Improvement of salt tolerance of Arabidopsis thaliana seedlings inoculated with endophytic Bacillus cereus KP120

Yaran Zhang1*, Zengyuan Tian2*, Yu Xi1, Xiaomin Wang1, Shuai Chen1, Mengting He2, Yange Chen2 and Yuqi Guo1*

1School of Life Sciences, Zhengzhou University, Zhengzhou, People’s Republic of China; 2School of Agricultural Sciences, Zhengzhou University, Zhengzhou, People’s Republic of China

ABSTRACT
In our previous reports, an endophytic bacterium, Bacillus cereus KP120 was isolated from the halophyte species Kosteletzkya virginica. In this study, the effect of KP120 colonization on Arabidopsis thaliana seedlings was investigated. Our results showed that inoculation with KP120 could promote the growth of A. thaliana seedlings plants under salt-stress conditions, compared with uninoculated controls. After salt treatment, chlorophyll, proline, the activity of antioxidant enzymes, indole-3-acetic acid and 1-aminocyclopropane-1-carboxylate-deaminase in plants inoculated were increased significantly but malondialdehyde content was decreased compared with the plants under salt stress lonely. Similarly, under non-salt stress, physiological indices above except for MDA in plants inoculated with KP120 were increased compared with control. B. cereus also induced the up-regulation of key genes involved in IAA biosynthesis, responses, transport, down-regulated expression of genes related with ethylene synthesis and response. Our work principally demonstrates that Bacillus cereus KP120 significantly enhances plant growth and increases plant tolerance to salt stress.

Introduction
In modern agricultural production, soil salinization is a compelling worldwide environmental problem (Yang et al. 2020) that inhibits plant growth and development (Sharameti et al. 2008), and decreases the yield of crops, including maize, wheat, cotton, soybean, rice, and more (Baek et al. 2020; Fan 2020). Furthermore, salt stress may damage plant physiological processes such asphotosynthesis, protein synthesis, and energy metabolism (Song et al. 2016) because of over-accumulation of ROS, osmotic stress, water deficits, and membrane degeneration (Abdel Latef et al. 2019). Therefore, it is necessary to alleviate the adverse effect of salinity stress by different strategies.

Often, genetic modification can be used to improve plant tolerance. However, this approach is time-consuming and costly (Dong et al. 2019). The utilization of plant growth-promoting bacteria (PGPB) is to mitigate severe salt stress in a cost-effective and environmentally friendly approach (Qin et al. 2016). Beneficial microorganisms can colonize and proliferate in the host plant tissues and protect plants from salt stress through various direct and indirect mechanisms (Jaemsaeng et al. 2018; Singh et al. 2019; Yao et al. 2010). Salt stress, manifesting in water uptake reduction via osmotic stress, triggers a range of metabolic and molecular cascades such as inhibition of photosynthetic activity, indole-3-acetic acid (IAA)-mediated responses followed by stimulation of SOD, POD and CAT activities, incensement of membrane permeability, and accumulation of osmolytes like proline. PGPB has been also shown to alleviate salt stress in plants by producing different bioactive secondary metabolites, i.e. volatile organic compounds (VOCs) (Khan et al. 2012), and increasing the activity of antioxidant enzymes, including peroxidase and catalase, that counteract stress-induced reactive oxygen (Bacon and White 2016).

PGPB has been found to alleviate the adverse effect of salinity stress in plants such as Piriformospora indica (Mohd et al. 2017), Bacillus flexus (Xiong et al. 2020), Aspergillus terreus (Khushdhil et al. 2019), Streptomyces sp. (Jaemsaeng et al. 2018) and Pseudomonas putida (Kumar et al. 2020). PGPB enhances salt stress tolerance by modulating the levels of phytohormones (e.g. IAA, gibberellins, ethylene), or by maintaining K+/Na+ balance (Abhinandan et al. 2018; Khan et al. 2012). In addition to plant growth-promoting bacteria, endophytic fungi in ryegrass has been reported to significantly increase phenol content and antioxidant enzyme activity (Qawasmeh et al. 2012), which counteracts plant growth and development repression by reactive oxygen species (ROS) (Khan et al. 2020; Zheng et al. 2016). Exopolysaccharides (EPS) are mainly secreted by microorganisms during growth and metabolism and released into the surrounding environment. Some studies have shown that the production of EPS in bacteria is one of the strategies used by plants to survive under stress conditions (Kumari and Khanna 2015), by increasing microbial ability to attach to plant rhizospheres, and improving nutrient utilization and water absorption through biofilm formation on the root surface. For example, Sun Liang found that EPS producing bacteria Pantoea alhagi NX-11 could promote rice growth and reduce the toxic effect of salt stress, compared with the EPS-deficient strain NX-11eps− (Sun et al. 2020). The
protective mechanism was believed to relate to the high molecular weight of EPS helping maintain high moisture content in the rhizosphere. As an acidic polysaccharides with negative charges, EPS has strong adsorption capacities for metallic cations such as Na⁺ and Mn²⁺ (Sun et al. 2020).

Plant hormones can alleviate plant damage caused by high salinity to some extent. Plant cell growth, development, division, and nutrient absorption are all related to plant hormones. High salinity limits the synthesis of auxin (Cackett et al. 2022). Furthermore, the synthesis, transport, metabolism, and activity regulation of plant auxin were affected under abiotic stress (Mateo-Bonmati et al. 2021). Auxin (IAA) is widely distributed in higher plants and plays a key role in physiological processes such as cell growth, cell division, and embryonic development. The YUC gene family catalyzes the process of indole-3-pyruvate (IPA) producing auxin and regulates the synthesis of IAA. PIN is an important carrier element to regulate the polar transport of auxin, which is closely related to the growth and development of plants. Auxin regulates plant growth by inducing a series of responsive genes, among which SAUR (Small Auxin-up RNA) is one of the early corresponding genes of auxin (Hagen and Guilfoyle 2002) involved in the regulation of various biological processes (Li et al. 2017).

Some plant rhizosphere-promoting bacteria (PGPB) use 1-aminoacyclopropane-1-carboxylate (ACC) as the source to synthesize ACC deaminase, which can reduce the ethylene concentrations of plants and stimulate plant growth. Bacillus cereus can secrete ACC deaminase, which can significantly promote the growth of plants (Jaemsang et al. 2018; Singh et al. 2020) such as tomatoes, cucumbers, wheat, beans, and other crops. Ethylene is synthesized from methionine by catalysis mediated by S-adenosyl-L-methionine synthase, 1-aminoacyclopropane-1-carboxylic acid synthase (ACS), and 1-aminoacyclopropane-1-carboxylic acid oxidase (ACO) (Liu et al. 2019). ACO and ACS are the rate-limiting enzymes that regulate ethylene biosynthesis, and several regulators influence ethylene production by changing the activities and gene expression levels of ACS and ACO. Ethylene response factors (ERFs) participate in abiotic and biotic stress responses and play key roles in various stresses, especially salt stress (Han et al. 2020). Similarly, EILs have a conserved binding sequence of plant-specific transcription factors in the downstream gene promoter involved in ethylene response (Liu et al. 2019).

In previous studies, we have isolated and identified an endophytic bacterium, B. cereus KP120, from the salt-tolerant Kosteletzkya pentacarpos (Han et al. 2015). In the present study, we aim to investigate whether the PGPB B. cereus KP120 can alleviate the adverse effects of salt stress on the growth of Arabidopsis thaliana plants. Physiological indices including chlorophyll, proline, EPS content, and plant growth and development under salt stress were investigated. Additionally, IAA content in A. thaliana seedlings was examined, and the expression of SAUR family genes and key genes in auxin synthesis (YUCCA) and transport (PIN) were analyzed. Similarly, the content of ACC deaminase, the expression of some genes involved in the degradation of precursors in ethylene synthesis (ACO, ACS) and in ethylene signal response pathways (ERF and EIL) were analyzed. Our results help elucidate the molecular basis of growth in plants inoculated with B. cereus KP120.

Material and methods

Cultivation of Bacillus cereus KP120

Bacillus cereus KP120, isolated and identified from the salt-tolerant Kosteletzkya pentacarpos, was used in the present study (Han et al. 2015). Bacterial strains were grown in 50 mL LB medium at 37 °C for 12 h.

Plant materials and growth conditions

The Arabidopsis thaliana used in this study was a wild type of Columbia stored in our laboratory. Arabidopsis thaliana seeds were surface-sterilized with 75% ethanol for 1 min, followed by NaClO (5%) for 10 min, and then washed at least 5–10 times with sterilized water (Woo et al. 2020). The seeds were placed on Murashige and Skoog (MS) agar medium (pH 5.8–6.0) for 7 days at 28°C. The seedlings were moved into soil for further assessment (Egamberdieva et al. 2017).

Treatment with B. cereus KP120 and NaCl

Seven-day-old Arabidopsis plants were initially treated with either sterile water or strain KP120, then used for further treatment with salt stresses. For salt stress, from 7 days after inoculation with the bacteria, each plant in a pot was treated with 250 mM NaCl solution or sterile water. After 1 week of growth, the Arabidopsis seedlings were randomly divided into four groups: non-inoculated control group (CK); group treated with 250 mM NaCl solution (Salt); inoculated with B. cereus KP120 (BC); and group treated with 250 mM NaCl solution, then inoculated with B. cereus KP120 (BCS).

Measurement of chlorophyll, proline and malondialdehyde content

Chlorophyll content in leaves of control and Bacillus cereus-treated Arabidopsis was quantified according to the method of Moran et al (Moran 1982). The proline contents of Arabidopsis seedlings were determined according to the method described by Jaemsang et al (Jaemsang et al. 2018). Leaf malondialdehyde (MDA) content was estimated by the method of thiobarbituric (TBA) (Diao et al. 2015).

Measurement of antioxidant enzyme and ACC deaminase activity

To quantify protective enzyme activity, fresh roots and leaves samples (0.5 g) were immediately pulverized with liquid nitrogen. The samples were added to 50 μM potassium phosphate buffer, and then were centrifuged for 20 min at 12,000 g (4 °C). Afterwards, the supernatant was collected as a crude enzyme extract.

The method in (Donahue et al. 1997) was carried out to determine the SOD activity by Nitroblue tetrazolium photochemical reduction method at 560 nm. Catalase activity (CAT) was quantified by determining the disintegration of hydrogen peroxide at 240 nm as described in (He et al. 2014). The ascorbate peroxidase (APX) activity was calculated by the decline in optical density at 240 nm according to the method of He et al. (2014). The activity of peroxidase
(POD) was analyzed by the guaiacol method (Fujita et al. 1995). The optical density at 240 nm was used to estimate the activity.

The method of Penrose and Glick – 2, 4-Dinitrophenylhydrazine Colorimetry was applied to measure the activity of ACC deaminase (Penrose and Glick 2003). That is, the quantification of ACC deaminase production was estimated through the amount of α-ketobutyrate released as a result of the hydrolysis of ACC by ACC deaminase.

**Secretion of indole acetic acid (IAA) in strain KP120 and measurement of IAA in leaves and root**

IAA production was assessed according to Gordon and Weber (Saleem et al. 2021). B. cereus KP120 was inoculated into 50 ml LB medium supplemented with tryptophan and incubated at 37°C at 150 rpm on a rotary shaker for 12 h. 100 μL of bacterium suspension was added into a tube supplemented with 100 μL of Salkowski’s reagents followed by incubation at room temperature for 15 min to have color reaction. Color change from pale yellow to pinkish red was the indication of IAA production. The amount of IAA produced by the B. cereus KP120 was calculated using a standard curve of commercial IAA at 530 nm in spectrophotometer UV-1800PC.

IAA content in Arabidopsis seedlings was measured via the ELISA kit. IAA was extracted according to a modification of the method of Ertani et al. (2019).

**Extraction and measurement of EPS in Bacillus cereus KP120**

The isolated strain Bacillus cereus KP120 was inoculated in the fermentation medium at 37 °C in an orbital shaker at 180 rpm. After a 40 h incubation period, the culture medium was boiled 4 times for 30 min each time. After ultrasonic extraction for 30 min, the medium was centrifuged at 1800g for 20 min at 4 °C. The supernatant was evaporated on a rotary evaporator and then added three volumes of 95% ethanol overnight at 4 °C. The precipitated EPS was collected by centrifugation at 1800g for 20 min at 4 °C. The precipitate was dissolved in 800 μL distilled water, and the phenol-sulphuric acid method was used for determining the content of the exopolysaccharide (Adesulu-Dahunsi et al. 2018).

**RNA isolation and RT-qPCR analysis**

Total RNA was isolated from Arabidopsis plants using HiFi-MMLV cDNA kit CW0744s according to the manufacturer’s instructions. Reverse transcriptase quantitative PCR was performed using an Ultra SYBR Mixture (LOW ROX) CW2601M). RT-qPCR analyses were performed using Rotor-Gene (RG-3000). The data were normalized to an internal control gene, AT-actin. The primer sequence information for analysis is shown in Table S1.

**Statistical analysis**

The obtained data were statistically analyzed by ANOVA method and turkey test with Graphpad Prism 8. All statistical experiments were performed for three biological replicates. The data were presented as the mean values ± S.E.

**Results**

**Effect of Bacillus cereus KP120 on A. thaliana growth under salt stress**

During the salt stress condition, the treated plants shriveled and displayed chlorosis in leaves compared with those grown under normal conditions. However, the application of the endophytic KP120 improved the growth of A. thaliana under both normal and salt-stress conditions (Figure 1). In normal conditions (without NaCl), the root length, plant height, leaf number, and branch number of seedlings inoculated with strain KP120 increased by 8.86%, 9.75%, 12.50%, and 75.18%, respectively, compared with the control group. Under salt-stress conditions, root lengths, plant height, leaf number, and branch number of seedlings inoculated with KP120 increased significantly by 14.40%, 182.24%, 14.28%, and 53.84% compared with the control seedlings (Figure 2c–f).

Colonization of B. cereus KP120 (+KP120) increased significantly fresh and dry weight of shoot under normal (control) and salt stress (salt) condition. Inoculated plants had obvious enhancements in total fresh and dry mass, which was 1.5–2.2 times and 2.5–2.8 times that of uninoculated plants without NaCl, respectively. Under salt-stress treatment, after application of strain KP120, all growth parameters of A. thaliana were increased (Figure 2a–d).

**Bacillus cereus KP120 enhanced proline and chlorophyll, while decreased MDA under salt stress**

The chlorophyll content in salt stress conditions was lower than that in control conditions. However, the chlorophyll content of A. thaliana inoculated with strain KP120 increased by 23.14% and 30.48% compared with that of non-inoculated under non-salt conditions and salt-stress conditions, respectively (Figure 3a). These results indicate that KP120 enhanced plant tolerance to salt stress by means of chlorophyll accumulation.

A slight increase in proline content was observed in the plants inoculated with KP120 under non-salt stress or salt stress treatment in leaves and significantly increase in roots under salt treatment. The proline content in A. thaliana leaves and roots were increased by 1.3-fold and 2.0-fold in inoculated plants when compared with non-inoculated plants, respectively (Figure 3b). Taken together, these results indicate that KP120 improved salt tolerance by increasing proline content.

There was no obvious difference in malondialdehyde (MDA) content under normal conditions with strain KP120 treatment compared with that inoculated with KP120. Compared with control, MDA content was significantly increased by about 3.63-fold (leaves) and 2.27-fold (roots) in salt conditions, respectively. However, the MDA content decreased notably by 76.66% in leaves, and 53.87% in roots in the plants inoculated with strains KP120 under salt-stress conditions (Figure 3c). These results indicate that strains KP120 improved salt tolerance by membrane oxidative damage under salt-stress conditions.

**Enhancement of the antioxidant enzyme activities in inoculated plant**

Previous studies suggested that antioxidant enzyme activities have a positive effect on B. cereus-induced abiotic stress...
resistance (Fan et al. 2020). Our results clearly showed that the SOD and POD activities in the roots and leaves of colonized plants were higher than the activities of all other treatments (including only salt, no salt, no strain KP120) under salt-stress conditions (Figure 4a and b). A similar result was observed for the CAT and APX activity (Figure 4c and d). Enzyme activity of SOD, POD, CAT, and APX increased by about 26.92%, 46.36%, 11.81%, and 76.85% in the roots of salt-treated plant, respectively, after \textit{B. cereus} KP120 colonization. Therefore, these results indicate that KP120 promoted plant tolerance to salt stress through the accumulation of antioxidant enzymes.

\textbf{IAA production of \textit{Bacillus cereus} and increases in IAA content of \textit{Arabidopsis thaliana} inoculated with KP120 under salt stress}

The concentration of IAA was about $0.98 \times 10^{-13}$ µg/mL, suggesting that \textit{B. cereus} KP120 has certain ability for IAA secretion. The concentration of IAA in both leaves and roots was lower in the salinity treatment compared with control treatment (Figure 5a). On the other hand, IAA concentration significantly increased by 8.41% (leaves) and 35.83% (roots) in plants treated with KP120, compared with non-inoculated plants under salt stress conditions. Similarly,
under normal conditions, the application of strain KP120 induced higher IAA concentration in *A. thaliana* plants compared with non-inoculated plants.

**Bacillus cereus** **KP120 to reduced ACC content in Arabidopsis thaliana under salt stress**

As shown in Figure 6(a), there was a significant positive correlation between the level of α-ketobutyrate and the activity of ACC deaminase in *Arabidopsis* seedlings under control and salt stress conditions. In stress conditions, the concentration of α-ketobutyrate decreased by 6.27% and 19.59% in *A. thaliana* leaves and roots, respectively, compared with the unstressed conditions (Figure 5b). This shows that the plant produced more ethylene precursor substance ACC, resulting in an increase in ethylene content under salt stress conditions. Compared with controls, the ACC content of plants inoculated with *B. cereus* KP120 was reduced. In particular, the amount of α-ketobutyrate increased by 17.52% in the roots of plants inoculated with strains KP120 under salt stress conditions (Figure 5b). Overall, these results suggest that strains KP120 reduced ethylene precursor ACC content, thus decreasing ethylene concentrations.

**The production of EPS by cultured Bacillus cereus KP120 strain**

Because the composition of the medium plays an important role in the yield of EPS in *B. cereus* KP120, the components of culture medium (C and N sources and inorganic salts) were optimized. With the optimal medium, the accumulation of EPS reached 37.80 mg/L in the fermentation broth, which was 3.9-fold higher than the initial yield of 9.64 mg/L. These results suggest that *B. cereus* KP120 can produce EPS.

**Effect of B. cereus KP120 colonization in seedlings under salt stress on the expression of genes involved in IAA and ethylene signal pathway**

Under different conditions, the expression levels of some genes in the SAUR gene family of *Arabidopsis thaliana* change significantly. To further study the expression changes of SAUR gene family members in *Arabidopsis thaliana* after inoculation with *B. cereus* KP120 under saline conditions, the relative expression levels of the measured genes were normalized and analyzed. Fifty members of SAUR gene family in *Arabidopsis thaliana* can be detected in roots and leaves. As shown in Figure 6a, the expression of SAUR04, SAUR14, SAUR15, SAUR49, SAUR51, SAUR54, SAUR60, SAUR69, SAUR72, and SAUR79 were significantly down-regulated in leaves and roots under saline conditions (Figure 6a), while the genes were up-regulated after colonization with *B. cereus* KP120. In addition, after inoculation with *B. cereus* KP120 under normal conditions, the expression of SAUR12, SAUR49, SAUR62, SAUR69, SAUR71, SAUR78, and SAUR79 were significantly up-regulated in the *Arabidopsis* seedlings. After inoculation with *B. cereus* KP120, the expression of SAUR04, SAUR09, SAUR14, SAUR15, SAUR23, SAUR27, SAUR29, SAUR31, SAUR32, SAUR42, SAUR45, SAUR51, SAUR53, SAUR54, SAUR60, SAUR65, SAUR76, and SAUR72 were significantly up-regulated in the *Arabidopsis* seedlings under salt stress conditions. In summary, after inoculation with *B. cereus* KP120 under saline conditions, the expression profiles of many members of the SAUR gene family in *Arabidopsis thaliana* change significantly (Figure 6a).

The YUCCA genes encode a flavin monooxygenase-like enzyme that plays a key role in auxin biosynthesis and regulates many aspects of plant growth. Our results demonstrate that the expression of YUCCA2 and YUCCA6 were significantly down-regulated in the *Arabidopsis* seedlings under the salt stress conditions. However, after inoculation with *B. cereus* KP120, the expression of YUCCA2 and YUCCA6 was up-regulated (Figure 6b). The PIN gene family is involved in various developmental processes in plants. Our results demonstrate that the expression of PIN2, PIN4, and PIN5 was lower in seedlings under salt stress compared with the control plants. However, these genes were up-regulated after colonization with *B. cereus* KP120 (Figure 6b). Therefore, the colonization of *B. cereus* KP120 in *Arabidopsis* seedlings regulated the expression of some genes to increase the content of IAA in seedlings.

As shown in Figure 6c, most of the key genes in ethylene synthesis (*ACO12, ACO9, ACS5, ACS1*, etc.) and signal transduction (*ERF8, ERF5, EIL1*) were significantly changed under saline conditions. The expression of *ACO3, ACO6, ACO9, ACO12, ACO13, ACS1, ACS2, ACS5*, and *ACS6* was significantly up-regulated in seedlings under saline conditions, while these genes were down-regulated after colonization with *B. cereus* KP120 (Figure 6c). This suggests that these two gene families may be involved in the salt response in *Arabidopsis*. Similarly, our results revealed that the expression of *ERF1, ERF, ERF5, EIL1*, and *EIL3* was up-regulated in seedlings under salt stress compared with the control plants. However, these genes were down-regulated after colonization with *B. cereus* KP120 (Figure 6c). This indicates
that these genes play important and specific roles in Arabidopsis responses to salt stress.

**Discussion**

Soil salinization is one of the most important abiotic stresses that seriously affect crop production. Two-thirds of the world’s countries and regions have been affected by soil salinization (Ripa et al. 2019). Presently, research shows that PGPB can promote plant tolerance to salt stress (Kumar and Verma 2018; Mesa-Marín et al. 2019). Bacillus contains a substantial number of PGPR strains, which are capable of promoting plant growth by suppressing phytopathogens (Ding et al. 2016; Madriz-Ordeñana et al. 2022; Zhou et al. 2021), causing the death of nematodes (Gao et al. 2016), producing various valuable enzymes and metabolites, degrading heavy metals (Jan et al. 2019) and alleviating abiotic stress to promote plant growth (Vilchez et al. 2018). Soil salinity impacts plant growth through chlorophyll degradation and severely reduced photosynthesis (Zouhaier et al. 2015). In our study, inoculation with *B. cereus* KP120 increased chlorophyll, suggesting that KP120 can counteract the suppression of photosynthesis under salt stress conditions. Hence, root length, shoot length, and biomass of *Arabidopsis thaliana* seedlings treated with *B. cereus* KP120 were increased compared with that non-inoculated plants, implying that the strain KP120 has the potential to cope with the negative effects of salinity stress.

Salt stress disturbs the balance of active oxygen metabolism system in plants, resulting in the generation of reactive oxygen species (ROS), which induces membrane lipid peroxidation in plant tissues, resulting in the destruction of a series of biochemical processes and subsequently reduced plant growth (Jan et al. 2019; Khan et al. 2020). MDA is one of the main products of membrane lipid peroxidation and can reflect the extent of lipid peroxidation (Wani et al. 2019). The antioxidant enzymes of the ROS scavenging in plants are comprised of SOD, POD, CAT and APX. Most

Figure 4. The antioxidant enzyme activities in leaves and roots of *Arabidopsis thaliana* under normal (control) and salt stress (salt), with inoculation with (+KP120) and without (-KP120) *B. cereus* KP120. SOD activity (a), POD (b), CAT (c) and APX (d) activity of the leaves and roots. The data represents means ± standard error (SE). Different letters indicate significant differences by Turkey’s test (*P* value < 0.05).

Figure 5. The IAA and a-ketobutyrate contents of *Arabidopsis thaliana* after inoculation with (+KP120) and without (-KP120) *B. cereus* KP120 under normal (control) and salt stress (salt). (a) represent IAA contents of the leaves and roots; (b) represent a-ketobutyrate contents: the leaves and roots. The data represents means ± standard error (SE). Different letters indicate significant differences by Turkey’s test (*P* value < 0.05).
plants cannot produce an adequate amount of antioxidants to decrease oxidation damage under stress conditions. Our study clearly showed that the SOD, POD, CAT and APX activities in the roots and leaves of inoculated plants under salt stress conditions are higher than that of non-inoculated plants. KP120 must induce all of these plant antioxidant enzymes. Therefore, reduction of MDA content and mitigation of oxidation damage were observed. Proline, a widely distributed osmotic regulating substance, plays a key role in the scavenging free radicals, protecting plant from osmotic stress under stress conditions (Shin et al. 2020). Proline content is used not only as a marker of plant salt stress, but as signal molecule during stress owing to plant growth regulator by triggering cascade processes (Park et al. 2020). In our study, the presence of _B. cereus_ KP120 led to an increase in proline content, which may help plants prevent osmotic stress under salt stress conditions.

IAA is a plant hormone involved in regulating plant life activities in plants and affects the development of the root system of the host plant under abiotic stress (Etesami et al. 2015). Some evidence suggests that IAA production is beneficial to improve plant-microbe interactions (Kumar et al. 2017). IAA produced by PGPB plays a significant role in the enhancement of root elongation, lateral roots, and root surface area, therefore helping provide soil nutrients and water for plants (Chen et al. 2017; Orozco-Mosqueda et al. 2020). In our results, _B. cereus_ KP120 produced IAA, which may have directly promoted seedling growth. In addition, _B. cereus_ KP120 promoted increase in IAA content of plants. It appeared that IAA accumulation promoted the growth of _Arabidopsis thaliana_ seedlings or mitigated salt-induced damage in the plant. Moreover, our findings show a reduction of ACC in plants inoculated with KP120, which would decrease plant ethylene levels through...
catabolizing ACC into ammonia and alpha-ketobutyrate, and significantly improve stress resistance and crop yields under various abiotic stresses (Ali and Kim 2018; Zheng et al. 2021). Ethylene levels were likely reduced and salt-induced damage mitigated in plants under treatment with KP120.

EPS are a type of extracellular polymeric substances. It is well known that some endophytes can produce extracellular polysaccharides such as *Glucanacetobacter diazotrophicus* (Meneses et al. 2017), *Azobacter chroococcum* (Rojas-Tapias et al. 2012), *Rhodotorula* sp. (Silambarasan et al. 2019), and *Bacillus licheniformis* (Singh and Jha 2016). EPS facilitates microbe–plant interaction, enhances cell adhesion, retains water, forms a protective barrier, and provides a source of nutrients to support plant growth (Bhat et al. 2021). Bacterial EPS has been shown to bind to sodium ions, thus maintaining Na+/K+ balance, and consequently improving plant salinity tolerance (Jhuma et al. 2021; Singh and Jha 2016). Previous reports also show that bacterial EPS have strong antioxidant activities and scavenging activities on superoxide and hydroxyl radicals and play an important role in sustaining plant growth in salt stress environments (Zheng et al. 2016). We find that KP120 produced EPS, which may help *B. cereus* KP120 colonize plants to confer salt tolerance by maintaining Na+/K+ balance and promoting scavenging activities on superoxide and hydroxyl radicals.

Because of increases in the total amount of IAA and ACC-deaminase in plants inoculated with KP120, we performed real-time RT–PCR to investigate the expression of genes involved in auxin synthesis and transport, IAA signal pathway, ethylene synthesis, and ethylene response in *Arabidopsis* seedlings inoculated with *B. cereus* KP120. These analytical results can help us shed light on the molecular mechanism of endophytic bacteria-related plant growth. We assessed the expression of key genes involved in tryptophan-dependent IAA biosynthetic pathways, and auxin-responding factor families such as flavin monoxygenase-like enzyme (YUCCA) and small auxin-upregulated RNAs (SAURs) (Cackett et al. 2022). SAURs may be the largest family of early auxin response genes and play multi-functional roles in plants (Van Mourik et al. 2017). In addition to auxin induction, the *Arabidopsis* SAURs gene also responds to abscisic acid, gibberellin, ethylene, and other abiotic stresses (anaerobic, low temperature, drought, salt), indicating that SAUR genes participate in the regulation of abiotic stress-tolerance responses (Stamm and Kumar 2013). The expression of most SAUR genes is reduced under salt stress in non-inoculated *A. thaliana* seedlings. However, SAUR gene expression was increased under salt stress with the inoculation of *B. cereus* KP120. This demonstrates that KP120 regulates SAURs. Similarly, we observe that the transcript level accumulation of different YUCCA genes was higher in seedlings inoculated with *B. cereus* KP120 under saline conditions. PIN proteins play a critical role in facilitating auxin efflux from cells. Once IAA is biosynthesized, it is transported with the help of cell-to-cell auxin transport mediated by PINs (Stamm and Kumar 2013). Consistent with the up-regulation of SAURs and YUCCA, the expression of auxin transport genes, particularly PIN2, PIN4, and PIN5 were also up-regulated in inoculated plants under saline conditions. These results indicate that KP120 promotes plant growth under saline conditions through improvements in IAA synthesis and transport.

*ACO* and *ACS* are two of the rate-limiting enzymes in the biosynthesis of ethylene, and they play an essential role in the regulation of plant growth and development (Liu et al. 2019; Sofy et al. 2021). It is well known that expression of ACC-deaminase from *B. cereus* can improve the growth performance of *A. thaliana* under normal and salt stress conditions (Zhang et al. 2019). In this study, salt stress increased the expression of *ACS* genes and *ACO* genes in *Arabidopsis*, while these *ACO* and *ACS* genes were down-regulated in *Arabidopsis* seedlings with inoculation with *B. cereus* KP120 under saline conditions. Ethylene response factors (ERFs) are widely involved in the response of plants to various stresses (Jiang et al. 2019). EIL proteins are the key components of ethylene signal transduction (Liu et al. 2019), which play an important role in plant response to abiotic stress. In our study, we observed down-regulation of *ERF* and *EIL* genes in *Arabidopsis* seedlings inoculated with *B. cereus* KP120, which suggests that inoculation with *B. cereus* KP120 improved the tolerance of seedlings to salt stress by decreasing ethylene synthesis.

Conclusion

Salt stress-mediated decreases in the growth of *A. thaliana* seedlings were significantly alleviated with the supplement of the beneficial *B. cereus* KP120. The beneficial role of KP120 was reflected by increased proline, chlorophyll, EPS production, and antioxidant enzyme activity, and decreased MDA content in *A. thaliana* seedlings. These effects all promote plant growth and enhance plant tolerance to salt stress. In addition, the IAA and ACC-deaminase producing strain of KP120 protects *A. thaliana* seedlings from salt stress through the down-regulation of genes encoding *ACS*, *ACO*, and *ERF* and overall decreases in ACC and ethylene biosynthesis. In addition, there is up-regulation of genes encoding IAA as well as the concentration of IAA in seedling roots to enhance *A. thaliana* seedling response to salt stress. Our results clarify the function of endophytic bacteria isolated from coastal halophytes *K. virginica*, and can guide their application as biostimulators in crops to improve salt tolerance in saline soil areas.

Acknowledgements

This work was supported by the scientific and technological projects (172102110132) in Henan province, China.

Disclosure statement

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

Contributions

Yuqi Guo and Zengyuan Tian designed the research, performed data analyses. Yran Zhang performed the most of the experiments. All authors reviewed and approved the final manuscript.

Notes on contributors

Yaran Zhang obtained her Master’s degree in Engineering, Zhengzhou University. She worked on plant-microbe interactions and molecular mechanisms of plant stress resistance.
References

Abdel Latef AAH, Mostofa MG, Rahman MM, Abdel-Farid IB, Tran L-SP. 2019. Extracts from yeast and carrot roots enhance maize performance under seawater-induced salt stress by altering physio-chemical characteristics of stressed plants. J Plant Growth Regul. 38 (3):966–979.

Abhinandan K, Skori L, Stanic M, Hickerson NMN, Jamshed M, Samuel MA. 2018. Abiotic stress signaling in wheat – An inclusive overview of hormonal interactions during abiotic stress responses in wheat. Front Plant Sci. 9:734.

Adesulu-Dahunsi AT, Sanni AI, Jeyaram K, Ojediran JO, Ogunsakin AO, Banwo K. 2018. Extracellular polysaccharide from Weissella confusa OF126: production, optimization, and characterization. Int J Biol Macromol. 111:514–525.

Ali S, Kim W-C. 2018. Plant growth promotion under water: decrease of waterlogging-induced ACC and ethylene levels by ACC deaminase-producing bacteria. Front Microbiol. 9:1096.

Bacon CW, White JF. 2016. Functions, mechanisms and regulation of endophytic and epiphytic microbial communities of plants. Symbiosis. 68(1):87–98.

Baek D, Kokubuzaman M, Khan A, Kim MC, Park HJ, Yun D-J, Chung YR. 2020. Plant-growth promoting Bacillus oryzicola YC7007 modulates stress-responses gene expression and provides protection from salt stress. J Microbiol Biotechnol. 31(8):1045–1059.

Bhagat N, Raghav M, Dubey S, Bedi N. 2021. Bacterial exopolysaccharides: insight into their role in plant abiotic stress tolerance. J Agric Food Chem. 43(9):10077–10086.

Bhagat N, Raghav M, Dubey S, Bedi N. 2021. Bacterial exopolysaccharides: insight into their role in plant abiotic stress tolerance. J Microbiol Biotechnol. 31(8):1045–1059.

Cackett L, Cannistraci CV, Meier S, Ferrandi P, Pencik A, Gehring C, Novák O, Ingle RA, Donaldson L. 2022. Salt-specific gene expression reveals elevated auxin levels in Arabidopsis thaliana plants grown under saline conditions. Front Plant Sci. 13:804716.

Chen C, Xiao L, Lu Y, Cheng J, Shen X, Wang Y, Zhang L. 2017. Pentocaa alhagi, a novel endophytic bacterium with ability to improve growth and drought tolerance in wheat. Sci Rep. 7:45164.

Diao Q, Song Y, Qi H. 2015. Exogenous spermidine enhances chilling tolerance of tomato (Solanum lycopersicum L.) seedlings via involvement in polyamines metabolism and physiological parameter levels. Acta Physiol Plant. 37:11.

Ding H, Niu B, Fan H, Li Y, Wang Q. 2016. Draft genome sequence of Bacillus subtilis 105 H, a plant-growth-promoting rhizobacterium of wheat. Genome Announc. 4(3).

Donahue JL, Okpodu CM, Cramer CL, Grabau EA, Alscher RG. 1997. Responses of antioxidants to paraquat in pea leaves (relationships to resistance). Plant Physiol. 113(1):249 LP–249257.

Dong Z-Y, Narsing Rao MP, Wang H-F, Fang B-Z, Liu Y-H, Li L, Xiao M, Li W-J. 2019. Transcriptomic analysis of two endophytes involved in enhancing salt stress ability of Arabidopsis thaliana. Sci Total Environ. 686:107–117.

Egamberdieva D, Wirth SJ, Shurigin V V, Hashem A, Abd Allah EF. 2017. Endophytic bacteria improve plant growth, symbiotic performance of chickpea (Cicer arietinum L.) and induce suppression of root rot caused by Fusarium solani under salt stress. Front Microbiol. 8:1887.

Ertani A, Nardi S, Francioso O, Sanchez-Cortes S, Di Foggia M, Schiavon M. 2019. Effects of two protein hydrolysates obtained from Chickpea (Cicer arietinum L.) and Spirulina platensis on zea mays (L.) plants. Front Plant Sci. 10:954.

Etesami H, Alkhani HA, Hosseini HM. 2015. Indole-3-acetic acid (IAA) production trait, a useful screening to select endophytic and rhizosphere competent bacteria for rice growth promoting agents. MethodsX. 2:72–78.

Fan C. 2020. Genetic mechanisms of salt stress responses in halophytes. Plant Signal Behav. 15(1):1704528.

Fan D, Subramanian S, Smith DL. 2020. Plant endophytes promote growth and alleviate salt stress in Arabidopsis thaliana. Sci Rep. 10 (1):12740.

Fujita S, Saari Nb, Maegawa M, Tetsuka T, Hayashi N, Tono T. 1995. Purification and properties of polyphenol oxidase from cabbage (Brassica oleracea L.). J Agric Food Chem. 43(5):1138–1142.

Gao H, Qi G, Yin R, Zhang H, Li C, Zhao X. 2016. Bacillus cereus strain S2 shows high nematicidal activity against Meloidogyne incognita by producing sphingosine. Sci Rep. 6:28736.

Hagen G, Guilloyte T. 2002. Auxin-responsive gene expression: genes, promoters and regulatory factors. Plant Mol Biol. 49(3):373–385.

Han D, Han J, Yang G, Wang S, Xu T, Li W. 2020. An ERF transcription factor gene from Malus baccata (L.) Borkh., MBERF1, affects cold and salt stress tolerance in arabidopsis. Forests. 11(5):514.

Han G, Tian Z, Liu K, Zhang J, Chang Y, Guo Y. 2015. Effects of endophytic bacteria of Kosteletskyia pentacarpos with ACC deaminase activity on salt tolerance in wheat. J Plant Physiol. 2. P2122–P2202. (In Chinese).

He J, Ren Y, Chen X, Chen H. 2014. Protective roles of nitric oxide on seed germination and seedling growth of rice (Oryza sativa L.) under cadmium stress. Ecotoxicol Environ Saf. 108:114–119.

Jaensaeng R, Jantusiriyarat C, Thamchaipenet A. 2018. Molecular interaction of 1-aminoacyclop propane-1-carboxylate deaminase (ACCD)-producing endophytic Streptomyces sp. GMK 336 towards salt-stress resistance of Oryza sativa L. cv. KDM105. Sci Rep. 8(1):1950.

Jan M, Shah G, Masood S, Iqbal Shinwari K, Hameed R, Rha ES, Jamil M. 2019. Bacillus cereus enhanced phytoremediation ability of rice seedlings under cadmium toxicity. Biomed Res Int. 2019:8134651.

Jhuma TA, Rafeya J, Sultana S, Rahman MT, Karim MM. 2021. Isolation of endophytic salt-tolerant plant growth-promoting rhizobacteria from Oryza sativa and evaluation of their plant growth-promoting traits under salinity stress condition. Front Sustain Food Syst. 6:879351.

Jiang M, Ye ZH, Zhang HJ, Xiao LX. 2019. Broccoli plants over-expressing an ERF transcription factor gene BoERF1 facilitates both salt stress and Sclerotinia stem rot resistance. J Plant Growth Regul. 38 (1):1–13.

Khan AL, Hamayun M, Kang S-M, Kim Y-H, Jung H-Y, Lee J-H, Lee I-J. 2012. Endophytic fungal association via gibberellins and indole acetic acid can improve plant growth under abiotic stress: an example of Paecilomyces formosus LHL10. BMC Microbiol. 12:3.

Khan MA, Asaf S, Khan AL, Adhikari A, Jan R, Ali S, Imran M, Kim K-M, Lee I-J. 2020. Plant growth-promoting endophytic bacteria augment growth and salinity tolerance in rice plants. Plant Biol. 22 (5):850–862.

Khan MA, Asaf S, Khan AL, Jan R, Kang SM, Kim KM, Lee IJ. 2020. Extending thermotolerance to tomato seedlings by inoculation with SA1 isolate of Aspergillus terreus and comparison with exogenous humic acid application. PLoS One. 15(4):e0232228.

Khushidil F, Jan FG, Jan G, Hamayun M, Iqbal A, Hussain A, Bibi N. 2019. Salt stress alleviation in Pennisetum glaucum through secondary metabolites modulation by Aspergillus terreus. Plant Physiol Biochem. 144:127–134.

Kumar A, Singh S, Gaurav AK, Srivastava S, Verma JP. 2020. Plant growth-promoting bacteria: biological tools for the mitigation of salinity stress in plants. Front Microbiol. 11:1216.

Kumar A, Verma JP. 2018. Does plant–microbe interaction confer stress tolerance in plants: a review. Microbiol Res. 207:41–52.

Zengyuan Tian is Associate Professor at Zhengzhou University. His research interests lie in the area of maize heterosis, epigenetic regulation and molecular mechanisms of plant stress resistance.

Yu Xi is Associate Professor at Zhengzhou University. His research interests are environmental microbiology and ecological toxicology.

Xiaomin Wang obtained her Master’s degree in Engineering, Zhengzhou University. Her research interests are plant-microbe interactions and molecular mechanisms of plant stress resistance.

Shuai Chen obtained his Master’s degree in Engineering, Zhengzhou University. He worked on plant-microbe interactions and molecular mechanisms of plant stress resistance.

Mengting He obtained her Master’s degree in Agriculture Sciences, Zhengzhou University. Her research interests are plant-microbe interactions and molecular mechanisms of plant stress resistance.

Yange Chen obtained her Master’s degree in Agriculture Sciences, Zhengzhou University. Her research interests are plant-microbe interactions and molecular mechanisms of plant stress resistance.

Yuqi Guo is Associate Professor at Zhengzhou University. Her research interests are plant-microbe interactions, molecular mechanisms and signal transduction of plant stress resistance, extraction and application of plant active ingredients.
Kumar K, Manigundan K, Amarenas N. 2017. Influence of salt tolerant *Trichoderma* spp. on growth of maize (*Zea mays*) under different salinity conditions. J Basic Microbiol. 57(2):141–150.

Kumari P, Khanna V. 2015. ACC-deaminase and EPS production by salt tolerant rhizobacteria augment growth in chickpea under salinity stress. Int J Bio-Resource Stress Manag. 6(5):558–565.

Li X, Liu G, Geng Y, Wu M, Pei W, Zhai H, Zang X, Lingli L, Zhang J, Yu S, Ju J. 2017. A genome-wide analysis of the small auxin-up RNA (SAUR) gene family in cotton. BMC Genomics. 18(1):815.

Li C, Li Dzhin J-P, H Frei J, Wong C, Long D, Yu M, Zhan A, Mullbery EIL3 confers salt and drought tolerances and modulates ethylene biosynthetic gene expression. Uversky V, editor. PeerJ.

Madriz-Ordeñana K, Pazarlar S, Jörgensen HL, Nielsen T K, Zhang Y, Nielsen K L, Hansen I H, Thorald-Christensen H. 2022. The *Bacillus cereus* Strain EC9 Primes the Plant Immune System for Superior Biocontrol of *Fusarium oxysporum*. Plants. 11(5):687.

Mateo-Bonomi E, Casanova-Sáez R, Simusra J, Ljung K. 2021. Redefining the roles of UDP-glycosyltransferases in auxin metabolism and homeostasis during plant development biotechnology. bioRxiv. 2021.06.24.270121.

Meneses C, Gonçalves T, Alquéres S, Rousu L, Serrato R, Vidal M, Balldini J. 2017. Gluconacetobacter diazotrophicus exopolysaccharide protects bacterial cells against oxidative stress in vitro and during rice plant colonization. Plant Soil. 416(1):133–147.

Mesa-Marin J, Perez-Romero JA, Mateos-Naranjo E, Bernabeu-Meana M, Pajuelo E, Rodriguez-Llorente ID, Redondo-Gomez S. 2019. Effect of plant-growth-promoting rhizobacteria on *Salicornia ramosissima* seed germination under salinity, CO2 and temperature stress. Agronomy. 9(10):655.

Mohd S, Shukla J, Kushwaha AS, Mandrak K, Shankar J, Araria N, Saxena PN, Narayan R, Roy SK, Kumar M. 2017. Endophytic fungi *Piriformospora indica* mediated protection of host from arsenic toxicity. Front Microbiol. 8:7574.

Moran R. 1982. Formulæ for determination of chlorophyllous pigments extracted with n-dimethylformamide. Plant Physiol. 69 (6):1376–1381.

Orozco-Mosqueda MdC, Glick BR, Santoyo G. 2020. ACC deaminase-containing plant growth-promoting rhizobacteria. *Microbially mediated plant growth-promoting rhizobacteria*.

Park M-H, Park C-H, Sim YB, Hwang S-J. 2020. Response of *Scedesmus quadricauda* (Chlorophyceae) to salt stress considering nutrient enrichment and intracellular proline accumulation. Int J Environ Res Public Health. 17(10):3624.

Penrose DM, Glick BR. 2003. Methods for isolating and characterizing ACC deaminase-containing plant growth-promoting rhizobacteria. Physiol Plant. 118(1):10–15.

Qawasmeh A, Obied HK, Raman A, Wheatley W. 2012. Influence of fungal endophyte infection on phenolic content and antioxidant activity in grasses: interaction between *Lolium perenne* and different strains of *Nestotyphodium loli*. I Agric Food Chem. 60(13):3381–3388.

Qiu Y, Denghun M, Pan X, Yuan Z. 2016. Microbially mediated plant salt tolerance and microbe-based solutions for saline agriculture. Biotechnol Adv. 34(7):1245–1259.

Ripa FA, Cao W-D, Tong S, Sun J-G. 2019. Assessment of plant growth-promoting and abiotic stress tolerance properties of wheat endophytic fungi. Biomed Res Int.

Shin YK, Bhandari SR, Cho MC, Lee JG. 2020. Evaluation of chlorophyll fluorescence parameters and proline content in tomato seedlings grown under different salt stress conditions. Hortic Environ Biotechnol. 61(3):433–443.

Silambarasan S, Logeswari P, Cornejo P, Kannan VR. 2019. Evaluation of the production of exopolysaccharide by plant growth promoting yeast *Rhodotorula* sp. strain CAH2 under abiotic stress conditions. Int J Biol Macromol. 121:55–62.

Singh RP, Jha PN. 2016. A halotolerant bacterium *Bacillus licheniformis* HSW-16 augments induced systemic tolerance to salt stress in wheat plant (*Triticum aestivum*). Front Plant Sci. 7:1890.

Singh S, Singh UB, Trivedi M, Sahu PK, Paul S, Paul D, Saxena AK. 2019. Seed biopriming with salt-tolerant endophytic *Pseudomonas geniculata*-modulated biochemical responses provide ecological fitness in maize (*Zea mays L.*) grown in saline sodic soil. Int J Environ Res Public Health. 17(1):253.

Singh S, Singh UB, Trivedi M, Sahu PK, Paul S, Paul D, Saxena AK. 2015. Seed biopriming with salt-tolerant endophytic *Pseudomonas geniculata*-modulated biochemical responses provide ecological fitness in maize (*Zea mays L.*) grown in saline sodic soil. Int J Environ Res Public Heal. 17(1):253.

Sofy MR, Aboseidah AA, Heneidak SA, Ahmed HR. 2021. ACC deaminase containing endophytic bacteria ameliorate salt stress in *Pisum sativum* through reduced oxidative damage and induction of antioxidative defense systems. Environ Sci Pollut Res. 28(30):40971–40991.

Song J, Zhou J, Zhao W, Xu H, Wang F, Xu Y, Wang L, Tian C. 2016. Effects of salinity and nitrate on production and germination of dimorphic seeds applied both through the mother plant and exogenously during germination in *Saeseda salsa*. Plant Species Biol. 31(1):19–28.

Stamm P, Kumar PP. 2013. Aixin and giberellin responsive Arabidopsis SMALL AUXIN UP RNA36 regulates hypocotyl elongation in the light. Plant Cell Rep. 32(6):759–769.

Sun L, Le I, P, Wang G, Ma J, Zhan Y, Jiang K, Xu Z, Xu H. 2020. The endophyte *Pantoea allihagi* NX-11 alleviates salt stress damage to rice seedlings by secreting exopolysaccharides. Front Microbiol. 10:3112.

Van Mourik H, Van Dijk ADJ, Stortenbeker N, Angenent GC, Bemer S. 2017. Divergent regulation of Arabidopsis SAUR genes: a focus on the SAUR10-clade. BMC Plant Biol. 17(1):245.

Vilchez J, Tang Q, Kaushal R, Chen S, Liu R, Zhang H. 2018. Genome sequence of *Bacillus cereus* strain TGI-6, a plant-beneficial rhizobacterium that is highly salt tolerant. Genome Announc. 6(19):doi:10.1128/genomeA.00351-18.

Wani AS, Ahmad A, Hayat S, Tahir I. 2019. Epibrassinolide and proline alleviate the photosynthetic and yield inhibition under salt stress by acting on antioxidant system in mustard. Plant Physiol Biochem. 135:385–394.

Woo O-G, Kim H, Kim J-S, Keum HL, Lee K-C, Sul WJ, Lee J-H. 2020. *Bacillus subtilis* strain GT9 confers enhanced tolerance to drought and salt stresses in *Arabidopsis thaliana* and *Brassica campestris*. Plant Physiol Biochem. 148:359–367.

Xiong Y-W, Li X-W, Wang T-T, Gong Y, Zhang C-M, Xing K, Qin S. 2020. Root exudates-driven rhizosphere recruitment of the plant growth-promoting rhizobacterium *Bacillus flexus* KLBMP 4941 and its growth-promoting effect on the coastal halophyte *Limonium sinense* under salt stress. Ecotoxicol Environ Saf. 194:101374.

Yang Z, Li J-L, Liu L-N, Xie Q, Sui N. 2020. Photosynthetic regulation under salt stress and salt-tolerance mechanism of sweet sorghum. Front Plant Sci. 10:1722.

Yao I, Wu Z, Zheng Y, Kaleem I, Li C. 2010. Growth promotion and protection against salt stress by *Pseudomonas putida* Rs-198 on cotton. Eur J Soil Biol. 46(1):49–54.

Zhang S, Gan Y, Xu B. 2019. Mechanisms of the IAA and ACC-deaminase producing strain of *Pantoea allihagi* NX-11 alleviates salt stress damage to rice seedlings by secreting exopolysaccharides. Front Microbiol. 10:3112.

Zhou H, Ren Z H, Zu X, Yu X Y, Zhu H J, Li X J, Zhong J, Liu E M. 2021. Patterns in the microbial community of salt-tolerant plants and the functional genes associated with salt stress alleviation. *Front Microbiol*. 12:769–781.

Zhou H, Ren Z H, Zu X, Yu X Y, Zhu H J, Li X J, Zhong J, Liu E M. 2021. Efficacy of Plant Growth-Promoting Bacteria *Bacillus cereus* YN917 for Biocontrol of Rice Blast. Front Microbiol. 12. doi:10.3389/fmicb.2021.684888.

Zhou H, Ren Z H, Zu X, Yu X Y, Zhu H J, Li X J, Zhong J, Liu E M. 2021. Efficacy of Plant Growth-Promoting Bacteria *Bacillus cereus* YN917 for Biocontrol of Rice Blast. Front Microbiol. 12. doi:10.3389/fmicb.2021.684888.