



Enhancement of growth and salt tolerance of tomato seedlings by a natural halotolerant actinobacterium *Glutamicibacter halophytocola* KLBMP 5180 isolated from a coastal halophyte

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Abstract

Background and aims Soil salinity stress affects the health and growth of crops. The use of plant growth-promoting rhizobacteria (PGPR) to improve the salt tolerance of plants is gaining acceptance worldwide. Here, a halotolerant, plant growth-promoting actinobacterium *Glutamicibacter halophytocola* KLBMP 5180, recently isolated from the root of a coastal halophyte *Limonium sinense*, was investigated for its capacity on the growth of tomato seedlings under the condition of saline stress.

Methods Tomato seedlings were inoculated with strain KLBMP 5180 and irrigated with 2% NaCl salt-stress treatment. Plant growth and physiological responses were determined after harvest. The genome of strain KLBMP 5180 was sequenced and analyzed.

Results High salinity significantly reduced the growth and biomass of tomato seedlings. However, KLBMP 5180 inoculation significantly improved tomato growth in terms of seedling fresh weight and height, root length and fresh weight, and number of fibrous roots, along with increased osmolyte content (proline) and antioxidant defense enzymes and regulation of ion homeostasis

under salt stress. From the genome, we identified a series of genes that may contribute to plant growth promotion, including genes for nitrogen fixation, biosynthesis of siderophores and exopolysaccharides. Additionally, several genes related to high salinity tolerance, such as Na⁺/H⁺ antiporter, K⁺ transporter, glycine-betaine synthesis and transport, and several heavy metal resistance and biodegradation genes were also identified in the genome of strain KLBMP 5180.

Conclusion Our results demonstrate that the halotolerant strain KLBMP 5180 can be used to improve tomato seedling growth in saline soil and act as a potential agricultural biofertilizer agent in future applications.

Keywords Salt stress · Tomato seedling · *Glutamicibacter halophytocola* · Plant growth promotion · Genome analysis

Introduction

Soil salinity is one of the serious abiotic stresses affecting crop performance, as it inhibits seed germination and seedling growth and leads to yield reduction (Cuartero et al. 2006). Worldwide, large areas of soil have been salinized. It is estimated that more than 50% of the agricultural land will be salinized by 2050 (Jamil et al. 2011). High salinity in soil decreases the ability of plants to absorb water and nutrients, and destroys the balance of ions and osmosis in cells (Shilpi and

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Narendra 2005). Plants have evolved complex physiological, biochemical, and molecular level strategies to respond to salt stress, including accumulation of osmotic regulators (e.g., proline, trehalose, and glycine-beta-ine), and production of protective antioxidant enzymes and secondary metabolites (e.g., peroxidases, catalases, superoxide dismutase, and flavonoids) to scavenge reactive oxygen species (ROS). In addition, plants can resist salt stress by controlling the Na⁺ homeostasis and ionic balance, and regulating signal transduction pathways related to plant phytohormones, such as abscisic acid (ABA), salicylic acid (SA), and jasmonic acids (JA) (Mickelbart et al. 2015; Caarls et al. 2015). Therefore, it is very urgent and important to take effective approaches to improve the salt tolerance of crops.

Some traditional strategies, e.g., modern genetic engineering and genome editing techniques have been used to improve salt stress in crops (Wei et al. 2017; Li et al. 2018). At present, genetically modified crops are not yet widely accepted. Therefore, using an environment-friendly approach to improve the salinity tolerance of crops and remediate saline soils is still challenging (El-Esawi et al. 2018). The use of beneficial plant rhizospheric microorganisms and endophytes has shown a great potential in enhancing plant growth and health under both normal and various stress conditions without harming the environment (Wani et al. 2015; Berg et al. 2016; Qin et al. 2017; Zhang et al. 2019). Beneficial endophytes have been successfully used in improving crop and plant growth as well as amelioration of stress-induced damage, such as salinity (Qin et al. 2014; Barnawal et al. 2017), drought (Sheibani-Tezerji et al. 2015), and heavy metal (Płociniczak et al. 2018). They are known to improve plant growth and stress tolerance via a range of direct and indirect mechanisms, including fixing nitrogen, producing phytohormones including indole acetic acid (IAA), solubilizing phosphate and potassium, synthesizing 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase, siderophores, extracellular hydrolytic enzymes, and antibiotics (Qin et al. 2011; Glick 2014; Ma et al. 2016).

Tomato is an important and nutritious vegetable crop, which is popular all over the world. However, due to salinization of soil and irrigation water, tomato production has been greatly restricted, leading to yield reduction (Turhan and Seniz 2012). Several studies have used plant growth promotion bacteria to alleviate salt stress and promote tomato growth (Kim et al. 2014;

Palaniyandi et al. 2014; Win et al. 2018). However, there were few reports on the use of natural salt-tolerant PGPR strains. Previously, we obtained several halotolerant plant growth promotion (PGP) endophytic and rhizospheric bacteria from coastal halophytes. Inoculation of *Limonium sinense* and wheat seedlings under greenhouse conditions showed significant PGP effect under salt stress (Qin et al. 2014; Wang et al. 2017; Gong et al. 2018). Moreover, a new endophytic actinobacterium, *Glutamicibacter halophytocola* KLBMP 5180 (Feng et al. 2017), isolated from the root tissues of the halophyte *Limonium sinense*, significantly promoted host growth under NaCl stress via complex physiological and molecular mechanisms (Qin et al. 2018). Thus, our results revealed that this natural halotolerant strain is a promising candidate for plant growth promotion agent, which could be used for the crop growth under salt stress conditions. However, its mechanisms of salt tolerance and PGP properties remain unknown.

Therefore, the aims of the present study were (1) to evaluate the plant growth promotion effect with and without inoculation of strain KLBMP 5180 in tomato seedlings under the stress condition of 2% NaCl in greenhouse, (2) to investigate the effects on the physiological changes (osmolyte, antioxidant defense enzymes, and ion contents) of tomato seedlings (leaves and stems) after KLBMP inoculation in greenhouse under salt stress, and (3) to explore the plant growth promotion and salt-tolerant mechanisms of strain KLBMP 5180 by genome sequencing, annotation and analysis.

Materials and methods

Strain type and the culture condition

The halotolerant PGP strain, *G. halophytocola* KLBMP 5180, was previously isolated from the coastal halophyte *Limonium sinense* (Feng et al. 2017) and was obtained from the Key Laboratory of Biotechnology for Medicinal Plants of Jiangsu Province (Xuzhou, China). The strain was cultured in a 250 mL Erlenmeyer flask containing 100 mL yeast extract-malt extract medium broth (ISP 2, International *Streptomyces* Project; Shirling and Gottlieb 1966) at 150 rpm and 28 °C for 5 days.

Construction of rifampicin-resistant *G. halophytocola* KLBMP 5180

The rifampicin-resistant derivatives of strain *G. halophytocola* KLBMP 5180rif were developed by inoculation in ISP 2 broth containing 50 $\mu\text{g mL}^{-1}$ rifampicin. Then, the culture was spread on ISP 2 agar plates containing 50 $\mu\text{g mL}^{-1}$ rifampicin and was incubated at 28 °C for 36 h. The colonies obtained were further inoculated in ISP 2 broth containing 100 $\mu\text{g mL}^{-1}$ rifampicin, and colonies were further selected on higher concentration rifampicin at an interval of 50 $\mu\text{g mL}^{-1}$. After repeats of “inoculation broth-spreading agar,” the 300 $\mu\text{g mL}^{-1}$ rifampicin-resistant strain KLBMP 5180rif was obtained.

Strain inoculation and tomato seedlings salt stress

Seeds of the tomato (Jingpeng No.1) purchased from Shouguang Jinkai Seed Industry Co., Ltd. (Shouguang, China), were surface sterilized with 75% ethanol for 3 min, followed by rinsing three times with sterile water. After that, seeds were sown in plastic pots containing sterilized soil for germination and seedling growth in an illumination incubator (25 °C, 14/10 h light/dark, relative humidity 60%) for 5 days. Then, tomato seedlings with identical growth size were selected and transferred into plastic cups (bottom diameter: 4 cm, depth: 7.6 cm) containing sterile soil (70 g) for further cultivation for 3 days under the same greenhouse conditions. For tomato seedling inoculation, the PGP strain cells (cultured in ISP 2 broth as described above) were harvested by centrifugation (4500 rpm, 10 min), washed once with sterile distilled water and then re-suspended in sterile distilled water to the final concentration ($\text{OD}_{600}=0.8$). Then, seedlings were inoculated with 35 mL of KLBMP 5180rif suspensions (five inoculations, once every two days) or with sterile water as the control (ten biological replicates for each inoculated and non-inoculated). Five days after inoculation, seedlings were root-irrigated with 35 mL of 200 mM NaCl every two days (a total of five irrigations) to a final 2% NaCl in the soil. After seven days of salt stress, seedling fresh weights and heights, root fresh weights and length, and number of fibrous roots were measured.

Strain rhizosphere colonization

Root colonization and survival rate of inoculated KLBMP 5180rif were checked by a dilution plating technique. Determination of the number of colonies forming units (CFU) was performed on ISP 2 agar plates containing 200 $\mu\text{g mL}^{-1}$ rifampicin using rhizosphere soils of inoculated tomato seedlings at 2, 7, and 13 days after salt stress.

Plant physiological measurements

To measure the plant growth and physiological traits, five seedlings from each replicate were randomly selected. The total chlorophyll estimation of the leaves for different treatments was done according to the method of Ali et al. (2014). The proline content of leaves and stems was determined by spectrophotometric analysis at 520 nm using a kit (A107, Nanjing Jiancheng Bioengineering Institute, Nanjing, China). Malondialdehyde (MDA) concentration was measured according to the thiobarbituric reaction (Heath and Packer 1968). Total soluble sugar of the leaves and stems was estimated by the phenol-sulfuric acid method (Dubois et al. 1956). For antioxidant enzyme extraction, fresh plant tissues (0.5 g) were homogenized and extracted in 5–10 mL of ice-cold 50 mM phosphate buffer (pH 7.0) supplemented with 1% polyvinylpyrrolidone and 0.1 mM EDTA. The crude extract was centrifuged at 10,000 \times g for 20 min at 4 °C, and the obtained supernatant was used for the antioxidant assay. Peroxidases (POD), catalases (CAT), and superoxide dismutase (SOD) were measured as described by previous methods (Beauchamp and Fridovich 1971; Kar and Mishra 1976; Singh and Jha 2017). For leaf and stem ion content, tissues were first oven-dried and HNO_3 -treated according to the method of Zhang et al. (2014). The Na^+ , K^+ , and Ca^{2+} contents of leaves and roots were analyzed according to detection kits (C002 for Na^+ , C001–2 for K^+ , and C004–1 for Ca^{2+} , Nanjing Jiancheng Bioengineering Institute, China) according to the manufacturer’s instructions.

Genomic sequencing, assembly, and analysis

Genomic DNA of strain KLBMP 5180 was extracted according to the previous method (Qin et al. 2015). Then, the genome was sequenced by integrating the Illumina Miseq and Pacific Bioscience (PacBio) RS II sequencing platform at Majorbio Biotech Co., Ltd.

(Shanghai, China) according to standard protocols. The reads were assembled by software SOAPdenovo v2.04 (Li et al. 2010) and Celera Assembler v8.0 (Myers et al. 2000) after the quality control. SOAP GapCloser V1.12 was used to close gaps after assembly. The protein coding sequences (CDS) were predicted by Glimmer 3.02 (Delcher et al. 2007) and Prokaryotic Genome Annotation Pipeline (PGAP) on NCBI (Pruitt et al. 2012). The function annotation of the genome sequence was based on a BLAST search against the different function databases: GO (<http://www.geneontology.org/>), COG (<http://www.ncbi.nlm.nih.gov/COG/>), and KEGG (<http://www.genome.jp/kegg/>). A circular genome map with functional annotation was plotted using Circos software (Krzywinski et al. 2009). The secondary metabolite biosynthesis was predicted according to antiSMASH 4.0 (Blin et al. 2017). The genome sequences have been deposited at GenBank under the accession numbers CP012750 for chromosome and CP012751 for plasmid.

Data analysis

Data were analyzed using the GraphPad Prism 5.0 software. Results are expressed as mean values \pm standard deviation (SD) for three independent replicates. The statistical significance between treatments was assessed by one-way analysis of variance. $P < 0.05$ was considered statistically significant.

Results

Effect of strain inoculation improves tomato growth under NaCl stress

After 7 days of the NaCl treatment, the plant growth and physiological parameters were statistically analyzed. Results showed that inoculation of strain KLBMP 5180 significantly promoted tomato seedling growth under both non-saline and salt stress conditions (Fig. 1a and b). Plant growth was significantly inhibited when exposed to a high concentration of NaCl. However, KLBMP 5180-inoculated seedlings had significantly higher biomass (seedlings and root fresh weight and number of fibrous roots) and heights than the control (Fig. 2a–e). Fresh root weights were found to have increased by 28.6% and 26.5% with and without NaCl stress, respectively (Fig. 2e). The total chlorophyll

content of leaves treated with 200 mM NaCl was not affected (Fig. 2f).

Effect of strain inoculation on tomato antioxidants, proline, and soluble sugars

Strain KLBMP 5180 did not improve the soluble sugar content of the leaves and stems with or without NaCl stress. Inoculation with KLBMP 5180 significantly increased the proline content in the leaves and stems under both non-saline and salt stress conditions. Proline content in leaves and stems was increased by 110% and 86.7% ($P < 0.05$), respectively, under 0 mM NaCl, whereas it was increased by 40.4% and 39.2% ($P < 0.05$), respectively, under the 200 mM NaCl stress treatment. With KLBMP 5180 inoculation, the MDA content was decreased by 15.8% in stems compared with that of the control under NaCl stress conditions (Table 1).

Under salt stress, KLBMP 5180 significantly increased the accumulation of antioxidant enzymes. KLBMP 5180 inoculation increased the stem SOD activity by 57.1% and 37%, respectively, and slightly increased leaf SOD activity by 7.6% and 9.4%, respectively, under both non-saline and salt stress conditions (Fig. 3a). Considering the POD activity, higher activity of 35.2% and 160.8% was observed significantly in leaves and stems, respectively, under NaCl stress treatments, compared to the control seedlings (Fig. 3c). Strain KLBMP 5180 significantly increased the stem CAT accumulation 4.8-fold and 5.3-fold, compared to non-inoculated plants, with 200 mM NaCl and without NaCl treatments, respectively. In leaves, CAT activity was also increased 1.47-fold and 0.4-fold under both non-saline and salt stress conditions (Fig. 3b). Overall, the results indicated that inoculation with KLBMP 5180 increased host proline and antioxidants as well as reduced lipid peroxidation, therefore protecting tomato seedlings from salt stress.

Effect of strain inoculation on tomato ion accumulation

The seedling ion profile was significantly altered in response to strain KLBMP 5180 inoculation. Na^+ content in plant stems and leaves increased significantly after salt stress. With KLBMP 5180 inoculation, the content of Na^+ in leaves and stems was decreased by 96.5% and 23.5%, respectively, compared to the uninoculated seedlings (Fig. 4a). There was no significant

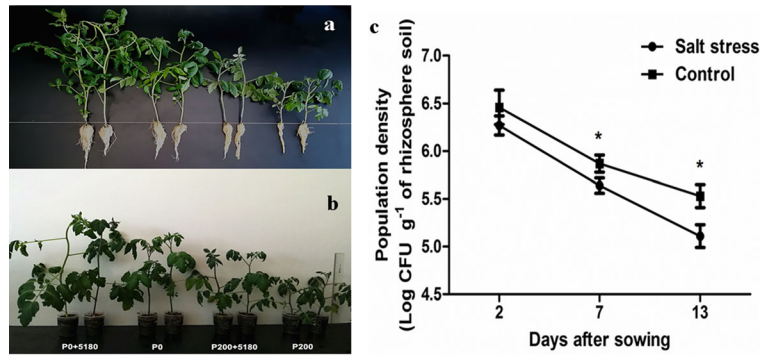


Fig. 1 Effect of *G. halophytocola* KLBMP 5180 strain inoculation on the growth of tomato seedlings with and without the NaCl stress condition, and its rhizosphere colonization density. **a**, aerial part; **b**, whole seedlings differences in control and strain KLBMP 5180 inoculation (P0 and P200 represent 0 and 200 mM NaCl

stress, and P0 + 5180 and P200 + 5180 represent strain KLBMP 5180 inoculation under 0 and 200 mM NaCl stress, respectively); and **c**, rhizosphere colonization density of strain KLBMP 5180 under 0 and 200 mM NaCl stress conditions. The asterisk (*) indicates $P < 0.05$ (*t* test) for treatment versus control

difference for K^+ concentration in leaves under both non-saline and salt stress conditions. However, K^+ content in the stems of inoculated seedlings was significantly higher under both 0 and 200 mM NaCl stress, compared to the un-inoculated plants (Fig. 4b). The K^+/Na^+ ratio was also calculated from the Na^+ and K^+ concentrations. NaCl stress decreased the K^+/Na^+ ratio in

leaves and stems, strain KLBMP 5180 inoculation increased the stem K^+/Na^+ ratio by 102.5% and 170.5% and the leaf K^+/Na^+ ratio by 10.2% and 33.3% under 0 and high NaCl stress treatments, respectively (Fig. 4d). At the same time, the content of Ca^{2+} was increased under salt or salt-free conditions. Ca^{2+} content in tomato stems was increased by 4.1-fold and 0.3-fold, whereas

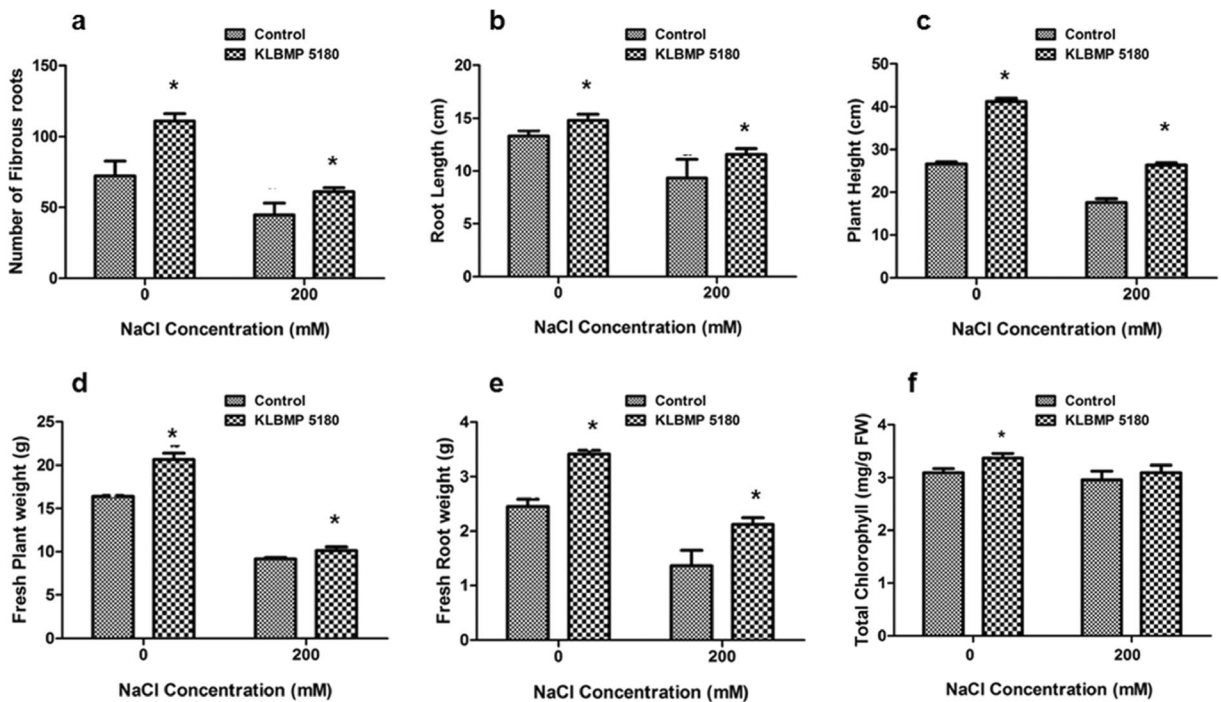


Fig. 2 Effect of *G. halophytocola* KLBMP 5180 strain inoculation on the growth of tomato seedlings with and without the NaCl stress condition. **a** number of fibrous roots; **b** root length; **c** plant height; **d** plant fresh weight; **e** root fresh weight; and **f** total

chlorophyll content. Values are means, and bars indicate SDs. The asterisk (*) indicates $P < 0.05$ (*t* test) for treatment versus control

Table 1 Effects of *G. halophytocola* KLBMP 5180 inoculation on the content of soluble sugar, proline, and MDA of tomato seedlings. Values are means \pm SD; different letters indicate significant difference between means at $P < 0.05$

Types	Soluble sugar (mg/g FW)		Proline (mg/g FW)		MDA ($\mu\text{mol/g FW}$)	
	Stem	Leaf	Stem	Leaf	Stem	Leaf
Control	15.66 \pm 0.87 ^{ab}	16.54 \pm 0.78 ^b	2.28 \pm 0.31 ^a	3.08 \pm 0.11 ^a	3.24 \pm 0.29 ^a	2.67 \pm 0.34 ^a
Control + KLBMP 5180	13.58 \pm 1.04 ^a	13.31 \pm 1.12 ^a	4.81 \pm 0.61 ^b	5.75 \pm 0.13 ^b	5.94 \pm 0.23 ^b	3.65 \pm 0.37 ^b
NaCl (200 mM)	20.88 \pm 0.98 ^c	17.74 \pm 0.39 ^b	8.19 \pm 0.52 ^c	10.00 \pm 0.16 ^c	7.66 \pm 0.81 ^b	3.48 \pm 0.78 ^b
NaCl + KLBMP 5180	16.57 \pm 1.39 ^b	16.41 \pm 1.02 ^b	11.50 \pm 0.82 ^d	13.92 \pm 0.21 ^d	6.61 \pm 0.69 ^b	3.37 \pm 0.52 ^b

in leaves, it was increased by 3.2-fold and 0.3-fold, under salt-free and salt stress conditions, respectively (Fig. 4c), when compared to un-inoculated seedlings.

Colonization of tomato by *G. halophytocola* KLBMP 5180

Strain KLBMP 5180 was found only colonizing the rhizosphere soil, and not in the endosphere of tomato seedlings. Colonization efficiency of strain KLBMP 5180 in the rhizosphere soil of tomato seedlings was measured by plate counting method. Obviously, the rhizosphere colonization density of strain KLBMP 5180rif was higher under salt-free than salt stress condition. After different days of salt stress, KLBMP 5180rif population density ($\log \text{CFU g}^{-1}$) decreased from 6.27 to 5.11 in the rhizosphere soil, whereas without salt stress, its density decreased from 6.46 to 5.53 (Fig. 1c). No bacterial colonies were observed on rifampicin-nutrient agar plates from un-inoculated control seedlings rhizospheric soil.

Genome characteristics of strain *G. halophytocola* KLBMP 5180

The complete genome of strain *G. halophytocola* KLBMP 5180 consists of a 3,911,798-bp circular chromosome and one 6626-bp circular plasmid (Fig. 5a and b). The G + C content of the chromosome and the plasmid was 60% and 53.7%, respectively. The chromosome contains 3624 CDSs, 19 rRNA, and 65 tRNA genes, whereas the plasmid contains 8 CDSs (Table 2). Five secondary metabolism-related gene clusters related to siderophore, non-ribosomal peptide synthetase (NRPS), betalactone, and terpene biosynthesis were detected in the genome (Table 3). The similarity of these gene clusters is relatively low, ranging from 6 to 75%,

suggesting that strain KLBMP 5180 has the potential to produce new secondary metabolites.

Genes related to PGP and salt environment adaption

Among these CDSs, 1503 genes were classified into 21 COG functional categories. Most of the genes were associated with functions such as amino acid transport and metabolism, carbohydrate transport and metabolism, translation, ribosomal structure and biogenesis, cell cycle control, cell division, chromosome partitioning, and inorganic ion transport and metabolism (Fig. 6a). The cellular component, molecular function and biological process of the genome information were also classified via the GO database (Fig. 6b). From the genome, many genes located in the chromosome were detected to be involved in plant growth promotion, including nitrogen fixation (*nifU*), IAA secretion (*iaaM*), siderophore (*sbnA*), spermidine (*speB*), and phenazine (*phzCEF*) biosynthesis (Table 4). In addition, genome analysis revealed the presence of entire genes responsible for the biosynthesis of exopolysaccharide (EPS), which could protect bacterial cells against oxidative stress and enhance plant growth under stress conditions (Meneses et al. 2017). These genes are involved in four distinct steps for the biosynthesis of EPS, including biosynthesis of nucleoside diphosphate sugars (NDP-sugars), assembly on lipid-acceptor, modification, and transport of EPS (Table 5). Furthermore, *G. halophytocola* KLBMP 5180 contains many genes related to salt tolerance. For example, genes encoding Na^+/H^+ antiporter and K^+ transporter can be activated under salt stress and thus avert the ingress of Na^+ . The key genes (*betABP*) for glycine-betaine synthesis and transport were found in the genome, which are considered as effective genes responsible for salt tolerance (Liu et al. 2016). In addition, the genome has a set of heavy

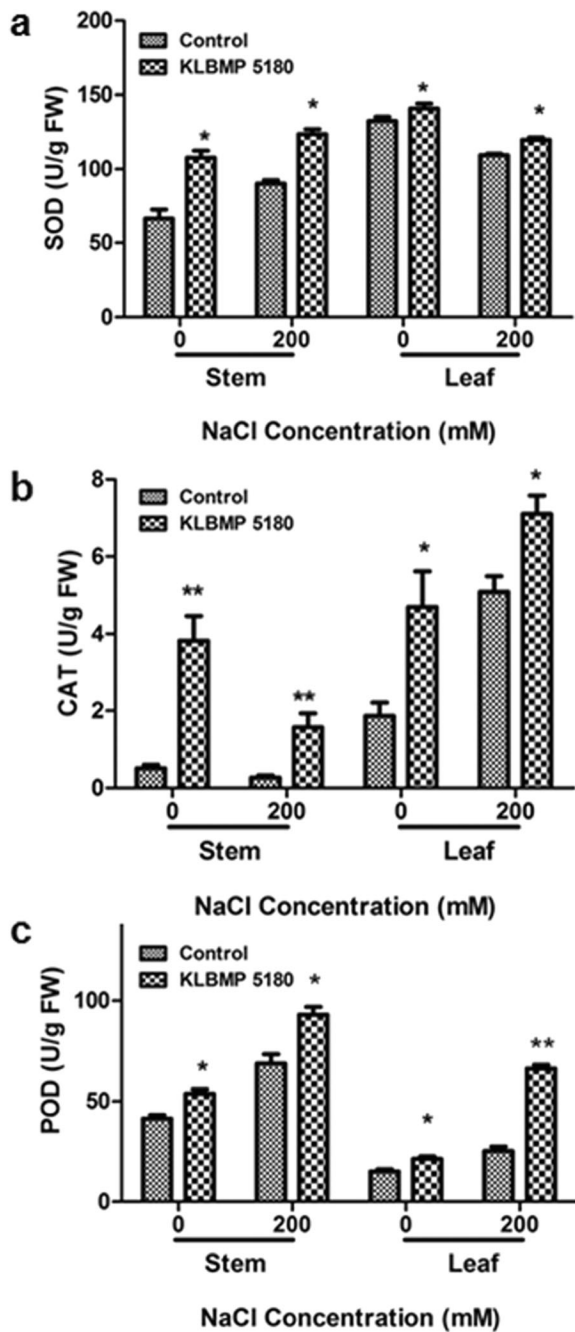


Fig. 3 Effect of *G. halophytocola* KLBMP 5180 strain inoculation on the seedling antioxidant defense enzymes content with and without the NaCl stress condition. a, SOD; b, CAT; and c, POD. One asterisk (*) and two asterisks (**) indicate $P < 0.05$ and $P < 0.01$ (t test), respectively, for treatment versus control

metal resistance genes that are resistant to arsenic, copper, tellurium, and cobalt-zinc-cadmium. We also found that this genome has various biodegradation genes that

are involved in phenylacetic acid, phenol, 4-hydroxybenzoate, and chitin degradation (Table 4).

Discussion

Salt stress is one of the main abiotic stress factors limiting crop yield worldwide (Rozema and Flowers 2008). Tomato is a favorite crop all over the world, but its growth is sensitive to salt stress. At present, using PGPR to alleviate the damage to plants caused by abiotic stress is gaining increased interest and has been considered as a promising alternative for agricultural growth. Several studies have already been conducted on PGP microorganisms and their effects on tomato plant growth under the condition of salt stress (Palaniyandi et al. 2014; Fan et al. 2016; Damodharan et al. 2018; Van Oosten et al. 2018). These strains are mainly from the genera *Streptomyces*, *Bacillus*, *Pseudomonas*, *Azotobacter*, and *Arthrobacter* and showed vital PGP traits, including IAA production, nitrogen fixation, and siderophore and ACC deaminase biosynthesis. The salt-tolerant actinomycete, *G. halophytocola* KLBMP 5180, which was previously found to have multiple PGP traits and tolerate 10% NaCl, significantly promoted the growth of halophyte *Limonium sinense* (Qin et al. 2018), meriting further exploration of its potential for PGP effects for crops under saline soil conditions. Our current study showed that this strain significantly promoted the growth of tomato seedlings under high salt stress and can colonize successfully the rhizosphere soil of non-host plant tomatoes with or without salt stress (Fig. 1), although the direct evidence still needs to be confirmed by scanning electron microscopy or the *GFP*-marked method.

The strain KLBMP 5180 is a new member of the genus *Glutamicibacter* (Feng et al. 2017), which was recently reclassified from the genus *Arthrobacter* (Busse 2016). Members of the genus *Arthrobacter* are widely distributed in different ecological environments and display many ecological functions, such as plant growth promotion, biodegradation, and bioremediation (Cycoń et al. 2017; Viegas et al. 2019). Previous studies have also found that strains of *Arthrobacter* spp. could promote plant growth under salt stress condition (Fan et al. 2016; Van Oosten et al. 2018). However, there are only a few reports on the study of the natural halotolerant endophyte-origin *Arthrobacter* spp. and their PGP effect under salt stress. Recent studies have shown that salt-

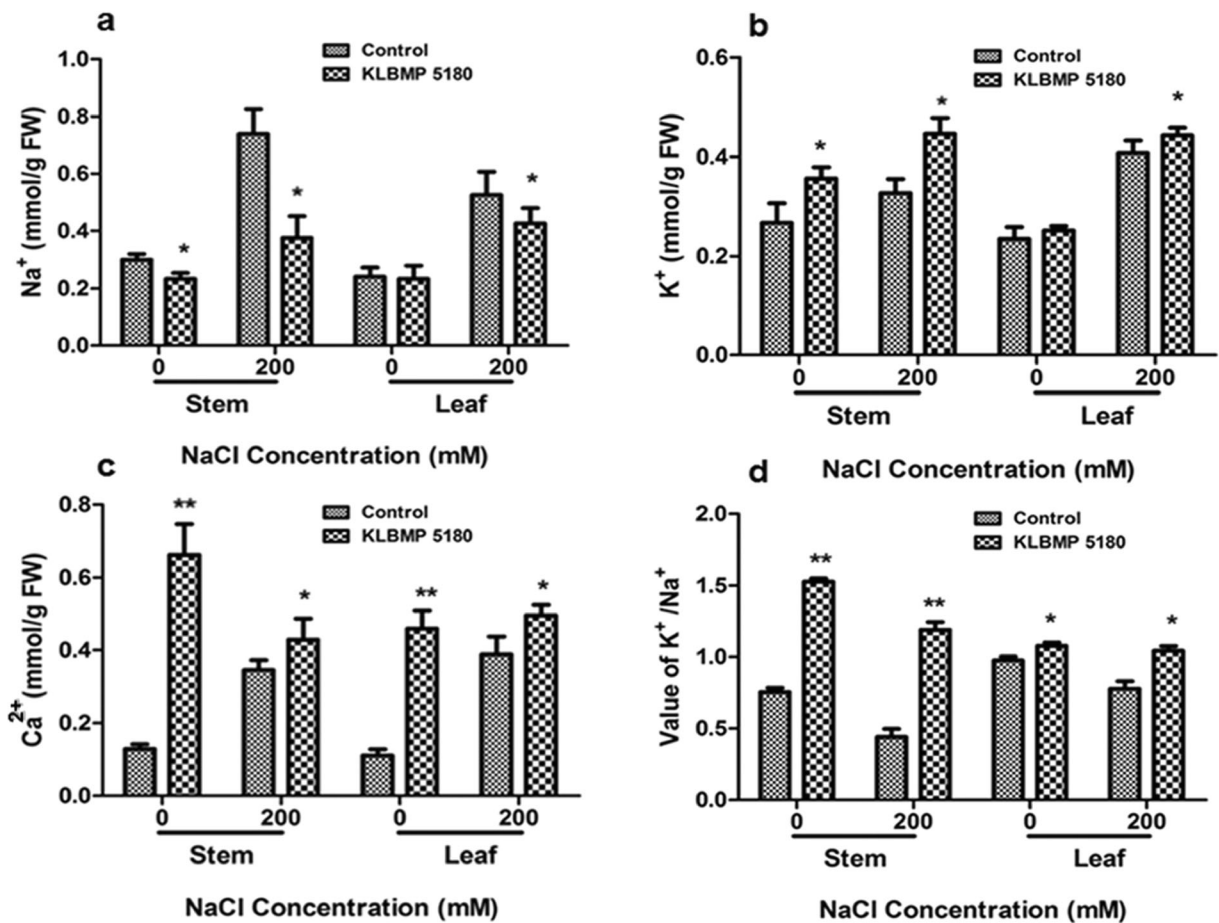


Fig. 4 Effect of *G. halophytocola* KLBMP 5180 strain inoculation on tomato seedling Na^+ , K^+ , and Ca^{2+} content and K^+/Na^+ ratio with and without the NaCl stress condition. a, Na^+ content; b, K^+ content; c, Ca^{2+} content; and d, K^+/Na^+ ratio. Values are

means, and bars indicate SEs. One asterisk (*) and two asterisks (**) indicate $P < 0.05$ and $P < 0.01$ (*t* test), respectively, for treatment versus control

tolerant PGPR strains are involved in conferring salinity tolerance in various crops (Sharma et al. 2016; Banik et al. 2018). Therefore, our experiments have proven the advantages and application potential of the halotolerant PGP bacteria in improving plant salt tolerance.

Proline acts as an osmoprotectant, which protects the plant cells from oxidative damage. The present study revealed that KLBMP 5180 inoculation enhanced the proline content of the leaves and stems. Reactive oxygen species (ROS) accumulation in NaCl-stressed plant cells leads to lipid peroxidation, which is estimated via the accumulation of MDA. Moreover, MDA content in stems was also decreased after KLBMP 5180 treatment, suggesting its ability to prevent soil NaCl-induced lipid peroxidation of cell membranes. Our results are in good agreement with previous studies (Akram et al. 2016; Pereira et al.

2016) in which maize and sunflower plants treated with PGPR show less accumulation of MDA and increased proline content under saline conditions. In this study, strain KLBMP 5180 inoculation significantly improved the POD, SOD, and CAT content in tomato seedlings under salinity stress (Fig. 3), which may thereby lead to low-level accumulation of ROS. This is in accordance with recent results in both *Enterobacter* sp. and *Streptomyces* KLBMP 5084 in which PGPR-inoculated plants exhibited higher antioxidant enzyme content (Qin et al. 2017; Sarkar et al. 2018). These results imply that *G. halophytocola* KLBMP 5180 could protect tomato seedlings and withstand salinity stress by regulating both osmoprotectants and ROS-scavenging enzyme accumulation.

Among the mechanisms used by PGPR, regulating ion balance and maintaining a high K^+/Na^+ ratio is considered as an important mechanism for eliminating

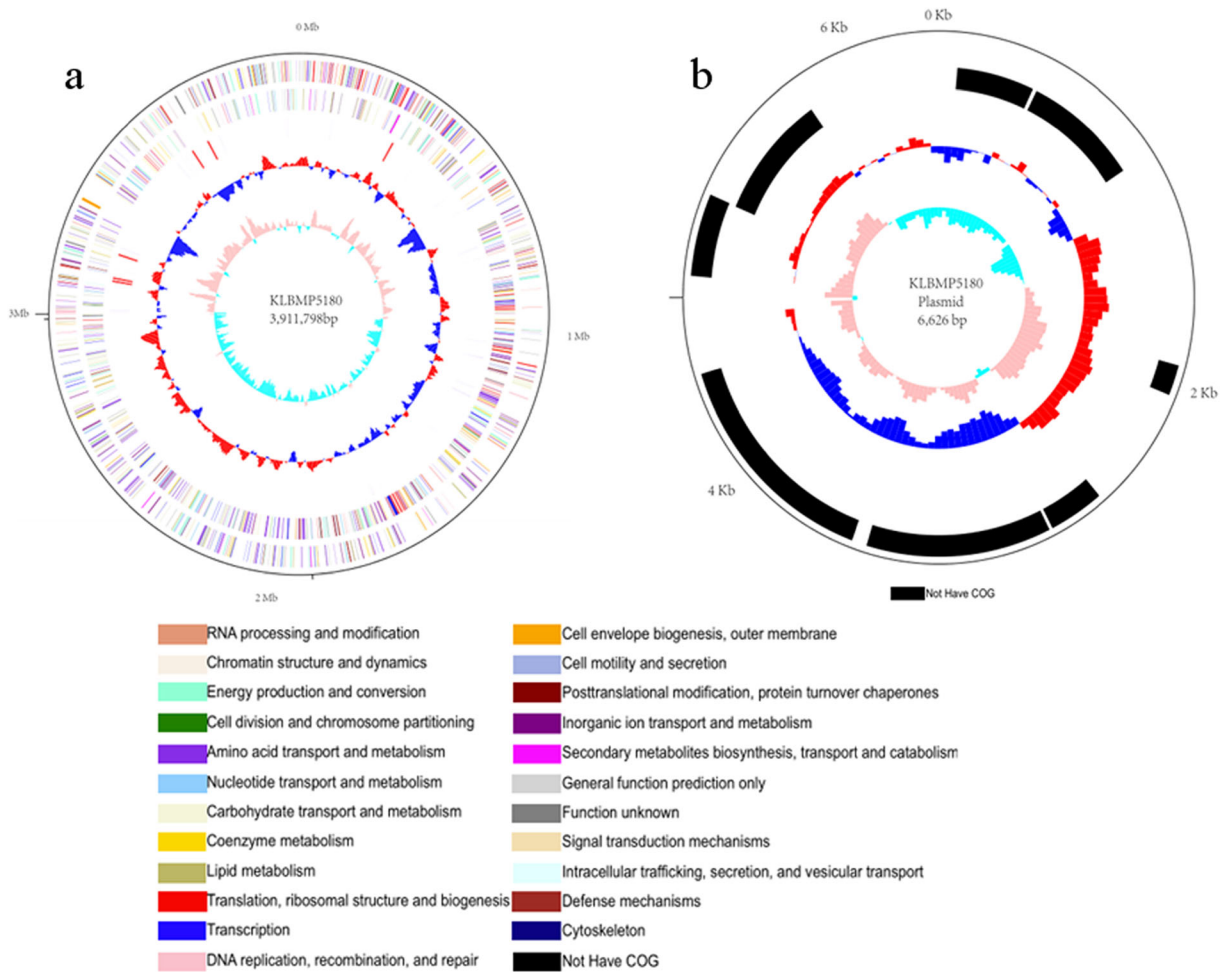


Fig. 5 Circular genome maps of the *G. halophytocola* KLBMP 5180 complete genome. **a** Genetic map of the circular chromosome; and **b** plasmid. From the outermost circle to the inner, each

circle contains information about rRNA/tRNA, reverse and forward CDS, and GC content and GC skew

salt stress toxicity and promoting plant growth (Munns and Tester 2008). In this study, the Na^+ concentration of

Table 2 General genomic features of strain *G. halophytocola* KLBMP 5180

Features	Chromosome	Plasmid
Genome size (bp)	3,911,798	6626
G + C content (%)	60.0	53.7
rRNAs	19	0
tRNAs	65	0
Other RNAs	3	0
Predicted CDSs	3624	8
Secondary metabolite gene clusters	5	0
GenBank accession	CP012750	CP012751

both leaves and stems of tomato seedlings increased with the rise in NaCl concentration. However, strain KLBMP-inoculated seedlings showed lower Na^+ concentration, increased K^+ uptake, and higher K^+/Na^+ ratio in both leaves and stems than non-inoculated seedlings under NaCl stress (Fig. 4). Our results are in accordance with recent studies that have reported that PGPR can promote various crops and plants growth and maintain lower Na^+ and Na^+/K^+ ratio to withstand salt toxicity (Ramadoss et al. 2013; Niu et al. 2016; Chen et al. 2016; Sharma et al. 2016). We also observed an increased Ca^{2+} accumulation after KLBMP 5180 inoculation as compared to the non-inoculated control under both the 0 and 200 mM NaCl treatments. As a secondary messenger signaling molecule, Ca^{2+} plays an important regulatory role in plant salt stress response. Maintenance of high

Table 3 Gene clusters of secondary metabolites of *G. halophytocola* KLBMP 5180 predicted by antiSMASH 4.0

Cluster ID	Cluster type	Similar known cluster	Ratio of genes show similarity (%)
1	Siderophore	Desferrioxamine (other)	75
2	NRPS-like	Streptomycin (saccharide)	14
3	Betalactone	Salinosporamide (nrps-polyketide)	6
4	Terpene	Carotenoid (terpene)	28
5	Betalactone	–	–

Note: –, no similar cluster predicted

Ca²⁺ accumulation can improve plant resistance to salt stress (Yang et al. 2016). The present study indicated that the PGP strain KLBMP 5180 might regulate tomato seedlings to selectively take up and transport Ca²⁺ to maintain a high Ca²⁺/Na⁺ ratio. However, detailed physiological and molecular mechanisms of salt tolerance mediated by this strain need to be further explored.

The developments of -omics techniques enable us to better understand the plant growth promotion and the environmental adaptation mechanisms of PGPR at the molecular level (Qin et al. 2016). Genome sequencing and analysis revealed that strain KLBMP 5180 harbors a series of genes related to plant growth promotion and salt stress tolerance. A single nitrogen fixation-related gene (*nifU*) was detected in the genome. However, there is no complete nitrogen fixation gene cluster in the KLBMP 5180 genome. The real nitrogen fixation capacity of this strain still needs to be confirmed by acetylene reduction tests. Strain KLBMP 5180 genome contains IAA, siderophores, and spermidine biosynthesis genes (Table 4). These genes have been demonstrated to be involved in the PGP effects of PGPR (Afzal et al. 2014; Wang et al. 2017). Recent studies have shown that the endophyte *Klebsiella* sp. LTGPAF-6F and the rhizobacterium *Bacillus amyloliquefaciens* SQR9 have the spermidine synthesis genes and induced growth, drought, and salt tolerance in wheat and *Arabidopsis* seedlings (Zhang et al. 2017; Chen et al. 2017). Therefore, whether strain KLBMP 5180 can improve the salt tolerance of tomato seedlings by secreting spermidine needs further detection. It is noteworthy to mention that in this strain, we have found complete gene clusters of EPS biosynthesis, including genes for NDP-sugars synthesis, assembly, modification, and transportation of the entire EPS synthesis process (Table 5). It has been demonstrated that bacterial EPS can help bacteria to resist

abiotic stresses, absorb sodium ions, resist ROS stress, promote plant growth, resist salt and drought stress (Liu et al. 2017; Lu et al. 2018), and contribute to PGPR root colonization (Santaella et al. 2008). For example, Meneses et al. (2017) reported that *Gluconacetobacter diazotrophicus* EPS protects bacterial cells against oxidative stress in vitro and during rice plant colonization. Our recent study also demonstrated that strain KLBMP 5180 secretes EPS (data not shown). Thus, in the present study, this positive effect may be correlated with the ability of *G. halophytocola* KLBMP 5180 to exhibit multiple PGP traits, which we speculate to be mainly due to EPS production.

The *G. halophytocola* KLBMP 5180 genome also has a series of genes involved in salinity resistance, including Na⁺/H⁺ antiporters, K⁺ transporter, and glycine-betaine synthesis and transporter encoding genes. These transporters act as regulating the outflow and uptake of protons and Na⁺/K⁺, maintaining intracellular ion balance, and therefore support the growth of bacteria under salt stress. These genes were also detected in recently described halotolerant PGPR strains (Liu et al. 2016; Wang et al. 2017). Moreover, some genes resistant to heavy metals were also detected. The presence of these genes reveals the diverse environmental adaptation capacity and mechanism of strain KLBMP 5180 and indicates that the strain has the potential in bioremediation of sites that have heavy metal contamination. Interestingly, some genes that encode the biodegradation process, such as phenylacetic acid, 4-hydroxyphenylacetate, and phenol degradation-related genes, were also present in the genome, indicating its biodegradation potential of organic pollutants. Therefore, combined with the PGP ability, this strain could be potentially used for phytoremediation and help sustainable development in agriculture as well as environmental

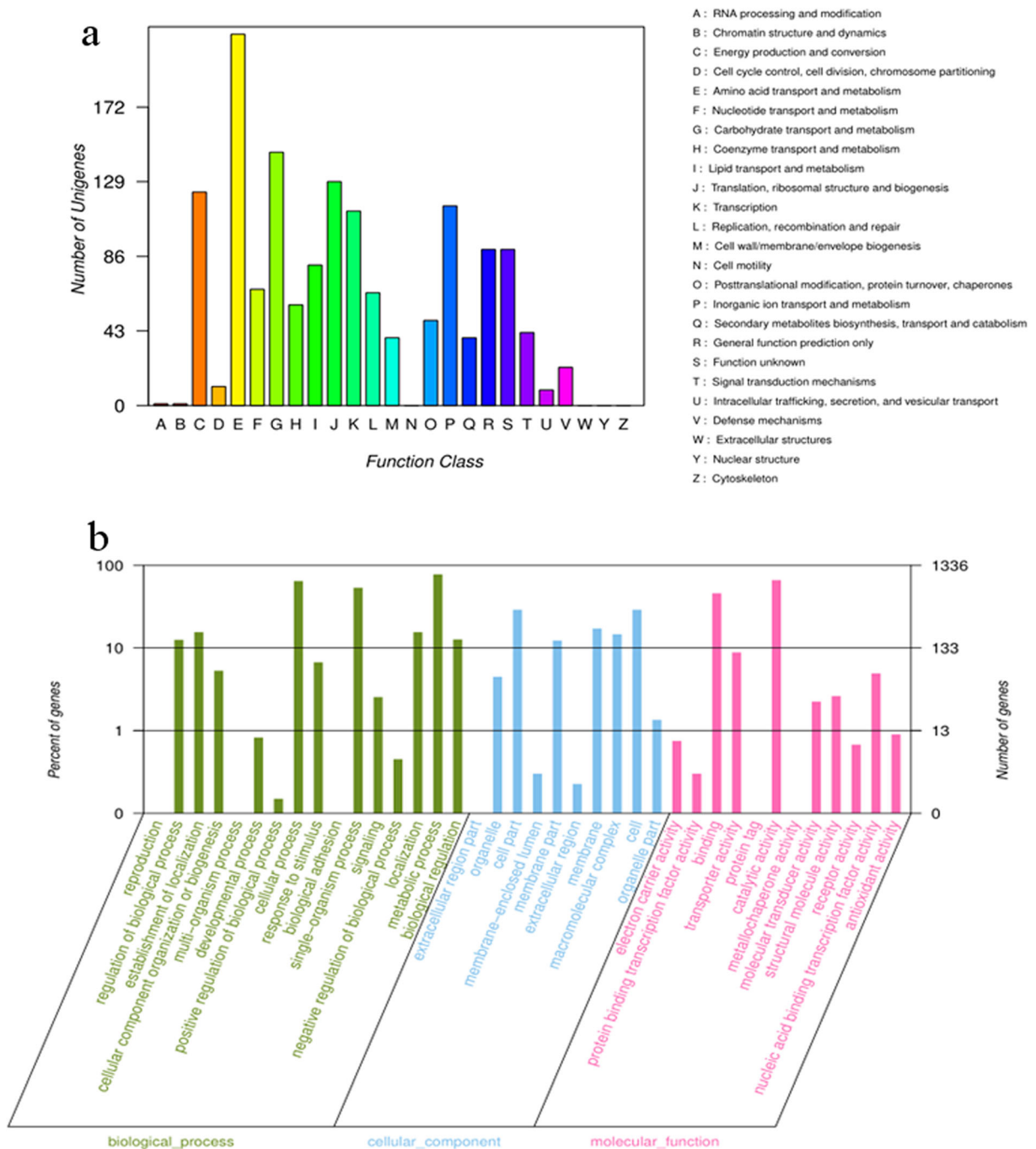


Fig. 6 Functional annotation of the *G. halophytocola* KLBMP 5180 strain genome against the COG (a) and GO database (b)

protection. In summary, the genomic information provides useful clues to explain the plant growth-promoting ability and environmental adaptability of the actinobacterium, and reveals some potential new functions, which is worthy of further exploration and research.

Conclusions

In conclusion, the PGP effect of a natural halotolerant actinobacterium *G. halophytocola* KLBMP 5180 was explored in tomato seedlings under the high salt stress condition. Current studies have proven that this strain

Table 4 Main genes related to plant growth promotion, salt tolerance, and environmental adaptation in the *G. halophytocola* KLBMP 5180 genome

KLBMP 5180 ORF	KEGG gene names	Gene annotation
Plant growth promotion		
orf00910_1	<i>nifU</i>	Nitrogen fixation protein
orf00160_1	<i>iaaM</i>	Tryptophan 2-monooxygenase
orf01050_1	–	Siderophore biosynthesis protein
orf03370_1	<i>sbnA</i>	Probable siderophore biosynthesis protein SbnA
orf01446_1	–	Siderophore synthetase
orf02828_1	<i>yusV</i>	Siderophore ABC transport system ATP-binding protein
orf02577_1	<i>fevA</i>	Siderophore ABC transporter substrate-binding protein
orf02839_1	<i>phzC/PhzF</i>	Phenazine biosynthesis protein
orf01146_1	<i>phzF</i>	Phenazine biosynthesis protein
orf01301_1	<i>phzF</i>	Phenazine biosynthesis protein
orf01959_1	<i>gabP</i>	GABA permease
orf02608_1	<i>gabT</i>	4-aminobutyrate aminotransferase
orf00712_1, orf00305_1	<i>speB</i>	Agmatinase
orf00190_1	–	Spermidine synthase
orf03602_1	<i>cobW</i>	Cobalamin biosynthesis protein CobW
Salt tolerance		
orf00911_1	<i>nhaA</i>	Na ⁺ /H ⁺ antiporter
orf02751_1	<i>mrpA</i>	K ⁺ /H ⁺ antiporter subunit A/B
orf02750_1	<i>mrpC</i>	Na ⁺ /H ⁺ antiporter subunit C
orf02749_1	<i>mrpD</i>	Na ⁺ /H ⁺ antiporter subunit D
orf02748_1	<i>mrpE</i>	Cation/proton antiporter
orf02747_1	<i>mrpF</i>	Cation/proton antiporter
orf02305_1	<i>mrp</i>	Sodium: proton antiporter ATP-binding protein Mrp
orf02746_1	<i>mrpG</i>	K ⁺ efflux system protein
orf02055_1, orf02160_1, orf02161_1,	<i>trkA</i>	K ⁺ transporter
orf02670_1	<i>trkB</i>	K ⁺ transporter
orf03234_1	<i>betA</i>	Choline dehydrogenase
orf00836_1	<i>betB</i>	Betaine-aldehyde dehydrogenase
orf00356_1, orf03439_1	<i>betP</i>	Glycine betaine transporter
orf03145_1	<i>opuD</i>	Glycine betaine transporter
orf01636_1	<i>proV</i>	Glycine betaine/L-proline ABC transporter
Biodegradation		
orf02646_1	<i>paaN</i>	Phenylacetic acid degradation protein
orf02640_1	<i>paaD</i>	Phenylacetic acid degradation protein
orf02630_1	<i>paaE</i>	Phenylacetic acid degradation protein
orf02458_1	–	4-hydroxyphenylacetate degradation bifunctional isomerase/ decarboxylase
orf03217_1	E1.14.13.7	Phenol 2-monooxygenase
orf00491_1	<i>pobA</i>	4-hydroxybenzoate 3-monooxygenase
orf03480_1	E3.5.1.-	Chitin deacetylase
Heavy metal resistance		
orf01772_1	–	Arsenic resistance protein
orf03413_1	<i>arsB</i>	Arsenite resistance protein
orf02767_1	<i>copD</i>	Copper resistance protein
orf02770_1	<i>pcoC</i>	Copper resistance protein C
rf00727_1	<i>czcD</i>	Cobalt-zinc-cadmium resistance protein
orf02081_1, orf02720_1	<i>terC</i>	Tellurium resistance protein

Table 5 Predicted genes involved in EPS biosynthesis from the *G. halophytocola* KLBMP 5180 genome

Steps of EPS biosynthesis	ORF and gene names	Gene annotation
Biosynthesis of NDP-sugars	orf01558_1, <i>galF</i>	UTP-glucose-1-phosphate uridylyltransferase
	orf03692_1, <i>galT</i>	Galactose-1-phosphate uridylyltransferase (EC 2.7.7.12)
	orf01519_1, <i>glf</i>	UDP-galactopyranose mutase
	orf02216_1, <i>murG</i>	UDP-N-acetylglucosamine transferase
	orf03690_1, <i>galE</i>	UDP-glucose 4-epimerase
	orf00834_1, <i>manC</i>	Mannose-1-phosphate guanylyltransferase
Assembly on lipid-acceptor	orf01792_1, <i>uppS</i>	Undecaprenyl pyrophosphate synthase
	orf01743_1, <i>bacA</i>	Undecaprenyl-diphosphatase
di-trans,octa-cis--undecaprenyl diphosphate	orf01054_1	Mannosyltransferase
di-trans,octa-cis--undecaprenyl phosphate Glycosyltransferases	orf00010_1, <i>mgtA</i> ; orf01518_1; orf01585_1, <i>gumL</i> ; orf00883_1	Glycosyltransferase
	orf01057_1	Glycosyltransferase family 1
	orf01763_1, <i>dpm1</i> ; orf03747_1, orf03386_1	Glycosyltransferase family 2
	orf03325_1, <i>qrfT</i>	Glycosyl transferase family 9
Modification	orf02820_1	Carbohydrate esterase, carboxylesterase
	orf02300_1	Carbohydrate esterase, metal-dependent phosphoesterase
	orf01919_1; orf03193_1; orf03722_1	Carbohydrate esterase, thioesterase
	orf02091_1; orf00734_1	Polysaccharide deacetylase
Transport of EPS	orf03696_1	ABC transporter, permease protein
	orf02951_1; orf02834_1	ABC transporter, ATP binding protein
	orf03695_1	ABC transporter, sugar binding protein
	orf03084_1; orf00584_1	GAF domain/GGDEF domain protein
	orf03365_1; orf02944_1; orf01445_1; orf00751_1; orf02244_1; orf03152_1; orf03345_1; orf01621_1	ABC transporter, lipoprotein

can also successfully colonize in the rhizosphere of non-host tomato plants and significantly enhance its growth under salinity stress. Therefore, this PGP strain has the potential for subsequent development as a new type of biofertilizer. Furthermore, we revealed that the strain could improve the salt tolerance of tomato seedlings

by regulating plant osmoprotectants and antioxidant enzymes accumulation, and ion balance and ultimately promote its growth under salt stress. Genome analysis also revealed the molecular mechanism of the strain's PGP and salt-alkaline tolerance capacity. In addition, unsolved problems remain, such as the potential PGP

capacity evaluation of the actinobacterium in the field condition, its phytoremediation of heavy metals and biodegradation of environmental organic pollutants, as well as whether the exopolysaccharide secreted by this strain is helpful to its rhizosphere colonization, recruitment, and salt stress adaptation is worthy of further study and experimental verification.

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Compliance with ethical standards

Conflict of interest None.

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