Based on these results, KB-10 and KB-25 were tentatively identified as *P. pseudoalcaligenes* and *P. putida*, respectively. Both isolates did not show any hemolytic activity on human blood agar plates (Table 2).

**Identification and hemolytic activity of selected PGPB strains**
Both KB-10 and KB-25 were cream colored, producing circular colonies with entire margins and smooth surfaces (Table 2). The elevation of KB-10 was flat, while KB-25 was convex (Table 2). Both isolates were gram-negative, rod-shaped, and motile, and reacted positively to the KOH lysis, catalase, oxidase, and ammonia production tests, but negatively to the HCN production test (Table 2). The biochemical results obtained from the VITEK 2 system showed that the isolates KB-10 and KB-25 were *Pseudomonas pseudoalcaligenes and P. putida*, respectively (Supplementary Table S1). In addition, the 16S rRNA gene of KB-10 and KB-25 was sequenced and the sequences were deposited in the GenBank database of NCBI under the accession numbers MG554687 and MG557689, respectively (Table 2). Blasting the 16S rDNA sequences of KB-10 (701 bp) and KB-25 (790 bp) against the sequences available at the GenBank showed 100% sequence homology with *P. pseudoalcaligenes* and *P. putida*, respectively (Table 2). The taxonomic positions of both isolates are presented in the phylogenetic tree (Figure 1). Based on these results, KB-10 and KB-25 were tentatively identified as *P. pseudoalcaligenes* and *P. putida*, respectively. Both isolates did not show any hemolytic activity on human blood agar plates (Table 2).

**Effects of selected PGPB isolates and Si treatment on coriander plants under non-saline and saline conditions**

**Effect on RWC**
Application of selected PGPB strains (KB-10 and KB-25) and Si fertilizer, alone or in combination, significantly (p 0.05) improved RWC in leaves as compared to negative control plants grown in non-saline (0 mM NaCl) conditions (Figure 2, Supplementary Table S2). Plants treated with both KB-10 and Si fertilizer had the highest RWC (about 91%), followed by plants treated with both KB-25 and Si (about 87%), whereas RWC was the lowest (about 80%) in negative control plants (Figure 2). However, salinity stress (75 mM NaCl) negatively affected RWC across all treatments (Figure 2). This effect was more pronounced in positive control plants as compared to plants treated with either bacterial strains.

### Table 1. Plant growth-promoting traits of isolated bacteria.

| Isolates | IAA production (µg mL⁻¹) | ACC deaminase activity (µmol α-ketobutyrate mg⁻¹ h⁻¹) | Phosphate solubilization (PSI in agar assay) |
|----------|--------------------------|----------------------------------------------------|---------------------------------------------|
| KB-1     | ND                       | ND                                                 | ND                                          |
| KB-2     | ND                       | ND                                                 | ND                                          |
| KB-3     | 61 ± 0.1                 | ND                                                 | ND                                          |
| KB-4     | 61 ± 1.2                 | ND                                                 | ND                                          |
| KB-5     | 61 ± 0.1                 | ND                                                 | ND                                          |
| KB-6     | ND                       | ND                                                 | ND                                          |
| KB-7     | ND                       | ND                                                 | ND                                          |
| KB-8     | ND                       | ND                                                 | ND                                          |
| KB-9     | ND                       | ND                                                 | ND                                          |
| KB-10    | 85 ± 0.7                 | ND                                                 | ND                                          |
| KB-11    | 85 ± 0.7                 | ND                                                 | ND                                          |
| KB-12    | ND                       | ND                                                 | ND                                          |
| KB-13    | 32 ± 0.3                 | ND                                                 | ND                                          |
| KB-14    | ND                       | ND                                                 | ND                                          |
| KB-15    | ND                       | ND                                                 | ND                                          |
| KB-16    | 83 ± 1                   | ND                                                 | ND                                          |
| KB-17    | 76 ± 0.1                 | ND                                                 | ND                                          |
| KB-18    | 76 ± 0.1                 | ND                                                 | ND                                          |
| KB-19    | ND                       | ND                                                 | ND                                          |
| KB-20    | ND                       | ND                                                 | ND                                          |
| KB-21    | ND                       | ND                                                 | ND                                          |
| KB-22    | ND                       | ND                                                 | ND                                          |
| KB-23    | ND                       | ND                                                 | ND                                          |
| KB-24    | ND                       | ND                                                 | ND                                          |
| KB-25    | 19 ± 0.3                 | 0.1                                                | 1.61 ± 0.06                                 |

Data presented as means ± standard error (n = 3). ND, not detected; IAA, Indole-3-acetic acid; ACC, 1-aminocyclopropane-1-carboxylic acid; PSI, phosphate solubilization index = (halo zone + colony diameter) / colony diameter.

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**Shetty et al. (1995):**
"determined using the following equation as described by Shetty et al. (1995):"

\[
\text{STI} = \frac{\text{DWS or DWT}}{\text{DWC}}
\]

(where, DWS indicates dry weight of uninoculated, Si non-treated, unstressed plants).
or Si fertilizer or both bacteria and Si fertilizer under salinity. Under saline conditions, treatment of plants with both KB-10 and Si fertilizer showed the highest RWC (about 86%), while positive control plants had the lowest RWC (about 69%) (Figure 2).

**Effect on photosynthetic pigments**

Concomitant to RWC, treatment of plants with PGPB strains and/or Si fertilizer resulted in a significant increase in photosynthetic pigments (total chlorophyl, Chl a, Chl b and carotenoids) as compared to negative control plants grown under normal conditions (Figure 3, Supplementary Table S3). Although salinity stress reduced the content of photosynthetic pigments in all treatments, plants treated with KB-10, KB-25, and/or Si fertilizer performed better than positive control plants (Figure 3). In both non-saline and saline conditions, the maximum amount of total chlorophyl, Chl a, Chl b and carotenoids was observed in plants treated with KB-10 and Si together. Combined application of KB-10 and Si increased about 114, 107, 145 and 85% total chlorophyl, Chl a, Chl b and carotenoids, respectively, as compared to negative control plants under non-stress conditions (Figure 3). Under salinity stress conditions, total chlorophyl, Chl a, Chl b and carotenoids increased by about 152, 144, 194 and 114%, respectively, in KB-10 and Si fertilizer treated plants as compared to positive control plants (Figure 3). Interestingly, all the measured parameters of photosynthetic pigments were higher in KB-10 and Si fertilizer treated plants as compared to both positive and negative control plants grown under either normal or stress conditions (Figure 3).

**Effect on TPC and POD enzyme activity**

There were no significant differences observed in TPC among different treatments under non-stress conditions, but it was significantly higher in positive control plants as compared to plants treated with bacterial strains and/or Si fertilizer under stress conditions (Figure 4, Supplementary Table S4). Plants treated with KB-25 along with Si fertilizer, followed by plants treated with KB-10 and Si fertilizer had the lowest amount of TPC, which were about 20 and 18%, respectively, lower as compared to positive control plants grown under saline conditions (Figure 4). On the other hand, POD level was similar in all treatments including negative control plants under non-saline conditions (Figure 4, Supplementary Table S4). Salinity stress significantly enhanced the enzyme level irrespective of the treatments; however, plants treated with PGPB and/or Si fertilizer exhibited higher enzyme activity in comparison to positive control plants (Figure 4). Under saline conditions, the maximum POD activity was recorded in KB-10 and Si fertilizer (combined) treated plants, which was about 50% higher as compared to positive control plants (Figure 4).

**Effect on plant growth and STI**

A significant decline in measured plant growth parameters including fresh and dry weights of shoots and roots was observed in plants exposed to salinity stress; however, plants treated with bacterial strains, and/or Si fertilizer performed significantly better as compared to positive control plants (Figure 5, Supplementary Figure S1, Supplementary Table S5). Under salinity stress, the highest shoot fresh and dry weights, root fresh and dry weights were recorded in plants treated with KB-10 and Si fertilizer together, which were
about 413, 638, 514 and 350%, respectively, higher as compared to positive control plants (Figure 5). Similarly, significant improvement in STI value was also recorded in plants treated with bacterial strains, and/or Si fertilizer (Figure 6, Supplementary Table S6). The lowest STI value was observed for positive control plants (0.437), whereas the highest STI value was recorded for plants treated with KB-10 and Si fertilizer together (2.978), followed by plants treated with KB-25 and Si (1.839) (Figure 6). These results indicate that inoculation of plants along with or without Si fertilizer enhances salinity tolerance in coriander plants.

Discussion

PGPB and Si fertilizer can confer plant tolerance to various abiotic stresses including salinity (Etesami 2018). In the present study, 25 potential PGPB strains were isolated from the alfalfa rhizosphere. Among the isolated bacteria, two promising isolates, namely KB-10 (the highest IAA-producing strain) and KB-25 (the only ACC deaminase-producing and P-solubilizing strain) were tentatively identified as *Pseudomonas pseudoalcaligenes* KB-10 and *P. putida* KB-25, respectively, based on their phenotypic, biochemical, and 16S rRNA gene sequence and phylogenetic relationship (Table 2, Supplementary Table S2, Figure S1). *Pseudomonas* is the most frequently reported genus as PGPB, and the ability of IAA production, ACC deaminase synthesis and P-solubilization by many *Pseudomonas* species has been documented by numerous researchers (Glick et al. 1995; Sharma et al. 2016; Egamberdieva et al. 2017; Khan et al. 2017). However, some strains of both *P. pseudoalcaligenes* and *P. putida* may cause nosocomial infections, particularly among the immunocompromised and hence, are considered as unusual human pathogens (Anaissie et al. 1987; Flores-Carrero et al. 2016). We observed that both isolates were non-hemolytic on human blood agar plates (Table 2). Generally, bacterial strains those exhibit β-hemolysis activity are considered as opportunistic human pathogens (Sum et al. 2017).

A pot experiment was carried out to evaluate the effectiveness of the two PGPB strains (KB-10 and KB-25) and/or Si fertilizer application in improving salinity tolerance in coriander plants. The results showed that inoculation of bacterial strains and/or treatment with Si fertilizer increased RWC in plant leaves (Figure 2, Supplementary Table S2). Measuring RWC is a very frequently used method to assess plant water status, and RWC is typically declined in plants subjected to salinity stress (Spomer 1985; Fahad et al. 2015). In saline conditions, increased RWC in cucumber due to PGPB inoculation, and in okra due to foliar application of Si was reported by Kang et al. (2014a) and Abbas et al. (2015), respectively. PGPB and Si may positively affect root hydraulic conductivity, osmolyte accumulation, and transpiration rate.
and thereby, regulate water potential in salt-stressed plants (Ilangumaran and Smith 2017; Etesami 2018).

Concentration of photosynthetic pigments is a useful indicator of plant responses to salinity stress (Percival et al. 2003; Habib et al. 2016). Enhanced chlorophyll concentrations might result in increased photosynthetic rate and consequently, enhanced plant growth under saline conditions (Kang et al. 2014a; Mahmood et al. 2016). In this study, photosynthetic pigments including total chlorophyll, Chl a, Chl b and carotenoids were decreased in plants when subjected to salinity stress indicating substantial impairment to the photosynthesis mechanisms; however, plants treated with PGPB and/or Si fertilizer had higher photosynthetic pigments concentration (Figure 3, Supplementary Table S3). Similar to our results, Zhang et al. (2014) reported that salinity stress decreased photosynthetic pigments concentration in cotton plants. The authors suggested that the decline in chlorophyll content could be associated with the suppression of specific enzymes that play an important role in synthesis of these pigments. The increased activity of chlorophyll degrading enzyme, chlorophyllase, in salt-stressed plants might be another probable reason for the reduced chlorophyll pigments (Reddy and Vora 1986; Abbas et al. 2015). Increased concentration of photosynthetic pigments in salinity-stressed mung bean plants treated with PGPB inoculants and/or foliar spray of Si fertilizer has been documented by Mahmood et al. (2016). In addition, the presence of K in the applied Si fertilizer might play a role in increasing chlorophyll contents. Wei et al. (2016) reported that application of exogenous K increased chlorophyll contents in Sophora alopecuroides plants subjected to salinity stress.

Increased ROS generation is one of the common phenomena in salinity-affected plants, which can damage lipids, proteins, DNA, and carbohydrates in plant cells (Yokoi et al. 2002; Yang and Guo 2018). Polyphenols are biosynthesized from the phenyl propanoid pathway that can play a pivotal role in ROS scavenging in plants (Sreenivasulu et al. 2000; Cheruiyot et al. 2007). Although there was no significant difference observed in TPC across all treatments under normal conditions, we observed enhanced TPC levels in case of all treatments under saline conditions. But the amount of TPC was significantly lower in PGPB and/or Si fertilizer treated plants as compared to positive control plants (Figure 4, Supplementary Table S4). The decreased level of TPC indicates that plants treated with PGPB and/or Si had a low level of salinity stress. Kang et al. (2014b) reported similar findings in soybean plants grown under saline conditions and inoculated with P. putida H-2-3. In contrast to our results regarding TPC in plants treated with Si fertilizer, Abbas et al. (2015) reported that foliar spray of Si (silicic acid, Si (OH)4) increased TPC in okra under both non-saline and saline conditions. This variation might be due to the differences in plant species and/or the type of Si solution applied.

POD is one of the major antioxidant enzymes that scavenges toxic H2O2 in the cytosol and chloroplasts of plant cells (Zhang et al. 2011). Treatment with PGPB and/or Si fertilizer elevated the POD activity in plants under saline conditions (Figure 4, Supplementary Table S4). Abd_Allah et al. (2018) also reported that salinity stress significantly increased POD activity in chickpea plants, and the level of POD was further elevated in plants inoculated with Bacillus subtilis BERA 71. Similarly, higher activity of POD enzyme
in Si treated okra and wheat plants as compared to non-Si treated control plants under salinity stress has been documented by Abbas et al. (2015) and Alzahrani et al. (2018), respectively. The mechanism of PGPB and Si induced POD activity is yet to be elucidated; however, several studies have reported that PGPB can stimulate various genes that encode different antioxidant enzymes in plants (Habib et al. 2016; Sharma et al. 2016). Additionally, both KB-10 and KB-25 exhibited catalase activity (Table 2). Most of the plant-associated aerobic bacteria are catalase positive and can help plants under stress conditions by scavenging H2O2 (Cowell et al. 1994; Sharma et al. 2016). These results indicate that plants treated with PGPB and/or Si convened less oxidative stress, which was correlated with the lower level of TPC in plants treated with PGPB and/or Si fertilizer as compared to positive control plants grown in saline conditions.

Our results showed that treatment of plants with PGPB strains and/or Si fertilizer significantly increased shoot and root biomass as compared to negative and positive control plants under both non-saline and saline conditions, respectively (Figure 5, Supplementary Table S5). The STI value was also higher in PGPB and/or Si fertilizer treated plants (Figure 6, Supplementary Table S6). Our findings are in agreement with the results of Mahmood et al. (2016), who reported that treatment with PGPB and/or Si fertilizer significantly increased plant biomass and STI of mung bean plants grown at different levels of salinity. In the present study, improved plant growth and biomass production due to PGPB treatment might be associated with the bacterial ability to synthesize IAA, ACC deaminase, and catalase enzyme. Bacterially-synthesized IAA along with plant endogenous IAA can improve root system architecture including

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**Figure 4.** Effect of PGPB (P. pseudoalcaligenes KB-10 and P. putida KB-25) and/or Silicon (Si) fertilizer treatment on total polyphenol content and peroxidase (POD) enzyme activity in the aerial parts of coriander under non-stress and salinity-stress conditions. Data presented are means (± standard error, n = 3). Bars labeled with different letters are significantly different according to DMRT test at P < 0.05.

**Figure 5.** Effect of PGPB (P. pseudoalcaligenes KB-10 and P. putida KB-25) and/or Silicon (Si) fertilizer treatment on plant biomass of coriander under non-saline and saline conditions. Data presented are means (± standard error, n = 4). Bars labeled with different letters are significantly different according to DMRT test at P < 0.05.
enhanced root growth and/or formation of lateral roots and root hairs that consequently increase water and nutrient uptake by plants (Patten and Glick 2002; Dimkpa et al. 2009; Yang et al. 2009). On the other hand, bacterial ACC deaminase can break down ACC, the immediate biosynthetic precursor of ethylene, into ammonia and α-ketobutyrate and consequently, decrease stress ethylene biosynthesis and thus, improve plant salinity tolerance (Honma and Shimomura 1978; Glick 2014). Additionally, the cumulative effect of increased RWC, photosynthetic pigments and POD activity in plants treated with PGPB and/or Si fertilizer might be attributed to improved growth and salinity tolerance in coriander. Ma and Yamaji (2006) suggested that the ameliorative effect of Si might be linked with its deposition in roots that reduces apoplastic bypass flow and provides metal binding sites and thereby, reduced salt uptake and root-to-shoot translocation. Also, additional K in the Si solution might help plants maintain Na⁺ and K⁺ homeostasis. In this regard, Wei et al. (2016) reported that application of K enhanced K⁺ / Na⁺ ratio and salinity tolerance in S. alopecuroides plants.

Interestingly, coriander plants inoculated with IAA-producing P. pseudoalcaligenes (KB-10) performed better compared to plants inoculated with IAA, ACC deaminase-producing, and P-solubilizing P. putida (KB-25) strain under both normal and saline conditions. That was probably because of higher (about 4.5-fold) IAA production ability by KB-10 than by KB-25. In addition, the amount of ACC deaminase produced and P-solubilized by KB-25 was very low in comparison with KB-10 than by KB-25. In addition, the amount of ACC deaminase can break down ACC, the immediate biosynthetic precursor of ethylene, into ammonia and α-ketobutyrate and consequently, decrease stress ethylene biosynthesis and thus, improve plant salinity tolerance (Honma and Shimomura 1978; Glick 2014). Additionally, the cumulative effect of increased RWC, photosynthetic pigments and POD activity in plants treated with PGPB and/or Si fertilizer might be attributed to improved growth and salinity tolerance in coriander. Ma and Yamaji (2006) suggested that the ameliorative effect of Si might be linked with its deposition in roots that reduces apoplastic bypass flow and provides metal binding sites and thereby, reduced salt uptake and root-to-shoot translocation. Also, additional K in the Si solution might help plants maintain Na⁺ and K⁺ homeostasis. In this regard, Wei et al. (2016) reported that application of K enhanced K⁺ / Na⁺ ratio and salinity tolerance in S. alopecuroides plants.

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Conclusion

This study showed that treatment of coriander plants with P. pseudoalcaligenes KB-10 or P. putida KB-25, alone or in combination with foliar spray of Si fertilizer, can improve plant growth by positively affecting RWC, photosynthetic pigments, TPC, POD enzyme activity, and root system under both normal and saline conditions. In addition, the data indicate that combined application of PGPB and Si fertilizer could be a promising and effective strategy to alleviate salinity stress in coriander. To the best of our knowledge, this is the first report on PGPB and/or Si fertilizer mediated salinity tolerance in coriander. However, further research is needed to validate the effectiveness of PGPB and/or Si fertilizer treatment in improving plant tolerance to salinity stress in field conditions.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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