Effect of Burkholderia sp. and Pseudomonas spp. inoculation on growth, yield, and absorption of inorganic components in tomato ‘Micro-Tom’ under salinity conditions

Hiroki Nakahara, Naotaka Matsuzoe, Takeshi Taniguchi, and Ping An

Arid Land Research Center, Tottori University, Hamasaka 1390, Tottori 680-0001, Japan

ABSTRACT

We screened four strains (Burkholderia sp. St-A, and Pseudomonas spp. St-B, St-C, and St-D) from 21 bacterial isolates isolated tomato cultivation fields based on their plant growth-promoting traits. Then, tomato (‘Micro-Tom’) seedlings inoculated with each of the four selected strains were grown under non-salinity and salinity (NaCl) treatment conditions. Under non-salinity conditions, St-C and St-D strains increased the total biomass of roots, stems, and leaves and fruit yield. Under NaCl treatment conditions, St-B, St-C, and St-D strains increased total biomass and fruit yield. In roots, Na content was not suppressed, but K, P, and water content were increased by bacterial inoculations. Correlation analysis showed a significant and positive relationship between fruit yield and root under both non-salinity and salinity conditions. This indicates that the maintenance of homeostasis and water relations in roots may contribute to the improvement of plant growth, including root and fruit yield, under salinity conditions.

1. Introduction

Approximately 1128 million hectares of soil worldwide are estimated to be negatively affected by salt (Wicke et al. 2011). In agricultural lands, salt damage is caused by the excessive use of chemical fertilizers, excessive irrigation in arid lands, and climate change, such as floods, tsunamis, and typhoon surges in coastal areas (Roy et al. 2014; Goto et al. 2015; Taylor and Krüger 2019). In salt-affected soils, the inhibition of water uptake or dehydration in plants occurs due to osmotic stress due to a reduction in the water potential of the soil. As a result, large amounts of Na enter plant cells, causing ion-specific toxicity, leading to protein degradation, disruption of ion homeostasis, the production of reactive oxygen species, the inhibition of photosynthesis, and a significant reduction in crop production (Muñns 2002; Muñns and Tester 2008). Increasingly unpredictable climate patterns due to global warming are likely to lead to an increase in salt-affected soils, which will have a negative effect on crop production. Thus, there is an urgent need to develop approaches that enable high crop productivity in salt-affected soils (Liu et al. 2020).

Tomato (Solanum lycopersicum L.) is one of the most important crops around the world. Tomatoes cultivated under salinity treatment conditions are sold at high prices in the market due to their high content of saccharides, organic acids, and amino acids, as well as their functional components, such as ascorbic acid and gamma-aminobutyric acid, and improved flavor (Zushi and Matsuzoe 2015; Nakahara et al. 2019). However, salinity stress can also cause losses in shoot biomass, fruit number, and fruit size, thus reducing tomato yields (Cuartero and Fernández-Muñoz 1998).

‘Micro-Tom,’ a model tomato cultivar, is a miniature-dwarf cultivar that has a short life cycle of 70–90 days, from sowing to fruit ripening, in small pots (Meissner et al. 1997). Using this cultivar, it is possible to study the effects of the growth and fruit yield of tomato in a short period, as well as grow a large number of plants in a growth chamber under constant environmental control. ‘Micro-Tom’ tomatoes have been used in many experiments to investigate the physiological response of tomato to biotic and abiotic stress (Takahashi et al. 2005; Yin et al. 2010), as well as to screen bacterial strains that improve the salinity tolerance or disease resistance of the tomato and determine the underlying mechanisms (Paliyandi et al. 2014; Nakahara et al. 2016).

A number of plant growth-promoting bacteria (PGPB) have been isolated, including those possessing plant growth-promoting (PGP) factors, such as siderophore production, which is an iron-supplementing molecule, indole acetic acid (IAA), which functions as a plant hormone for plant elongation, 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase, which is involved in the degradation of ACC, a precursor of ethylene, and phosphate solubilization, which assists in the supply of phosphorus from the soil (Hayat et al. 2010). Recently, several studies have attempted to improve the salinity tolerance of plants using various PGPB strains (Singh et al. 2018; Egamberdieva et al. 2019). Several bacteria, such as Achromobacter, Bacillus, Pseudomonas, Streptomyces, and Glutamicibacter strains with ACC deaminase, IAA, siderophores, and phosphate solubilizing ability, have been isolated as bacteria that improve the salinity tolerance of tomatoes (Mayak et al. 2004; Paliyandi et al. 2014; Singh et al. 2018; Yoo et al. 2019; Xiong et al. 2019; Gong et al. 2020); in particular, Pseudomonas strains...
have been extensively studied (Tank and Saraf 2010; Shen et al. 2012; Ali et al. 2014a, 2014b; Yan et al. 2014; Egamberdieva et al. 2017; Cordero et al. 2018; Rabhi et al. 2018; Win et al. 2018). However, most of these studies have investigated the enhancement of tomato growth, such as shoot biomass, and few studies, except Shen et al. (2012), have investigated the effects of bacterial inoculation on tomato yield under salinity treatment conditions in detail. Since fruit production is the most important aspect of tomato cultivation, there is a need to evaluate the effect of bacterial inoculation on both biomass of plant tissues and yield of fruits.

Ion-specific toxicity caused by NaCl treatment is a major factor inhibiting tomato growth, with Na accumulation in plant cells resulting in a reduced absorption of K, Ca, Mg, and NO₃, as well as inhibition of enzyme and protein synthesis, which are important for plant metabolism (Cuartero and Fernández-Muñoz 1998). The maintenance of ion homeostasis in tomatoes by bacterial inoculation has been investigated in several studies, with reports that it plays an important role in improving salinity tolerance in plants. For example, the inoculation of tomatoes with Pseudomonas migulae 8R6, P. fluorescens YsS6, and Glutamicibacter halophytocola KLBMP5180 strains was found to suppress shoot Na absorption and reduced direct Na toxicity (Ali et al. 2014a; Xiong et al. 2019). Additionally, it has been reported that the inoculation of tomato with Achromobacter piechaudii ARV8, Arthrobacter sp. PD1.5, Pseudomonas spp. RC5.5, OFT2, and OFT5, Bacillus aryabhattai H19-1, and B. mesonae H20-5 does not inhibit shoot Na absorption, but enhances K, P, and Ca absorption, thus maintaining ion balance and improving salinity tolerance (Mayak et al. 2004; Cordero et al. 2018; Win et al. 2018; Yoo et al. 2019). However, these reports only investigated the absorption of inorganic components in the shoots, with no studies investigating the absorption of inorganic components in the roots. Roots are the first plant part to be affected by bacterial infection and salinity stress; therefore, it is important to evaluate the effect of inorganic component absorption in roots.

The objective of this study was to determine the bacterial strains that improve the growth and yield of ‘Micro-Tom’ tomatoes under salinity stress conditions, as well as to determine the contribution of absorption of inorganic components in each plant tissue (roots, stems, and leaves) to the improvement of plant salinity tolerance by bacterial inoculations. Specifically, in this study, we isolated 21 bacterial strains from tomato cultivation fields and screened four bacterial strains with high PGP activities (siderophore, IAA, ACC deaminase activities, and phosphate solubilizing ability). In addition, we investigated the effect of the four bacterial strains on the growth and yield of the tomato cultivar ‘Micro-Tom’ and the water contents and the absorption of inorganic components of roots, stems, and leaves in tomatoes cultivated under non-salinity and salinity conditions. Through the research, we also tried to estimate the mechanism for the bacterial isolates to enhance plant growth under salinity condition and to find the plant trait that were not only enhanced by inoculated bacteria but also related to the tomato yield.

2. Materials and methods

2.1. Isolation of bacterial strains

Soil samples were collected from two tomato fields (32°37’51.1” N, 130°32’16.4” E and 32°59’21.1” N, 130°40’05.9” E) in Uki City, Kumamoto, Japan, in June 2018. After removing 2–3 cm of soil from the ground surface, soil samples near tomato roots were collected using a core sampler (height: 5 cm, volume: 100 cm³) from five points in each field. Water suspensions of each soil sample were serially diluted and plated on Pseudomonas CFC selective agar plates (Merck, Darmstadt, Germany) and incubated at 28°C for 48 h. There are many strains in Pseudomonas that promote plant growth (Tank and Saraf 2010; Shen et al. 2012; Ali et al. 2014a, 2014b; Yan et al. 2014; Egamberdieva et al. 2017; Cordero et al. 2018; Rabhi et al. 2018; Win et al. 2018). We thought that it would be easy to obtain bacterial strains with plant growth promoting activity in closely related to Pseudomonas spp., and we used strains isolated from Pseudomonas CFC selective agar plates. Bacterial colonies with different morphologies were isolated from each plate; a total of 21 isolates were cultured in BG broth (10 g L⁻¹ bacto peptone, 5 g L⁻¹ glucose, 1 g L⁻¹ yeast extract, and 1 g L⁻¹ casamino acid) at 28°C for 24 h with shaking at 130 strokes min⁻¹, and then stored in the culture supplemented with 15% glycerol at −80°C. The bacterial stocks were cultured on BGT agar plates (BG broth supplemented with 50 mg L⁻¹ tetrazolium chloride and 15 g L⁻¹ agar) at 28°C for 48 h. These were then used to evaluate the PGP activities of the bacterial strains.

2.2. Screening for plant growth promoting activities

2.2.1. Siderophore and phosphate solubilization

The siderophore production of bacterial colonies was evaluated using the chrome azurol S (CAS) assay (Schwyn and Neilands 1987). A single colony was transferred to CAS plates (3 g L⁻¹ casamino acids, 3 g L⁻¹ PIPES, 2 g L⁻¹ glucose, 1 g L⁻¹ bacto peptone, 1 g L⁻¹ NH₄Cl, 0.6 g L⁻¹ NaOH, 0.3 g L⁻¹ KH₂PO₄, 246.5 mg L⁻¹ MgSO₄·7H₂O, 14.8 mg L⁻¹ CaCl₂·2H₂O, 72.9 mg L⁻¹ HDTMA, 60.5 mg L⁻¹ CAS, 2.7 mg L⁻¹ FeCl₃·6H₂O, and 15 g L⁻¹ agar) and grown at 28°C for 48 h. Siderophore production was evaluated as positive when a halo (changed from blue to orange) around the colony was formed.

To determine the phosphate solubilization ability, a single colony was transferred to Pikovskaya’s agar plate (10 g L⁻¹ dextrose, 5 g L⁻¹ Ca₃(PO₄)₂, 0.5 g L⁻¹ yeast extract, 0.5 g L⁻¹ (NH₄)₂SO₄, 0.2 g L⁻¹ KCl, 0.1 g L⁻¹ MgSO₄·5H₂O, 0.1 mg L⁻¹ MnSO₄·5H₂O, 0.1 mg L⁻¹ FeSO₄·7H₂O, and 15 g L⁻¹ agar), and then grown at 28°C for 7 days. The phosphate solubilization ability was evaluated as positive when a clear zone was formed around the colony.

2.2.2. Indole acetic acid

The production IAA was determined as reported by Kurbachew and Wydra (2013). Isolates were cultured in BG broth supplemented with 3 mM tryptophan at 28°C for 48 h with shaking at 130 strokes min⁻¹. The culture was centrifuged at 8000 rpm for 5 min. Then, 1 mL of the resulting supernatant was mixed with 50 µL of ortho-phosphoric acid and 2 mL of Salkowski’s reagent (50 mL 35% perchloric acid and 1 mL 0.5 M FeCl₃·6H₂O) and incubated in the dark for 30 min. The resultant pink color was determined using a spectrophotometer (SH-9000; Corona Electric Co., Ltd., Ibaraki, Japan) at 535 nm. IAA concentration was calculated using a standard curve prepared from pure IAA.
2.2.3. ACC deaminase activity

The ACC deaminase activity of the isolates was determined by measuring the production of α-ketobutyrate generated by the cleavage of ACC by ACC deaminase, using the partially modified method with reference to Penrose and Glick (2003) and Ali et al. (2014b). Isolates were cultured in 4 mL of BG broth at 28°C for 15 h with shaking at 130 strokes min⁻¹. Once at the stationary phase, the bacterial cells were collected by centrifugation at 4200 rpm for 5 min and washed twice with 0.1 M Tris-HCl (pH 7.5), suspended in 2 mL of modified minimal medium supplied with ACC (5 g L⁻¹ glucose, 1.75 g L⁻¹ K₂HPO₄, 0.75 g L⁻¹ KH₂PO₄, 0.25 g L⁻¹ MgSO₄·7H₂O, 0.015 g L⁻¹ CaCl₂·2H₂O, and 0.3 g L⁻¹ ACC), and incubated at 28°C for 24 h with shaking. The bacterial cells were collected by centrifugation at 6000 rpm for 5 min, washed twice with 0.1 M Tris-HCl (pH 7.5), and resuspended in 200 μL of 0.1 M Tris-HCl (pH 8.5). The cells were labeled by adding 10 μL of tolueone, followed by vortexing at the highest speed for 30 s. Fifty microliters of the labeled cell suspension was incubated with 5 μL of 0.3 M ACC solution in a 1.5 mL microcentrifuge tube at 28°C for 30 min. The blank included 50 μL of 0.1 M Tris-HCl (pH 8.5) with 5 μL of 0.3 M ACC solution. The samples were then mixed thoroughly with 500 μL of 0.56 N HCl by vortexing, and the cell debris was removed by centrifugation at 8500 rpm for 5 min. A 500-μL aliquot of the supernatant was mixed with 400 μL of 0.56 N HCl and 150 μL of dinitrophenylhydrazine (DNF) reagent (0.01 g DNF in 10 mL of 2 N HCl) and incubated at 28°C for 30 min. To prepare the standard curve for the concentration of α-ketobutyrate, 500-μL aliquots of different concentrations (0–1 mM) of α-ketobutyrate solutions were mixed with 0.56 N HCl and DNF reagent. One milliliter of 2 N NaOH was added to the samples and standards, and the absorbance at 540 nm was determined using a spectrophotometer. The concentration of α-ketobutyrate in the samples was calculated using a standard curve.

The protein concentration in the labeled cell suspension was determined using the Bradford Protein Assay Kit (Takara Bio Inc., Shiga, Japan). A 100-μL aliquot of the labeled cell suspension was mixed with 100 μL of Bradford dye reagent and incubated at 25°C for 5 min. The resulting sample was analyzed using a spectrophotometer at 595 nm within 1 h of incubation. The protein concentration in the sample was calculated using a standard curve prepared from a standard solution of bovine serum albumin. The ACC deaminase activity was expressed in μmol α-ketobutyrate mg protein⁻¹ h⁻¹.

2.3. Identification and phylogenetic analysis of selected bacterial strains

2.3.1. DNA sequencing and putative identification of bacterial strains

Four bacterial strains screened for PGP activities were used for DNA sequencing. The genomic DNA of the selected strains was extracted using Quick-DNA Fungal/Bacterial MiniPrep Kit (Zymo Research, Irvine, CA, USA) according to the manufacturer’s instructions. The 16S rRNA gene was amplified using the universal primers 10F (5’-GTTGTGATCCTGCGCTA-3’) and 800R (5’-TACAGGG-TATCTAATCC-3’) with Takara Ex Taq DNA Polymerase (Takara Bio Inc.). PCR was conducted using a Takara PCR Thermal Cycler Dice Touch (Takara Bio Inc.) under the following conditions: one cycle at 94°C for 3 min; 30 cycles at 94°C for 30 s, 55°C for 1 min, and 72°C for 2 min; and final extension at 72°C for 7 min. The resulting PCR products were confirmed by the presence of a band under UV irradiation after 1% agarose gel electrophoresis with ethidium bromide staining, and then purified using ExoSAP-IT (Thermo Fisher Scientific Inc., Waltham, MA, USA). The sequences were obtained using the BigDye Terminators v1.1 Cycle Sequencing Kit (Thermo Fisher Scientific Inc.) and Illustra AutoSeq G-50 Dye Terminator Removal Kit (GE Healthcare, Chicago, IL, USA) and a DNA sequencer (Applied Biosystems 3130xl Genetic Analyzer; Thermo Fisher Scientific Inc.). The sequence of each bacterial strain was submitted to the DNA Data Bank of Japan (DDBJ) database under accession number LC653498–LC653501. This sequence was aligned with homologous sequences of the database for similarity searching using the BLASTn tool of the National Center for Biotechnology Information (NCBI) and Ribosomal Database Project (RDP) for putative identification at the genus level.

2.3.2. Phylogenetic analysis

Phylogenetic analyses were conducted to obtain further details on the taxonomic relatedness of the four bacterial strains. As reference sequences for phylogenetic analysis, the sequences of type-strains closely related to the test strains were searched in the Global Catalogue of Type-strain (gType) (Shi et al. 2021), and the sequences of type-strains were obtained from the NCBI database. Sequences were aligned using the multiple sequence alignment service obtained method with reference to Penrose and Glick (2003) and Ali et al. (2014b). Isolates were cultured in different concentrations (0–1 mM) of α-ketobutyrate, 500-μL aliquots of different concentrations (0–1 mM) of α-ketobutyrate solutions were mixed with 0.56 N HCl and DNF reagent. One milliliter of 2 N NaOH was added to the samples and standards, and the absorbance at 540 nm was determined using a spectrophotometer. The concentration of α-ketobutyrate in the samples was calculated using a standard curve.

The protein concentration in the labeled cell suspension was determined using the Bradford Protein Assay Kit (Takara Bio Inc., Shiga, Japan). A 100-μL aliquot of the labeled cell suspension was mixed with 100 μL of Bradford dye reagent and incubated at 25°C for 5 min. The resulting sample was analyzed using a spectrophotometer at 595 nm within 1 h of incubation. The protein concentration in the sample was calculated using a standard curve prepared from a standard solution of bovine serum albumin. The ACC deaminase activity was expressed in μmol α-ketobutyrate mg protein⁻¹ h⁻¹.

2.4. Effect of bacterial inoculations on the growth, yield, and inorganic content of tomato under non-salinity and salinity conditions

2.4.1. Plant materials and growth condition

The tomato cultivar (Solanum lycopersicum L.) ‘Micro-Tom’ was used in this study. Seeds were surface-disinfected first with 70% ethanol for 10 s, followed by 1% sodium hypochlorite for 10 min, and then washed twice in distilled water. They were germinated and grown in vermiculite in a growth chamber maintained at 28°C for 12 h in light and 22°C for 12 h in the dark. Seedlings were treated with liquid fertilizer (1/2 strength OAT B solution (N: 115 ppm, P: 46.5 ppm, K: 188.5 ppm, Ca: 109.5 ppm, Mg: 40 ppm, Fe: 1.45 ppm, Mn: 0.5 ppm, B: 0.5 ppm); OAT Agrio Co., Ltd., Tokyo, Japan) once at 14 days after sowing and grown until the three-leaf stage for 22 days.

2.4.2. Bacterial inoculation and salinity treatments

Four bacterial strains (St-A, St-B, St-C, and St-D) were selected from 21 strains based on the PGP activities of the bacterial strains. To prepare the bacterial inoculum, the selected bacterial stocks were streaked on BGT agar plates supplemented with 100 mM NaCl and cultured at 28°C for 48 h. A single colony was transferred to 4 mL of BG broth and cultured at 28°C for 24 h with shaking at 130 strokes
min\(^{-1}\) as a preculture. A 40-µL aliquot of preculture was added to 4 mL of BG broth and cultured at 28°C for 24 h with shaking. The bacterial cells were collected by centrifugation at 4500 rpm for 10 min and diluted with sterile distilled water (SDW) to an optical density of 0.12 at 600 nm (approximately 2 \times 10^7 CFU mL\(^{-1}\)).

For bacterial inoculation, the roots were washed gently with SDW to remove adhering vermiculite, and then soaked in 20 mL of the bacterial suspension for 30 min. Seedlings mock-inoculated with 20 mL of SDW served as the control. Inoculated seedlings were transplanted into 6-cm pots filled with commercial soil (Tanemaki Baido (main materials: peat moss, vermiculite, and perlite; N: 380 ppm, P: 290 ppm, K: 340 ppm); Takii Seed Co., Ltd., Kyoto, Japan) as salinity treatment. To prevent water and salinity runoff from the pots, a tray was placed under each pot, and bottom irrigation with tap water into the tray was conducted every day. The transplanted plants in salinity-treated soil were irrigated with 20 mL of 100 mM NaCl solution at 3 and 6 days after transplanting. Plants were grown in a growth chamber (28°C for 12 h of light and 22°C for 12 h in darkness) until harvest.

2.4.3. Measurement of growth and yield parameters

Tomato fruits were harvested 62 days after transplanting, and the number of fruits and weight was measured. Thereafter, plants were collected and the plant tissue of the leaves, stems, and roots were separated. The total number of leaves and stem length were measured. The root samples were carefully washed with tap water to remove adhering soil. Fresh biomass of each plant tissue was measured, and then their dry biomass was measured after drying in an oven at 80°C until there was no further decrease in the weight. The water content in each plant tissue was calculated using the following formula: water content in each plant tissue (%) = ((fresh weight − dry weight)/ fresh weight) \times 100.

2.4.4. Measurement of inorganic content

Dried samples of each plant tissue were digested with 5 mL of 70% HNO\(_3\) (1.42 g mL\(^{-1}\)) using a microwave digestion system (Ethos Up; Milestone, Sorisole, Italy), and then plant extracts were diluted with 1% HNO\(_3\). The inorganic content of plant extracts was measured using inductively coupled plasma-mass spectrometry (ICP-MS 8900; Agilent, CA, USA), and the Na, K, P, Mg, Ca, and Fe content were calculated using each standard curve prepared from a multi-element standard (XSTC-22; SPEX CertiPrep, NJ, USA).

2.4.5. Statistical analysis

The experiment was conducted using a completely randomized design with eight replicates per treatment. Two-way analysis of variance (ANOVA) was conducted to detect the effects of bacterial inoculation and salinity treatment. The mean values were compared using Tukey’s honestly significant difference (HSD) test at P < 0.05 under the non-salinity and salinity conditions, respectively. Pearson’s correlation coefficient was used to analyze the relationship (P < 0.05) among plant growth and fruit yield parameters under the non-salinity and salinity conditions, respectively. The values of water content in each plant tissue were calculated as percentages and arcsine-transformed before statistical analysis. All tests were performed using SPSS Statistics version 25 (IBM Co., NY, USA).

3. Results

3.1. Screening of isolated bacterial strains based on the plant growth promoting activities

Twenty-one bacterial strains were isolated from soil samples collected near tomato roots using Pseudomonas CFC selective agar plates. Then, the PGP activities (siderophore production, IAA production, phosphate solubilization, and ACC deaminase activity) of the strains were evaluated. As a result, four bacterial strains (St-A, St-B, St-C, and St-D) with potentially high PGP activities were selected (Table 1). All of bacterial strains had abilities of siderophore production and phosphate solubilization. The IAA production was highest in the order St-D > St-C > St-B > St-A. The ACC deaminase activity was highest in the order St-A > St-D > St-B > St-C.

The St-A strain was identified as *Burkholderia* sp., and St-B, St-C, and St-D were identified as *Pseudomonas* spp., based on the results of homology searches using the BLASTn and RDP tools. Phylogenetic trees were constructed based on the 16S rRNA sequences of St-A and representative *Burkholderia* type-strains (Figure 1A), and St-B, St-C, St-D, and representative *Pseudomonas* type-strains (Figure 1B). *Burkholderia* sp. St-A is closely related to *B. latens* R5630 T, *Pseudomonas* sp. St-B, and *P. putida* NBRC14164 T, *Pseudomonas* sp. St-C, and *P. taiwanensis* BCRC17751 T, and *Pseudomonas* sp. St-D and *P. guariconensis* PCAVU11 T are closely related. The similarity between test strains and the most closely related type-strain ranged from 98.93%–100%, with the coverage of 99%–100% (Supplemental Table 1).

3.2. Effect of bacterial inoculations on the growth of tomato under non-salinity and salinity conditions

Under non-salinity conditions, the plant growth parameters (except total biomass FW) of tomatoes inoculated with bacterial strains were not significantly different from those of the control plants (Table 2). However, total biomass FW was

| Table 1. Plant growth-promoting traits of selected bacterial strains. |
|----------------------|----------------------|----------------------|
| **Strain** | Diameter of clear zone (cm) | IAA production (µg mL\(^{-1}\)) | ACC deaminase activity (µmol α-ketobutyrate mg protein\(^{-1}\) h\(^{-1}\)) |
| St-A | 2.3 | 1.92 | 8.68 |
| St-B | 1.9 | 4.09 | 2.82 |
| St-C | 1.6 | 5.60 | 0.06 |
| St-D | 2.6 | 6.37 | 3.72 |
significantly increased in plant inoculated with St-D strain compared with the control.

In non-bacterial inoculation under salinity conditions (NaCl), the total number of leaves increased, and stem length, shoot biomass, and total biomass decreased compared with the non-salinity conditions (Table 2). Shoot FW and total biomass FW and DW were significantly increased in the plants inoculated with the St-D strains, and were slightly increased in inoculations of St-A, St-B, and St-C strain compared with the control.

3.3. Effect of bacterial inoculations on the biomass and water content of leaves, stems, and roots under non-salinity and salinity conditions

The effect on the biomass of individual plant tissues differed according to plant tissues, bacterial strains, and salinity conditions. Under the non-salinity conditions, leaf and stem biomass FW and DW were highest in plants with St-D inoculation (Figure 2A, C, and Figure 3A, C). Root biomass FW was significantly increased in the plants inoculated with St-C or St-D compared with the control (Figure 2E, 4C and 4D).

In the non-inoculated plants, the biomass FW of leaves, stems, and roots decreased by NaCl treatment in comparison with the control (Figure 2), while that of biomass DW decreased by 32.0%, 33.7%, and 51.0%, respectively (Figure 3). The effect of salinity stress on biomass reduction was greatest in roots than in leaves and stems. Under salinity conditions, leaf biomass FW was significantly increased (Figure 2B), and leaf biomass DW tended to increase in all bacterial inoculations compared with the non-inoculated NaCl treatment (Figure 3B). Stem biomass FW and DW were not significantly different after bacterial inoculation (Figure 2D and 3D). Root biomass FW was significantly increased in the plants inoculated with St-B, St-C, or St-D strains compared to non-inoculated plants (Figure 2F and Figure 4). However, root biomass DW was not significantly different among treatments (Figure 3F).

Under the non-salinity conditions, the water content in each plant tissue was not significantly different from that in the control and bacterial inoculations (Figure 5A, C, and E). Under salinity conditions, the water content in the leaves and stems was not increased by bacterial inoculations (Figure 5B, D); however, the water content in the roots was significantly increased after bacterial inoculation (Figure 5F).

3.4. Effect of bacterial inoculations on the yield of tomato fruits under non-salinity and salinity conditions

Under the non-salinity conditions, no significant difference was observed in the number of fruits per plant, fruit weight, or the yield of fruits after bacterial inoculation compared with the control. Under the non-inoculation conditions in NaCl treatment compared with the control under non-salinity conditions, the number of fruits, fruit weight per plant, and total fruit weight were reduced to 22.2%, 30.8%, and 45.3%, respectively (Table 3). Under salinity conditions, no significant difference was observed in terms of fruit weight and yield between the inoculated and non-inoculated plants; fruit number increased in plants inoculated with St-B, St-C, and St-D, with total fruit weight increasing by 15.4%, 18.4%, and 12.4%, respectively.

3.5. Effect of bacterial inoculations on inorganic content of tomato tissues under non-salinity and salinity conditions

In the leaves and stems in the NaCl treated plants, the Na, P, Ca, Mg, and Fe contents increased, while the K content decreased compared with non-salinity conditions (Tables 4 and 5). Na absorption in the leaves was slightly lower in tomatoes inoculated with St-B strain than in the non-inoculated plants under salinity conditions (Table 4). However, the contents of most inorganic components in the leaves and stems were not significantly different between non-inoculated and inoculated plants under salinity conditions.
non-salinity and salinity conditions, respectively (Tables 4 and 5).

In the roots of non-bacterial inoculation, the Na and Ca contents tended to increase with NaCl treatment, while the K and P contents tended to decrease compared with the non-salinity control (Table 6). The effect of bacterial inoculation on the absorption of inorganic components in roots was greater than that of the leaves and stems. In particular, in the roots of plants under salinity conditions, the Na, K, and P contents were significantly increased in all bacterial

### Table 2. Effect on plant growth of tomato seedlings by bacterial inoculations under non-salinity and salinity conditions.

| Treatment          | Total number of leaf | Stem length (cm) | Fresh weight (g) | Dry weight (mg) |
|--------------------|----------------------|------------------|------------------|-----------------|
|                    | Shoot                | Total biomass    | Shoot            | Total biomass   |
| Non-salinity condition |                      |                  |                  |                 |
| Control            | 8.3 A                 | 11.7 A           | 4.37 AB          | 5.01 B          | 426.3 AB        | 484.4 AB        |
| St-A               | 7.6 A                 | 11.3 A           | 3.84 B           | 4.57 B          | 363.8 B         | 417.9 B         |
| St-B               | 8.0 A                 | 11.1 A           | 4.07 B           | 4.79 B          | 381.8 B         | 438.5 B         |
| St-C               | 9.5 A                 | 12.2 A           | 4.62 AB          | 5.31 AB         | 473.1 AB        | 549.3 AB        |
| St-D               | 9.4 A                 | 12.9 A           | 5.22 A           | 6.10 A          | 549.5 A         | 624.2 A         |
| Salinity condition |                      |                  |                  |                 |
| NaCl               | 10.0 a                | 10.3 a           | 3.44 b           | 3.82 b          | 286.6 a         | 315.1 b         |
| St-A+NaCl          | 12.0 a                | 9.8 a            | 3.68 ab          | 4.16 ab         | 310.1 a         | 340.1 ab        |
| St-B+NaCl          | 9.6 a                 | 10.5 a           | 3.72 ab          | 4.33 ab         | 323.4 a         | 360.0 ab        |
| St-C+NaCl          | 10.1 a                | 10.3 a           | 3.88 ab          | 4.47 a          | 331.4 a         | 368.2 ab        |
| St-D+NaCl          | 11.3 a                | 10.8 a           | 4.07 a           | 4.63 a          | 361.1 a         | 396.9 a         |
| Bacterial inoculation (B) | n.s.                |                  |                  |                 |
| Salinity treatment (S) | ***                  |                  |                  |                 |
| n.s.               | ***                  |                  | ***              | ***             |
| B × S              | n.s.                 |                  | *                | n.s.            |

*Data show mean of 8 plants in each treatment. Different letters indicate significant differences (P < 0.05) according to the Tukey-HSD test in each cultivation condition.

*Results by two-way ANOVA show as ns, not significant; * and ***, significant difference at P < 0.05 and P < 0.001.

Figure 2. Effect of bacterial inoculations on biomass fresh weight (FW) of leaf, stem, and root in tomato seedlings under non-salinity and salinity conditions. Data show the results of mean and standard error of 8 plants for each treatment. Different letters indicate significant differences (P < 0.05) according to the Tukey-HSD test in each cultivation condition.
inoculations, and the Fe content was significantly increased in the St-D-inoculated plants. The Ca content was significantly decreased in St-A, St-C, and St-D inoculations under both non-salinity and salinity conditions compared with non-inoculated plants.

3.6. Correlation between plant growth and yield parameters of tomatoes

In the correlation analysis among the growth parameters (total number of leaves, stem length, leaf, stem, root, shoot, and total biomass FW/DW), a significant positive correlation \((r \leq 0.80, P < 0.05)\) was observed among most of the pairs of growth parameters under the non-salinity conditions (Figure 6A), while the numbers of the pairs indicated significant correlations decreased under the salinity conditions (Figure 6B).

Correlation analysis between yield parameters (number of fruits, fruit weight, and yield) and growth parameters revealed significant positive correlations between tomato yield, leaf number, and root DW under non-salinity conditions (Figure 6A). Under salinity conditions, significantly positive correlations were observed between yield vs. root biomass FW/DW and number of fruits vs. root FW/DW and total biomass DW (Figure 6B). Tomato yield was strongly correlated with fruit weight in the non-salinity conditions and with number of fruits in the salinity conditions (Figure 6).

4. Discussion

4.1. Bacterial production of plant growth-promoting activities and salt tolerance in plants

PGPB are present in the soil environment and often have PGP traits, such as siderophores, IAA, ACC deaminase, and phosphate solubilization (Hayat et al. 2010; Egamberdieva et al. 2019). Auxin and ethylene are plant hormones that are related to plant growth, fruit set, and fruit ripening (Srivastava and Handa 2005; Santner et al. 2009). The most important naturally occurring auxin is IAA (Santner et al. 2009). In this study, under non-salinity and salinity conditions, tomato growth was promoted the most after inoculation with *Pseudomonas* sp. St-D strain, which had the highest IAA production. In plants subjected to salinity stress, excessive ethylene is produced, which inhibits plant growth (Win et al. 2018). Ethylene is biosynthesized from methionine via the ACC in plants. ACC deaminase is an enzyme that

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**Figure 3.** Effect of bacterial inoculations on biomass dry weight (DW) of leaf, stem, and root in tomato seedlings under non-salinity and salinity conditions. Data show the results of mean and standard error of 8 plants for each treatment. Different letters indicate significant differences \((P < 0.05)\) according to the Tukey-HSD test in each cultivation condition.
Figure 4. Effect of bacterial inoculations on root biomass in tomato seedlings (A: St-A, B: St-B, C: St-C, and D: St-D) under non-salinity and salinity conditions. After the roots were washed and measured fresh weight, photographs were taken of the average samples in each treatment.

Figure 5. Effect of bacterial inoculations on water content of leaf, stem, and root in tomato seedlings under non-salinity and salinity conditions. Data show the results of mean and standard error of 8 plants for each treatment. Different letters indicate significant differences ($P < 0.05$) according to the Tukey-HSD test in each cultivation condition. Percentages were obtained by arcsine-transformed before statistical analysis.
The results of two-way ANOVA show as * significant with inoculation with Burkholderia sp. St-A strain did not improve under non-salinity conditions, while the biomass of leaf FW tend to increase under salinity treatment conditions compared to the control; however, yield did not improve. This indicates that the ability of bacteria to promote plant growth does not necessarily coincide with the results of the plant inoculation experiments. Barriuso et al. (2008) stated that testing these abilities in vitro is an effective strategy to isolate PGPB, but the biochemical traits shown in vitro are inducible under specific conditions (e.g. the use of specific media), which are not necessarily expressed in the soil and rhizosphere. Although many studies have evaluated only the bacterial ability of PGP traits for isolating PGPB strains, the results based on the experiments of inoculation into plants are most important. In addition, the majority of studies on tomato growth promotion by PGPB have only evaluated shoot biomass, and few studies have investigated its effects on fruit yield. In this study, the Pseudomonas spp. St-C and St-D strains were obtained, which enhanced tomato plant growth and yield under both non-salinity and salinity conditions.

### 4.2. Effect of bacterial inoculation as revealed by correlation of plant growth and yield parameters of tomatoes

Tomato yield is significantly correlated with the number of flowers, fruits, and fruit weight (Solieman et al. 2013). At low salinity concentrations, the number of fruits does not change and the yield reduction is caused by a decrease in average fruit weight. By contrast, at high salinity concentrations, the number of flowers, buds, and fruits decreases and the yield is reduced (van Ieperen 1996; Cuartero and Fernández-Muñoz 1998; Ali et al. 2014a). Correlation analysis among the yield parameters revealed that there was a significantly positive correlation between yield and fruit weight (Figure 6A), suggesting that the increase in fruit weight due to bacterial inoculation contributes to yield. Conversely, although the number of fruits and fruit weight were reduced by salinity treatment, there was a significantly positive correlation between yield and number of fruits (Figure 6B), suggesting that the improvement of fruit yield in salinity conditions by bacterial inoculation was more strongly related to fruit number than to fruit weight. In fact, the fruit weight under salinity conditions was not increased by bacterial inoculation, and the reduction in the number of fruits by salinity stress was alleviated by bacterial inoculation with Pseudomonas spp. St-B, St-C, and St-D strains, resulting in higher yields.

Wang et al. (2019) reported that root characteristics (e.g. root length, root volume, and root surface area) correlated very significantly with fruit yield and dry matter production in tomato cultivars with different water and fertilizer concentrations. In particular, a high correlation ($r = 0.971$) was observed between total root volume and fruit yield. In this study, root growth did not increase under salinity conditions by bacterial inoculation was more strongly related to fruit number than to fruit weight. In fact, the fruit weight under salinity conditions was not increased by bacterial inoculation, and the reduction in the number of fruits by salinity stress was alleviated by bacterial inoculation with Pseudomonas spp. St-B, St-C, and St-D strains, resulting in higher yields.
under salinity conditions, the increase in plant biomass and fruit yield in tomatoes inoculated with *Pseudomonas* spp. St-B, St-C, and St-D strains was attributed to an increase in root biomass. In this study, root growth promotion by bacterial inoculation was found to be one of the major factors responsible for the improvement of tomato growth and yield under salinity conditions.

### 4.3. Inorganic content of tomato tissues after bacterial inoculations

Plant growth inhibition under NaCl treatment conditions is caused by osmotic stress and ion-specific toxicity. In NaCl-treated soils, water uptake by plants is inhibited or dehydrated due to osmotic stress that occurs from the beginning of NaCl treatment because the water potential of the soil is reduced (Munns 2002; Munns and Tester 2008). To prevent osmotic stress, plants produce compatible solutes, such as sugars, organic acids, amino acids, and proline. Inorganic ions, such as Na⁺ and K⁺ ions, absorbed into plant cells also function effectively as osmoregulators in plants (Munns and Tester 2008; van Zelm et al. 2020). Ion-specific toxicity is mainly caused by toxicity from large amounts of Na⁺ entering plant cells, resulting in protein degradation, the disruption of ion homeostasis, the production of reactive oxygen species, and the inhibition of photosynthesis (Munns 2002; Munns and Tester 2008). As a general effect of Na⁺ on ion absorption in plants, it is known that NaCl treatment increases Na content and inhibits K, Ca, and Mg absorption in aboveground tissues (Cuartero and Fernández-Muñoz 1998; Mayak et al. 2004; Win et al. 2018). However, Cordero et al. (2018) reported that an increase in the Na content of tomato leaves due to NaCl treatment inhibited the absorption of K, but not Ca and Mg. Similar results were observed in this study, where NaCl treatment decreased K content, while the Ca and Mg contents were not decreased in neither the leaves, stems, nor roots.

There are two patterns of the effects of PGPB inoculation on the absorption of inorganic elements in tomato plants: (1) Na absorption is suppressed and direct Na toxicity and inhibition of other ion absorption are alleviated (Ali et al. 2014a; Xiong et al. 2019); (2) Na absorption is not suppressed and inhibition of other elements, such as K, P, and Ca, is enhanced (Mayak et al. 2004; Cordero et al. 2018; Win et al. 2018; Yoo et al. 2019). However, these studies only evaluated inorganic constituent absorption in the aboveground parts of tomato plants, and absorption by roots remains unclear. Plant roots are the first tissues to come into contact with soil, salt, and bacteria. In this study, the effect of salt treatment on biomass reduction was greater in roots than in leaves and stems. Therefore, there is a need to evaluate the absorption of inorganic components in the roots. In this study, the content of most inorganic components in the leaves and stems was not significantly different between the non-inoculation and bacterial inoculations (Tables 4 and 5). However, the absolute amount of inorganic components absorbed into the plant increased because the leaf weight was increased by bacterial inoculation. The absorption of inorganic components in roots was different from that in the leaves and stems: Na content was not suppressed, and K and P contents increased by bacterial inoculations (Table 6). The absorption of trace elements, such as Mg and Fe, also tended to increase in tomatoes inoculated with *Pseudomonas* spp. St-B, St-C, and St-D strains.

### Table 5. Effect on inorganic component contents (mg g stem DW⁻¹) in tomato stem by bacterial inoculations under non-salinity and salinity conditions.

| Treatment | Na | K | P | Ca | Mg | Fe |
|-----------|----|---|---|----|----|----|
| Control   | 3.3 A | 49.6 A | 7.0 A | 4.3 A | 3.1 A | 0.14 A |
| St-A      | 3.6 A | 46.7 AB | 5.8 AB | 3.5 AB | 2.7 A | 0.17 A |
| St-B      | 3.2 A | 43.5 AB | 6.1 AB | 3.3 AB | 2.8 A | 0.09 A |
| St-C      | 3.0 A | 38.0 B | 5.5 AB | 3.1 B | 2.4 A | 0.08 A |
| St-D      | 2.9 A | 36.1 B | 4.9 B | 3.2 AB | 2.4 A | n.s. |

Salinity condition

| Treatment | Na | K | P | Ca | Mg | Fe |
|-----------|----|---|---|----|----|----|
| NaCl      | 19.2 a | 40.0 a | 10.1 A | 4.8 a | 3.6 a | 0.19 a |
| St-A+NaCl | 18.3 a | 37.8 a | 10.0 A | 4.2 a | 3.1 a | 0.16 a |
| St-B+NaCl | 18.2 a | 37.2 a | 9.7 A | 4.6 a | 3.5 a | 0.16 a |
| St-C+NaCl | 18.0 a | 37.0 a | 9.5 A | 4.4 a | 3.4 A | 0.15 A |
| St-D+NaCl | 18.0 a | 38.3 a | 9.3 A | 4.7 A | 3.5 A | 0.15 A |

| Bacterial inoculation | Na | K | P | Ca | Mg | Fe |
|-----------------------|----|---|---|----|----|----|
| n.s.                 | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. |

**Results of two-way ANOVA show as * significant difference at P < 0.05, ** significant difference at P < 0.01, *** significant difference at P < 0.001, and n.s. not significant.

### Table 6. Effect on inorganic component contents (mg g root DW⁻¹) in tomato root by bacterial inoculations under non-salinity and salinity conditions.

| Treatment | Na | K | P | Ca | Mg | Fe |
|-----------|----|---|---|----|----|----|
| Control   | 4.5 A | 32.6 B | 7.7 B | 3.7 A | 4.8 A | 4.1 A |
| St-A      | 5.0 A | 43.8 A | 13.6 A | 2.9 C | 5.2 A | 2.9 A |
| St-B      | 4.7 A | 43.9 B | 8.0 B | 3.5 | 6.3 A | 4.8 A |
| St-C      | 5.4 A | 38.6 B | 7.6 B | 3.0 BC | 8.9 A | 8.9 A |
| St-D      | 4.9 A | 39.2 AB | 8.7 B | 2.7 C | 6.9 A | 6.5 A |

Salinity condition

| Treatment | Na | K | P | Ca | Mg | Fe |
|-----------|----|---|---|----|----|----|
| NaCl      | 17.1 b | 22.0 AB | 6.0 b | 5.3 a | 6.5 ab | 3.2 b |
| St-A+NaCl | 24.5 a | 38.4 a | 10.6 a | 3.8 b | 5.7 b | 3.6 ab |
| St-B+NaCl | 23.6 a | 35.7 a | 9.0 a | 4.4 ab | 11.1 a | 9.9 ab |
| St-C+NaCl | 24.8 a | 38.4 a | 10.0 a | 3.9 b | 8.5 ab | 6.7 ab |
| St-D+NaCl | 24.2 a | 38.9 a | 9.0 a | 3.9 b | 10.8 a | 10.4 a |

| Bacterial inoculation | Na | K | P | Ca | Mg | Fe |
|-----------------------|----|---|---|----|----|----|
| n.s.                 | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. |

Data show mean of 8 plants in each treatment. Different letters indicate significant differences (P < 0.05) according to the Tukey-HSD test in each cultivation condition.

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- Cuartero and Fernández-Muñoz 1998
- Egamberdieva et al. 2019
- Mayak et al. 2004
- Mayak et al. 2004
- Win et al. 2018
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- Cordero et al. 2018
- Cuartero and Fernández-Muñoz 1998
- Munns 2002
- Munns and Tester 2008
- Munns and Tester 2008
- Mayak et al. 2004
- van Zelm et al. 2020
- Cordero et al. 2018
- Mayak et al. 2004
- Win et al. 2018
- Yoo et al. 2019
suggest that the factor responsible for the improvement of salinity tolerance by bacterial inoculation does not involve the inhibition of Na absorption in plants, but rather the maintenance of homeostasis of ion absorption in roots, such as K and P.

The factors responsible for the improvement of plant salt tolerance after bacterial inoculation include not only an improvement in ion uptake, but also an increase in plant chlorophyll content, an improvement of photosynthetic parameters (leaf photosynthesis, stomatal conductance, and transpiration rates), which are reduced by salinity stress (Win et al. 2018), activities of transporters of Na⁺ and K⁺ into vacuoles and xylem cells to inhibit Na toxicity in cell, abscisic acid accumulation, the production of compatible solutes such as proline, and an enhancement of ROS-scavenging enzyme activities (Rabhi et al. 2018; Xiong et al. 2019; Yoo et al. 2019; Gong et al. 2020). However, our measurements were not sufficient to clarify the mechanistic relationships. Therefore, further studies are needed to clarify the mechanism of growth enhancement in tomato plants under salinity-treated conditions by inoculation with Pseudomonas spp. St-B, St-C, and St-D strains.

4.4. Conclusion

NaCl-treated tomatoes showed disrupted ion homeostasis (mainly suppression of K uptake), resulting in a significant reduction in root biomass and a decrease in aboveground biomass and yield (fruit weight and number). The plant roots showed the highest rate of growth reduction under salinity stress compared to the leaves and stems. Tomatoes inoculated with Pseudomonas spp. St-B, St-C, and St-D strains showed improved plant growth and yield under salinity treatment conditions. On the other hand, a weak effect was observed on the content of inorganic components in the leaves and stems of these plants. Although Na absorption was higher in roots, K, P, Mg, and Fe absorption were enhanced by bacterial inoculations. Root biomass showed a strong positive correlation with the total biomass and yield. In conclusion, in this study, the maintenance of ion homeostasis in roots and an increase in root biomass were suggested to be important factors for plant growth and yield enhancement under salinity treatment conditions in tomatoes inoculated with Pseudomonas spp. St-B, St-C, and St-D strains.

Acknowledgements

We would like to thank BEX Co., Ltd. (Tokyo, Japan, http://www.bexnet.co.jp) for DNA sequencing. H.N. appreciates the Research Fellowships for Young Scientists from the Japan Society for the Promotion of Science (JSPS).

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This study was supported in part by a Grant-in-Aid for JSPS Fellows (grant number 20J00615).
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