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Halotolerant plant growth-promoting bacteria *Enterobacter* sp. Av16 and *Acinetobacter* sp. Av23 enhance seed germination and seedling photosynthesis of *Apocynum pictum* under salt stress

Xue WANG[1*], Li JIANG[2*], Yao GE[1], Yiping ZOU[1], Qingsheng CAI[1], Yan XIA[1], Laiqing LOU[1✉]

[1]*College of Life Sciences, Nanjing Agricultural University, Nanjing 210095, China*
[2]*State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011, China*

Abstract: *Apocynum pictum* Schrenk, a halophyte, is commonly used as a traditional Chinese medicine, tea, and fiber crop. To improve the growth of *A. pictum* in saline soil, its responses to halotolerant plant growth-promoting bacteria (PGPB) were investigated at germination and during early growth stages. Inoculation with either *Enterobacter* sp. Av16 or *Acinetobacter* sp. Av23 significantly improved seed germination percentage and alleviated the adverse effects of salinity on seedling growth of *A. pictum*. Under salt stress, PGPB increased leaf area and improved photosynthetic pigments, including chlorophyll *a*+*b* and carotenoids, as well as intercellular carbon dioxide (C_i) and transpiration rate (T_r). More importantly, PGPB alleviated salt-induced damage to the photosynthetic apparatus by stabilizing the photosystems and optimizing electron transport processes. This was evidenced by increases in the density of reaction centers per cross-section (RC/CS_m) and the efficiencies of electron transfer to photosystem I (δR_o and ΦR_o). Consequently, PGPB improved chlorophyll fluorescence and key photosynthetic parameters, including the maximum quantum yield (ΦP_o), performance index on absorption basis (PI_{abs}), overall performance index (PI_{total}), and net photosynthetic rate (P_n). Furthermore, PGPB activated antioxidant enzymes, such as superoxide dismutase (SOD) and catalase (CAT), reducing the accumulation of reactive oxygen species (ROS) in *A. pictum*. In summary, PGPB enhanced *A. pictum* seed germination and photosynthetic capacity by stabilizing photosystems, improving stomatal gas exchange, and mitigating oxidative stress under salt stress. These findings highlight the potential of PGPB inoculation as a sustainable strategy to enhance salt resilience in *A. pictum*.

Key words: *Apocynum pictum* Schrenk; Salt stress; Plant growth-promoting bacteria (PGPB); Seed germination; Photosynthesis; Antioxidant enzyme

1 Introduction

Salt stress is one of the most serious adverse factors in the environment for plants. It causes ionic imbalance, a burst of reactive oxygen species (ROS), cell damage, and metabolic disorders in plants, resulting in growth inhibition and abnormal development (Ma et al., 2020).

Seed germination and photosynthesis, two important physiological processes of plants, were reported to be obviously suppressed under saline conditions (Tsai et al., 2019; Damalas and Koutroubas, 2025). Seeds subjected to salt stress have difficulty in absorbing water and accumulate large amounts of salt ions internally, which increases abscisic acid (ABA) content, disrupts the ion balance within the cells, and thereby hinders seed germination (Zhang et al., 2015; Fu et al., 2025; Ghosh et al., 2025). It is reported that salinization leads to a significant decrease in seed germination of various plants (Ding et al., 2018; Silva et al., 2018). Photosynthesis, which is sensitive to salt stress, is crucial for plant growth. Excess salt reduces photosynthetic pigments and stomatal conductance (G_s), destroys the ultrastructure of chloroplasts, and decreases the photosynthetic rate (Tsai et al., 2019; Zhu et al., 2019). Electron transportation in photosystem II (PSII) is one of the physiological processes most sensitive to salt stress. In some halophytes, such

✉ Laiqing LOU, loulq@njau.edu.cn
* The two authors contributed equally to this work
Laiqing LOU, https://orcid.org/0000-0003-2759-8412

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as *Cakile maritima* and *Haloxylon salicornicum*, high-salt stress suppresses the maximum quantum yield (ΦP_o), the quantum yield (ΦPSII) and/or electron transport of PSII (Debez et al., 2008; Panda et al., 2019).

Apocynum pictum is a perennial wild herb belonging to the Apocynaceae family. It is recognized as a stress-tolerant plant, exhibiting tolerance to drought, salt, and alkaline stresses (Jiang et al., 2021a). The plant is widely distributed across Asia, Europe, and North America. In China, *A. pictum* is found mainly in the northwestern regions, including Xinjiang, Qinghai, Gansu, and Inner Mongolia (Thevs et al., 2012; Xie et al., 2012). *A. pictum* is used mainly for medicinal purposes, production of tea and fiber, and ecological improvement of saline-alkali land (Xie et al., 2012). In recent years, the wild resources of *A. pictum* have been continuously declining. It is difficult to cultivate due to its lower germination percentage and survival percentage at the seedling stage when grown in saline land. This is mainly because it struggles to absorb water from the soil. Therefore, adopting efficient methods to improve the germination percentage and salt tolerance of *A. pictum* is crucial for protecting wild resources and restoring the ecosystem in saline soil.

Bacteria that exist in plant tissue or rhizospheric soil are biological factors that affect plant growth and regulate the plant's salt tolerance (Kou et al., 2024). Plant growth-promoting bacteria (PGPB) are a class of beneficial bacteria that can promote plant growth under various adverse conditions (Singh et al., 2018; Lee and Cho, 2025). Recent results showed that inoculation with PGPB enhanced the salt tolerance of plants such as maize, rice, and tomato (Hou et al., 2022; Mahmud et al., 2023; Abdelkefi et al., 2024). Thus, PGPB can potentially be applied to assist plants in improving plant growth and salt tolerance.

Most previous studies on PGPB have focused on glycophytes. However, the impact of PGPB on the growth of halophytes, particularly those being developed as cash crops, has rarely been investigated. In this study, we hypothesized that halotolerant bacteria with multiple plant growth-promoting traits can enhance the seed germination and seedling growth of halophytes. The objectives of this study were (1) to select and obtain appropriate bacterial strains that can be used to enhance the salt tolerance of *A. pictum* and aid in the restoration of saline land ecosystems, and (2) to elucidate the physiological responses of *A. pictum* inoculated with PGPB. This study advances our understanding of the role of PGPB in improving halophyte growth and potentially enriching beneficial bacterial resources for the cultivation of *A. pictum*.

2 Materials and methods

2.1 Plant and bacterial strains

Seeds of *A. pictum* were collected in November 2022 from the Fukang Field Research Station of the Chinese Academy of Sciences, Xinjiang, China. The bacterial strains were isolated from *Apocynum venetum* (red hemp, which belongs to the same genus as *A. pictum*), and the related rhizospheric soil was collected in April 2020 from saline fields in Dafeng (32°59′N, 120°49′E), Yancheng, Jiangsu, China.

2.2 Isolation of bacterial strains and analysis of plant growth-promoting traits

Bacterial strains in soil and plant tissues were isolated according to the methods described by Bharathi et al. (2004) and Tian et al. (2022), with some modifications. After that, four plant growth-promoting traits, including indole-3-acetic acid (IAA) secretion, phosphate solubilization, siderophore production, and nitrogen fixation of bacterial isolates, were analyzed (supplementary materials and methods). Bacterial isolates exhibiting three or more plant growth-promoting traits were selected to assess their ability to enhance the growth of *A. pictum* seedlings under salt stress.

2.3 Preparation of bacterial suspensions

Bacterial suspensions were prepared following the method of Tian et al. (2022) immediately before use (supplementary materials and methods).

2.4 Investigation of the plant growth-promoting ability of 11 bacterial strains

Eleven bacterial strains exhibiting more than three plant growth-promoting traits were used in this experiment. Seeds of *A. pictum* were surface-sterilized with 0.5% (5 g/L) NaClO for 15 min, thoroughly rinsed with sterilized distilled water (dH_2O), and then sown on 1/2 Murashige-Skoog (MS) solid medium (pH 6.8). After 10 d of growth, 15 uniform seedlings were transplanted into Petri dishes containing 1/2 MS solid medium (pH 6.8) supplemented with 150 mmol/L

NaCl, and 10 mL of bacterial suspensions with optical density at 600 nm (OD_{600}) of 0.3 were added to the surface of each Petri dish (Fig. S1). Each treatment had three replicates. The seedlings were grown vertically in a plant growth chamber at 30 °C/26 °C (day/night) with a 12-h light/night cycle, a light intensity of 350 μmol/(m^2·s), and a relative humidity of (60±5)%. Shoot elongation, as well as shoot and root biomass, were measured after 14 d of exposure to NaCl. Bacterial strains that significantly improved shoot elongation, as well as shoot and root fresh weight, were selected for further investigation.

2.5 Identification of bacterial strains

The bacterial strains Av16 (*Enterobacter* sp. Av16) and Av23 (*Acinetobacter* sp. Av23) were identified based on colony morphology, Gram staining, and 16S ribosomal DNA (rDNA) gene sequencing, followed by the National Center for Biotechnology Information (NCBI) BLAST analysis (supplementary materials and methods).

2.6 Effect of PGPB on the seed germination of *A. pictum*

Salt treatment concentrations that reduced seedling growth and seed germination potential by about 50% were selected according to the results of a pre-experiment under the same conditions (Fig. S2). After surface sterilization, the seeds were sown on 1/2 MS solid medium (pH 6.8) supplemented with different concentrations of NaCl (0, 200, or 400 mmol/L). Twenty-five seeds were evenly placed in the middle of each Petri dish (Fig. S1). Three treatments, −PGPB (without PGPB), Av16, or Av23, were designed for each NaCl concentration, resulting in a total of nine treatments for this experiment (Table S1). Each treatment had four replicates. For the Av16 or Av23 treatment, 10 μL of the corresponding bacterial suspensions were evenly spread over the surface of each Petri dish (Fig. S1). In contrast, for the −PGPB treatment, 10 μL of sterilized dH_2O was added instead. The seeds on 1/2 MS were incubated under the same conditions as described in Section 2.4. The number of germinated seeds was recorded daily for the first 5 d. Germination percentage, germination potential, and germination index were calculated according to the formulae described by Xiao and Wang (2020) (supplementary materials and methods). The lengths of the radicle and shoot were measured 14 d after the seeds were sown.

2.7 Effects of PGPB on the leaf morphology and photosynthetic parameters of *A. pictum* seedlings

After surface sterilization, the seeds were germinated and grown on wet gauze for 7 d. The seedlings were then transplanted to a plastic box containing 1.2 L of 1/4 Hoagland solution (pH 6.8) (Table S2), with the solution being renewed every 3 d. After another eight weeks, the uniform seedlings were selected and treated with NaCl and/or PGPB. Two concentrations (0 or 150 mmol/L) of NaCl and three PGPB treatments (−PGPB, Av16, or Av23) for each NaCl concentration were designed (Table S3). In total, six treatments with four replicates (four pots each containing seven seedlings) for each treatment were performed. The roots of *A. pictum* seedlings were immersed for 2 h in a suspension of *Enterobacter* sp. Av16 or *Acinetobacter* sp. Av23 (OD_{600}=1). Additionally, a 1% (volume fraction) bacterial suspension was added to 1/4 Hoagland solution for PGPB treatments every 3 d when the solution was renewed. The seedlings were grown under the same conditions as described in Section 2.4. The leaf morphology and photosynthetic parameters were assessed after two weeks of treatment with NaCl and/or PGPB.

To determine the leave morphology and photosynthetic parameters, the upper 3rd pair of leaves of four plants for each treatment were neatly lined up and photographed. Leaf length, leaf width, and leaf area were analyzed using ImageJ. Photosynthetic pigments were determined according to the method of Xiong et al. (2023). Photosynthetic gas exchange parameters were measured using a portable photosynthesis system (LI-6400, Li-Cor, Inc., Lincoln, NE, USA) between 9:00 a.m. and 12:00 p.m. with a light intensity of 800 μmol/(m^2·s), leaf temperature of 27 °C, and a CO_2 concentration of 380 μmol/mol. A multi-function plant efficiency analyzer (M-PEA, Hansatech Instruments Ltd., King's Lynn, Norfolk, UK) was used to measure the fast chlorophyll *a* fluorescence after the leaves had been in the dark for 30 min. F_o, F_k, F_j, and F_i represent the fluorescence intensity that was observed at 0.02 (o), 0.3 (k), 2 (j), and 30 (i) ms, respectively. The maximum fluorescence intensity was denoted as F_m. The chlorophyll fluorescence induction (OJIP)-test parameters in Table S4 were calculated according to the method described by Tsimilli-Michael

(2020), and the OJIP curves were normalized following Guo et al. (2023).

2.8 Effects of PGPB on ROS and antioxidant enzymes in *A. pictum* seedlings

Fifteen 10-d-old seedlings were transplanted to 1/2 MS solid medium (pH 6.8) containing either 0 or 150 mmol/L NaCl. Three PGPB treatments (−PGPB, Av16, or Av23) for each NaCl concentration with three replicates (three pots each containing seven seedlings) were designed (Table S3). A total of 10 mL bacterial suspension (OD_{600}=0.3) was spread onto the surface of agar in each Petri dish (Fig. S1). The seedlings were grown under the same conditions as described in Section 2.4. Histochemical localization and contents of hydrogen peroxide (H_2O_2) and superoxide ($O_2^{\cdot-}$) and activities of peroxidase (POD) and superoxide dismutase (SOD) were measured after 14 d of exposure.

Histochemical distribution of H_2O_2 and $O_2^{\cdot-}$ in the roots was determined by staining with 3,3'-diaminobenzidine (DAB) and nitroblue tetrazolium (NBT), respectively (Ramel et al., 2009). The content of H_2O_2 was analyzed using the KI chromogenic reaction (Sergiev et al., 1997). The content of $O_2^{\cdot-}$ was determined as described by Oracz et al. (2007). The activity of POD was assayed using guaiacol according to Castillo et al. (1984) and Poli et al. (2018). A quantitative NBT assay was used to determine SOD activity (Rao and Sresty, 2000).

2.9 Data analysis

Microsoft Excel 2019 and Sigmaplot 14.0 were used for data analysis and illustration. Data are presented as mean±standard deviation (SD). An analysis of variance (ANOVA) combined with Tukey's honestly significant difference (HSD) test in SPSS 26.0 was performed to compare significant differences among treatments at the significance level of P<0.05. A normality hypothesis test (Shapiro-Wilk) and a homogeneity of variances test (Levene's) were performed before applying ANOVA.

3 Results

3.1 Plant growth-promoting traits of bacterial strains

The plant growth-promoting traits of the bacterial strains are shown in Fig. S3 and Table S5. Among the 32 bacterial strains, 20 showed the ability to secrete IAA, with concentrations in tubes ranging from 13.9 to 109.0 μg/mL. A total of seven strains (Av05, Av06, Av13, Av16, Av17, Av18, and Av20) were able to excrete IAA at concentrations exceeding 50 μg/mL. Fifteen of the thirty-two strains had the ability to solubilize phosphate, with phosphate solubility indices ranging from 1.22 to 3.75. Among them, the strain Av23 exhibited the highest phosphate-solubilizing ability. Thirteen of the thirty-two strains had the ability to fix nitrogen, and ten produced siderophore. Eleven bacterial strains, each exhibiting more than three plant growth-promoting traits, were selected for further study.

3.2 Effects of screened PGPB on the growth of *A. pictum* seedlings

Fig. 1 illustrates the effects of 11 bacterial strains with growth-promoting potential on the growth of *A. pictum* seedlings under salt stress. Four of eleven strains significantly enhanced both shoot elongation and the shoot fresh weight of *A. pictum* seedlings. Only two strains significantly increased root fresh weight. Among the 11 strains, Av23 was the most efficient, increasing shoot elongation, shoot fresh weight, and root fresh weight of *A. pictum* seedlings by 106.0%, 62.3%, and 84.6%, respectively, compared to the non-inoculation treatment. Similarly, inoculation with strain Av16 led to marked increases in both shoot elongation and fresh biomass of *A. pictum* seedlings.

3.3 Identification of bacterial strains

Based on their morphological characteristics and Gram staining results, both Av16 and Av23 are rod-shaped, Gram-negative bacteria (Fig. S4 and Table S6). Av16 colonies appeared raised, opaque, and light yellow, with a wet and smooth surface on Luria-Bertani (LB) medium. The 16S rDNA sequence of Av16 was analyzed using the BLASTN tool of NCBI. The analysis revealed that Av16 belongs to *Enterobacter* sp. Phylogenic analysis indicated that Av16 was most closely related to *Enterobacter* sp. strain MBWS7 (OP990292.1) (Fig. 2). Consequently, Av16 was identified as *Enterobacter* sp. The Av23 colonies were flat, opaque, and light yellow, with a wet and smooth surface on LB medium. After analyzing its 16S rDNA sequence with the NCBI BLASTN tool, Av23 was identified as an *Acinetobacter* sp., most closely resembling *Acinetobacter* sp. S3.MAC.013 (HM063913.1) according to phylogenic analysis (Fig. 2).

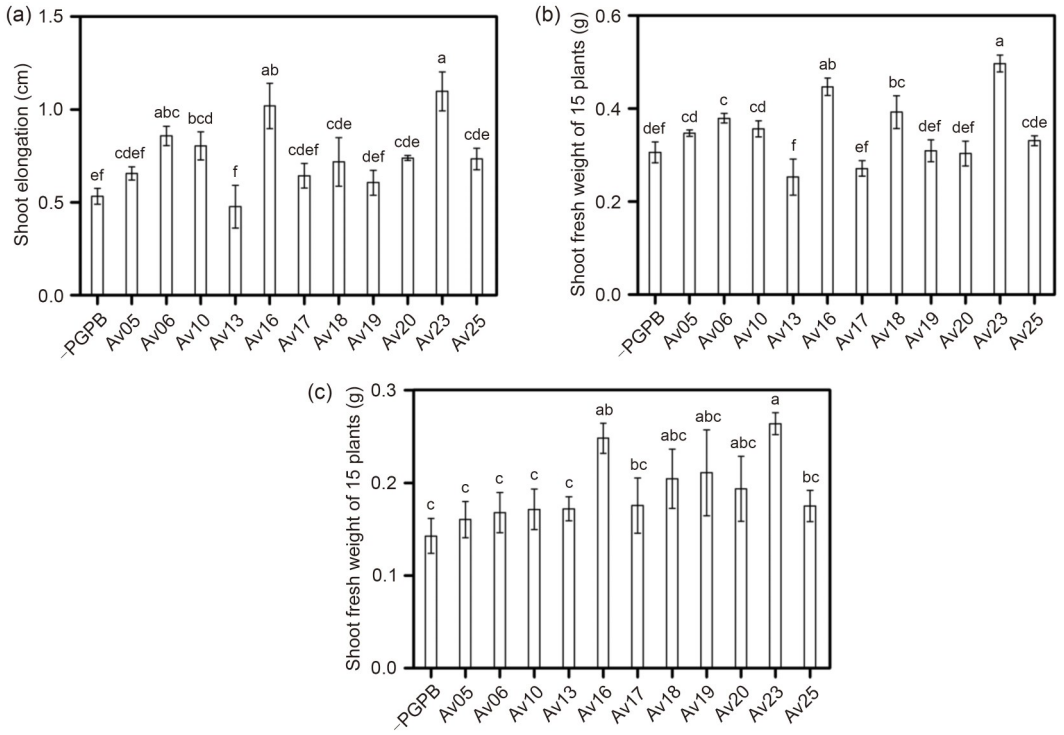

Fig. 1 Effects of 11 strains on the growth of *Apocynum pictum* seedlings under 150 mmol/L NaCl. (a) Shoot elongation; (b) Shoot fresh weight; (c) Root fresh weight. Data are expressed as mean±standard deviation (SD) (n=3). Different letters indicate significant differences between treatments (P<0.05). −PGPB: the treatment without plant growth-promoting bacteria.

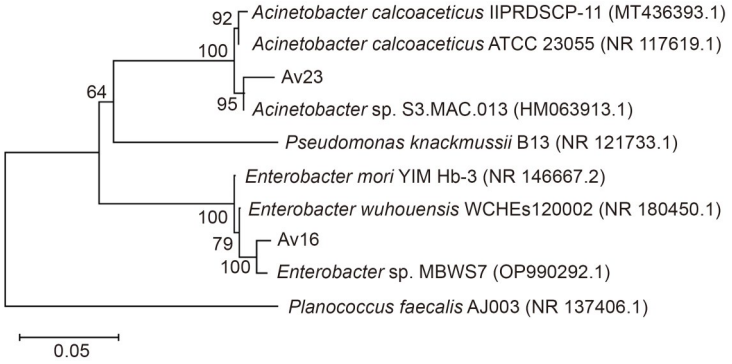

Fig. 2 Phylogenetic position of strains *Enterobacter* sp. Av16 and *Acinetobacter* sp. Av23. Bootstrap values (percentage of 1000 bootstrap replications) are shown at the branch points. The scale bar represents a phylogenetic distance of 0.05 substitutions per site.

3.4 Effects of *Enterobacter* sp. Av16 and *Acinetobacter* sp. Av23 on the germination of *A. pictum*

Salt stress inhibited seed germination, resulting in a significant decrease in the germination percentage, germination potential, and germination index as the NaCl concentration increased (Figs. 3a–3c). Salt stress delayed seed germination, with the highest germination percentages observed on the 3rd, 4th, and 5th days under 0, 200, and 400 mmol/L NaCl treatments, respectively (Fig. 3a). Inoculating seeds with *Enterobacter* sp. Av16 and *Acinetobacter* sp. Av23 enhanced the seed germination of *A. pictum* under all NaCl treatments. Compared to the non-inoculation control, the germination percentage, germination potential, and germination index were significantly increased after inoculation with *Enterobacter* sp. Av16 or *Acinetobacter* sp. Av23 (Figs. 3a–3c). Figs. 3d–3g present the growth

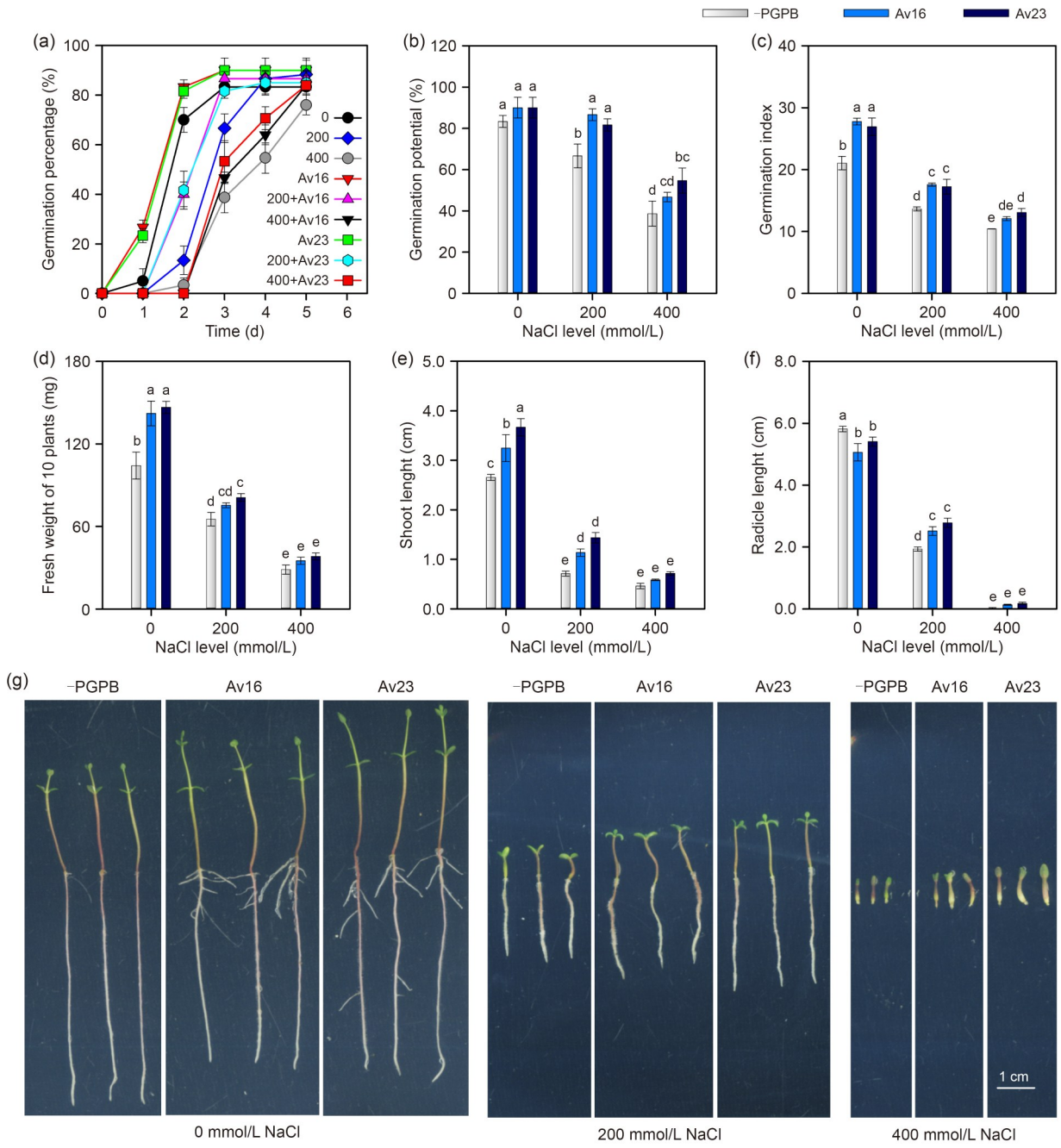

Fig. 3 Effects of *Enterobacter* sp. Av16 (Av16) and *Acinetobacter* sp. Av23 (Av23) on seed germination of *Apocynum pictum* under 0, 200, and 400 mmol/L NaCl. (a) Germination percentage (the values 0, 200, and 400 represent NaCl treatments at 0, 200, and 400 mmol/L, respectively); (b) Germination potential; (c) Germination index; (d) Fresh weight; (e) Shoot length; (f) Radicle length; (g) Phenotype. (d–g) Growth parameters were observed on 14 d after germination. Data are expressed as mean±standard deviation (SD) (n=4). Different letters indicate significant differences between treatments (P<0.05). PGPB: plant growth-promoting bacteria.

parameters of *A. pictum* seedlings 14 d after germination. NaCl with a concentration of 200 mmol/L caused a significant reduction of 37.4%, 73.2%, and 66.8% in the fresh weight, shoot length, and radicle length of *A. pictum* seedlings, respectively. Under the 400 mmol/L NaCl condition, the fresh weight and shoot length of *A. pictum* were inhibited by 62.6% and 85.4%, respectively. Inoculation with *Enterobacter* sp. Av16 or *Acinetobacter* sp. Av23 notably increased the fresh weight and shoot length in both the 0 and 200 mmol/L NaCl

treatments (P<0.05; Figs. 3d–3g). After inoculation with *Enterobacter* sp. Av16 and *Acinetobacter* sp. Av23, a decrease in radicle length and an increase in the number of lateral roots of *A. pictum* were observed in the absence of NaCl. However, in the presence of 200 mmol/L NaCl, the radicle length increased by 30.2% for Av16 and 44.0% for Av23 (P<0.05), but no lateral roots were observed despite inoculation with *Enterobacter* sp. Av16 or *Acinetobacter* sp. Av23 (Figs. 3f and 3g). At 400 mmol/L NaCl, radicle growth ceased and shoot growth of *A. pictum* was stunted during the germination stage (Figs. 3e–3g).

3.5 Effects of *Enterobacter* sp. Av16 and *Acinetobacter* sp. Av23 on leaf morphology and photosynthetic parameters of *A. pictum*

3.5.1 Leaf morphology and photosynthetic pigments

Eleven-week-old seedlings were used to study the effects of NaCl and/or PGPB on leaf morphology after a two-week treatment under hydroponic conditions. The results showed that both salt stress and PGPB affected the leaf morphology of *A. pictum* (Figs. 4a–4d). Sodium at a concentration of 150 mmol/L caused a significant reduction in leaf length and leaf area, but did not affect leaf width. Inoculation with either PGPB strain markedly enhanced leaf length, width, and area (P<0.05), regardless of salt stress exposure. Except for leaf area under NaCl exposure, there were no significant differences between the effects of the two PGPB strains. Inoculation with *Enterobacter* sp. Av16 and *Acinetobacter* sp. Av23 resulted in about 65.0% and 106.0% increases in leaf area, respectively, compared to the non-inoculation treatment under 150 mmol/L NaCl exposure.

The contents of photosynthetic pigments were significantly reduced by salt stress (Figs. 4e and 4f). Under salt stress, both PGPB strains increased the contents of chlorophyll (by 13.3%–19.6%) and carotenoids (by 18.3%–24.1%). However, they did not affect the contents of these pigments in the absence of NaCl.

3.5.2 Photosynthetic parameters

Salt stress significantly inhibited (P<0.05) four photosynthetic parameters, including the net photosynthetic rate (P_n), G_s, intercellular carbon dioxide (C_i), and transpiration rate (T_r) in both PGPB-inoculation

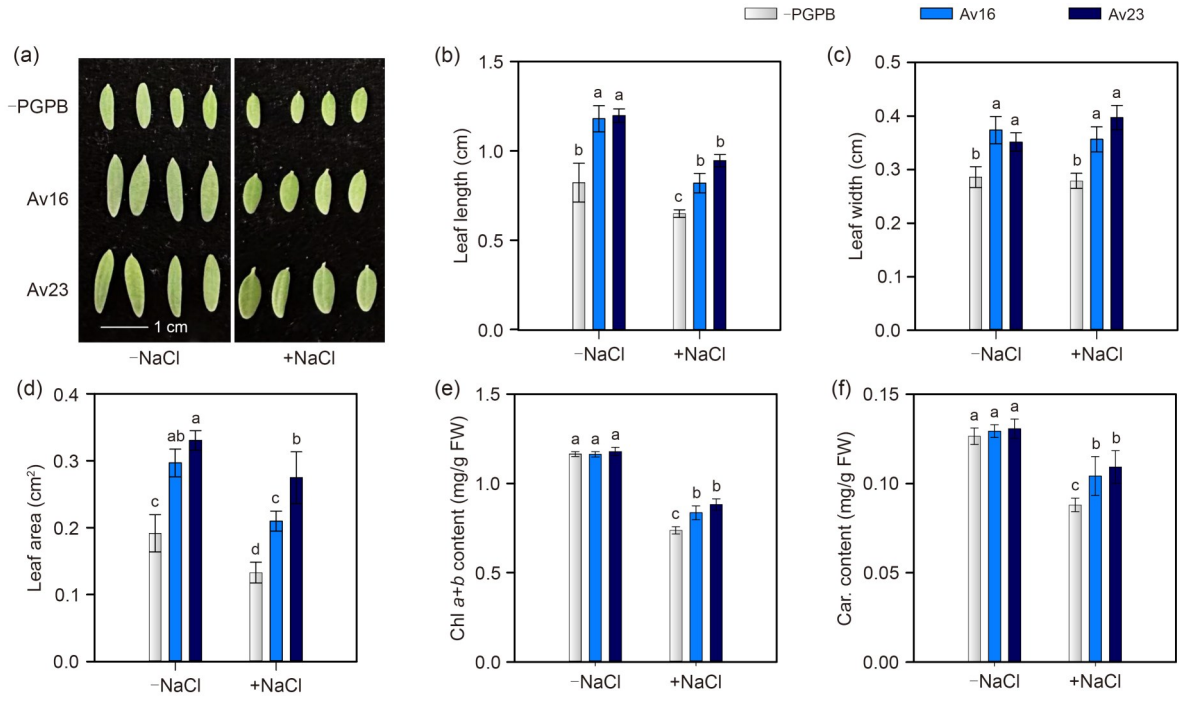

Fig. 4 Effects of *Enterobacter* sp. Av16 (Av16) and *Acinetobacter* sp. Av23 (Av23) on leaf morphology, chlorophyll content, and carotenoid content in *Apocynum pictum* leaves under different treatments. (a) Leaf morphology; (b) Leaf length; (c) Leaf width; (d) Leaf area; (e) Chlorophyll *a*+*b* content; (f) Carotenoid content. Data are expressed as mean±standard deviation (SD) (n=4). Different letters indicate significant differences between treatments (P<0.05). PGPB: plant growth-promoting bacteria; FW: fresh weight; Chl: chlorophyll; Car: carotenoid.

and non-inoculation treatments (Fig. 5). In the absence of NaCl, no significant differences were observed in these parameters between the treatments. However, under 150 mmol/L NaCl stress, seedlings inoculated with either PGPB strain exhibited significantly higher P_n, C_i, and T_r than non-inoculated seedlings, with increases of 20.2%–22.1%, 16.5%–18.9%, and 25.6%–28.7%, respectively, although G_s of inoculated seedlings was only slightly higher than that of non-inoculated individuals. G_s did not differ significantly between inoculated and non-inoculated seedlings, nor did four parameters differ between seedlings inoculated with *Enterobacter* sp. Av16 or those with *Acinetobacter* sp. Av23.

3.5.3 OJIP curves and chlorophyll fluorescence parameters

Figs. 6 and S5 show the chlorophyll fluorescence OJIP curve and OJIP-test parameters, respectively, which reflect the light re-emitted from PSII. Salt stress decreased the F_m, which was increased by PGPB, whereas the original fluorescence (F_o) of *A. pictum* seedlings remained unaffected by both PGPB and salt stress (Fig. S5a). As shown by the normalized curve, salt stress caused a rise of the relative variable fluorescence at time t (V_t) at K, J, and I phases (Figs. 6a and 6b). After inoculation with *Acinetobacter* sp. Av23, a decrease in V_t at the J phase was observed compared to treatments without PGPB. The results showed that salt stress and PGPB had opposite effects on the oxygen-evolving complex (OEC) activity and the electron transfer of PSII. The relative variable fluorescence of the O-J and O-I phases was normalized to obtain W_{OJ} and W_{OI}, respectively (Figs. S5b–S5f). Among all treatments, the highest W_{OJ} was observed with 150 mmol/L NaCl. ΔW_K, which is the W_{OJ} value at point K, reflects the activity of the OEC. Salt stress caused damage to the OEC, resulting in a significant increase of the ΔW_K value. Both Av16 and Av23 alleviated the injury to the OEC under salt exposure

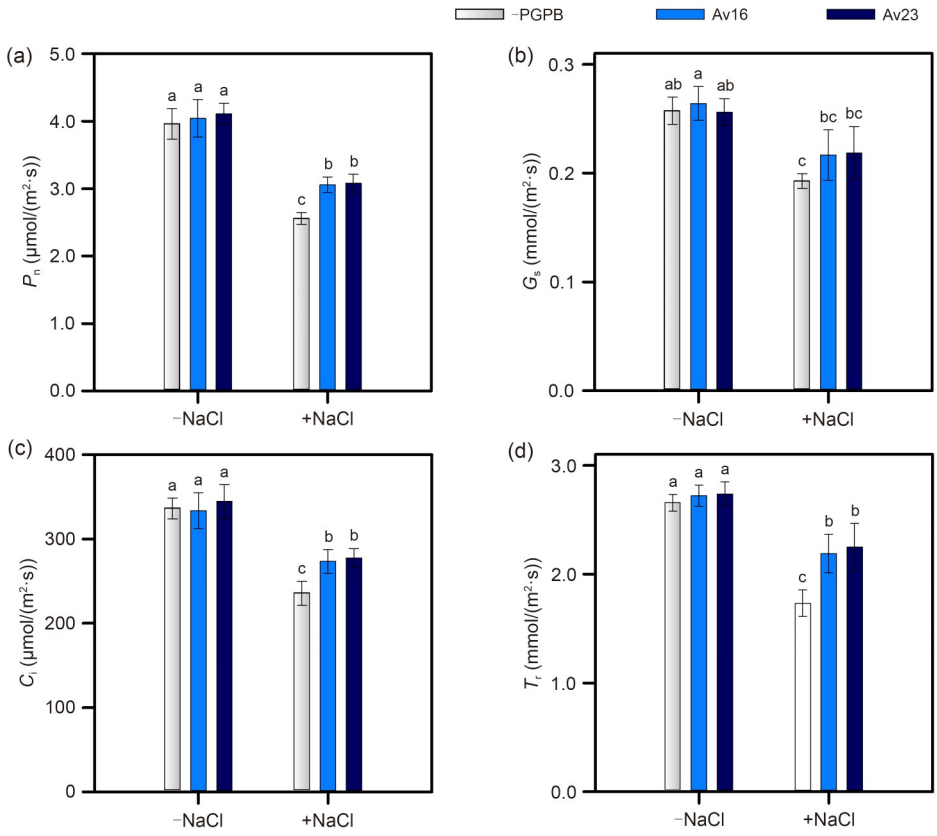

Fig. 5 Photosynthetic parameters of *Apocynum pictum* seedlings under different treatments. (a) Net photosynthetic rate (P_n); (b) Stomatal conductance (G_s); (c) Intercellular carbon dioxide (C_i); (d) Transpiration rate (T_r). Data are expressed as mean±standard deviation (SD) (n=4). Different letters indicate significant differences between treatments (P<0.05). PGPB: plant growth-promoting bacteria; Av16: *Enterobacter* sp. Av16; Av23: *Acinetobacter* sp. Av23.

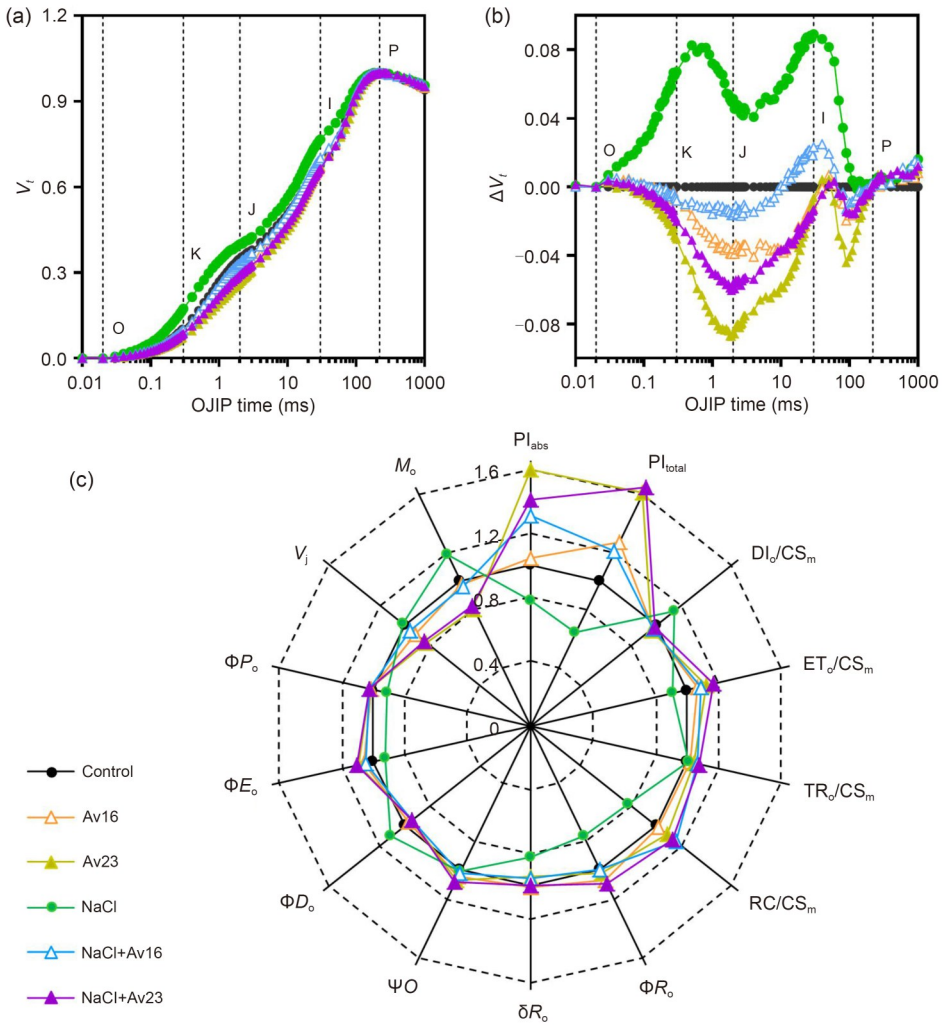

Fig. 6 Relative chlorophyll *a* fluorescence and fluorescence parameters of *Apocynum pictum* seedlings. The chlorophyll fluorescence induction (OJIP) curve was measured on the upper 3rd pair of leaves after dark adaptation for 30 min. Maximum fluorescence (F_m) was induced by applying a 1000-ms pulse of saturating light. The labels O, K, J, I, and P represent specific parameters at 0.02, 0.3, 2, 30, and 220 ms, respectively. (a) Normalized OJIP curves. V_t represents the relative variable fluorescence at time *t*. $V_t=(F_m-F_o)/(F_t-F_o)$, where F_o is original fluorescence and F_t is fluorescence intensity at time *t*. (b) $\Delta V_t=V_{t\,(treatment)}-V_{t\,(control)}$. (c) Relative chlorophyll *a* fluorescence parameters were calculated as the ratio of the parameter value in the treatment to that of the control. The data represent the means of four replicates. Av16: *Enterobacter* sp. Av16; Av23: *Acinetobacter* sp. Av23; M_o: initial slope of fluorescence transient (O-J), which reflects the net rate of PSII reaction center closure; V_j: relative variable fluorescence at 2 ms; ΦP_o: maximum quantum yield of primary photosystem II (PSII) photochemistry; ΦE_o: quantum yield for electron transport (*t*=0); ΦD_o: quantum yield for energy dissipation (*t*=0); ψO: probability that a trapped exciton moves an electron into the electron transport chain beyond quinone A (Q_A^-) at *t*=0; δR_o: efficiency with which an electron from PQH_2 is transferred to final PSI acceptors; ΦR_o: efficiency with which a PSII trapped electron is transferred to final PSI acceptors; RC/CS_m: amount of PSII RCs per CS at $t=t_{F_m}$; TR_o/CS_m: trapped energy flux cross-section (CS) at $t=t_{F_m}$; ET_o/CS_m: electron transport flux per CS at $t=t_{F_m}$; DI_o/CS_m: dissipated energy flux per active RC at $t=t_{F_m}$; PI_{abs}: performance index on absorption basis; PI_{total}: overall performance index.

(Figs. S5b and S5c). Inoculation with PGPB reduced W_{OI} at point J (W_J), indicating improved electron transfer from the reduced primary quinone (Q_A^-) to the secondary quinone (Q_B) on the acceptor side of PSII. No significant differences in ΔW_J were found between the control and NaCl treatment (Figs. 5Sd and 5Se). The lower W_{OJ} values on the W_{OJ} curve ($W_{OJ}\geqslant 1$) in the 150 mmol/L NaCl treatment showed that salt stress reduced the electron acceptor pool in photosystem I (PSI).

The OJIP parameters and their description are shown in Fig. 6c and Table S4. Salt stress reduced

the ΦP_o, quantum yield for electron transport (ΦE_o), efficiency of electron transfer to final PSI acceptors (δR_o and ΦR_o), density of active reaction centers per cross-section (RC/CS_m), electron transport flux per cross-section (ET_o/CS_m), performance index on absorption basis (PI_{abs}), and overall performance index (PI_{total}). Conversely, it increased the net closing rate of PSII RC (M_o) and the dissipated energy flux (ΦD_o and DI_o/CS_m). These results indicate that excess salt reduces the density of PSII RCs, and inhibits electron transfer in PSII and PSI, while increasing energy dissipation, leading to a dramatic decline in PI. Both PGPB strains mitigated the negative effects of salt on the photosystems, increasing ΦP_o, ΦE_o, δR_o, ΦR_o, RC/CS_m, and ET_o/CS_m, and enhancing the performance indices of *A. pictum* seedlings under salt stress.

3.6 Effects of *Enterobacter* sp. Av16 and *Acinetobacter* sp. Av23 on ROS and antioxidant enzymes of *A. pictum*

Salt stress induced an overproduction of ROS in the roots of *A. pictum* (Figs. 7a–7d). The roots of *A. pictum* treated with NaCl showed dark-brown and navy-blue staining, indicative of H_2O_2 and $O_2^{\cdot-}$ accumulation, respectively. The contents of H_2O_2 and $O_2^{\cdot-}$ increased significantly in the NaCl-treated roots compared to the untreated controls. Inoculation with both PGPB strains lessened the intensities of DAB and NBT staining, indicating reduced levels of H_2O_2 and $O_2^{\cdot-}$ in *A. pictum* roots under salt stress ($P<0.05$; Figs. 7a–7d). Salt stress and PGPB treatments under NaCl-treated conditions enhanced the activities of SOD and POD in the shoots and roots of *A. pictum*, except for SOD activity in the roots (Figs. 7e–7h). The results indicated that PGPB alleviated oxidative stress in *A. pictum* by increasing the activity of antioxidant enzymes.

4 Discussion

Excess salt hinders plant growth due to osmotic stress, ion imbalance, and oxidative stress (van Zelm et al., 2020). Seed germination and photosynthesis play key roles in plant colonization and ecological remediation of saline soils. In the present study, salt stress delayed seed germination and inhibited photosynthesis in *A. pictum* (Figs. 3, 5, and 6). These findings are consistent with previous studies that documented the inhibition of seed germination and/or a decrease in photosynthesis in various plants, including those within the genus *Apocynum* (Silva et al., 2018; Zhu et al., 2019; Jiang et al., 2021b).

Generally, bacteria with multiple plant growth-promoting traits play important roles in enabling plants to resist adverse environments, such as saline soils (Singh et al., 2018; Suman et al., 2022). In this study, of the 11 strains initially identified with at least three growth-promoting traits, only two strains (*Enterobacter* sp. Av16 and *Acinetobacter* sp. Av23) were confirmed to significantly promote the growth of *A. pictum* seedlings under salt stress (Table S5; Figs. 1 and 2). Consistent with our findings, salt-tolerant members of *Enterobacter* sp. and *Acinetobacter* sp. were shown to promote plant growth and/or salt resistance (Kang et al., 2023; Rahman et al., 2025). These bacteria are considered to have the potential to improve crop production, soil fertility, and ecosystem sustainability in saline environments.

PGPB has been reported to promote seed germination in *Arachis hypogaea*, *Achnatherum inebrians*, and rice (Jiang et al., 2019; Ju et al., 2021; Mahmud et al., 2023). In the present study, inoculation with *Enterobacter* sp. Av16 or *Acinetobacter* sp. Av23 significantly improved the germination percentage of *A. pictum* during the first 1–4 d by up to 41.3%, and enhanced germination potential, germination index, and seedling growth after 14 d of germination (Fig. 3). Similar findings have been reported previously. For instance, the results of Abdelkefi et al. (2024) showed that three PGPBs significantly enhanced the seed germination percentage of tomato by about 53.51%. These improvements may result from the effects of PGPB on phytohormones, including IAA, gibberellins (GAs), ABA, and ethylene, and are related to their ability to produce IAA (Table S5) (Aktar et al., 2023; Kang et al., 2023). The increased activity of antioxidant enzymes following PGPB inoculation also plays a role in enhancing seed germination and subsequent seedling growth (Fig. 7) (Ju et al., 2021; Hou et al., 2022; Azeem et al., 2025).

PGPB alleviated plant growth inhibition caused by salt stress. The shoot and root fresh weights of *A. pictum* inoculated with PGPB were 1.46–1.62 and 1.74–1.85 times higher, respectively, than those of non-inoculated plants (Fig. 1). Numerous studies showed that inoculation with PGPB resulted in a 24.0%–44.8% increase in the fresh weight of tomato and soybean seedlings (Kang et al., 2023; Abdelkefi et al., 2024).

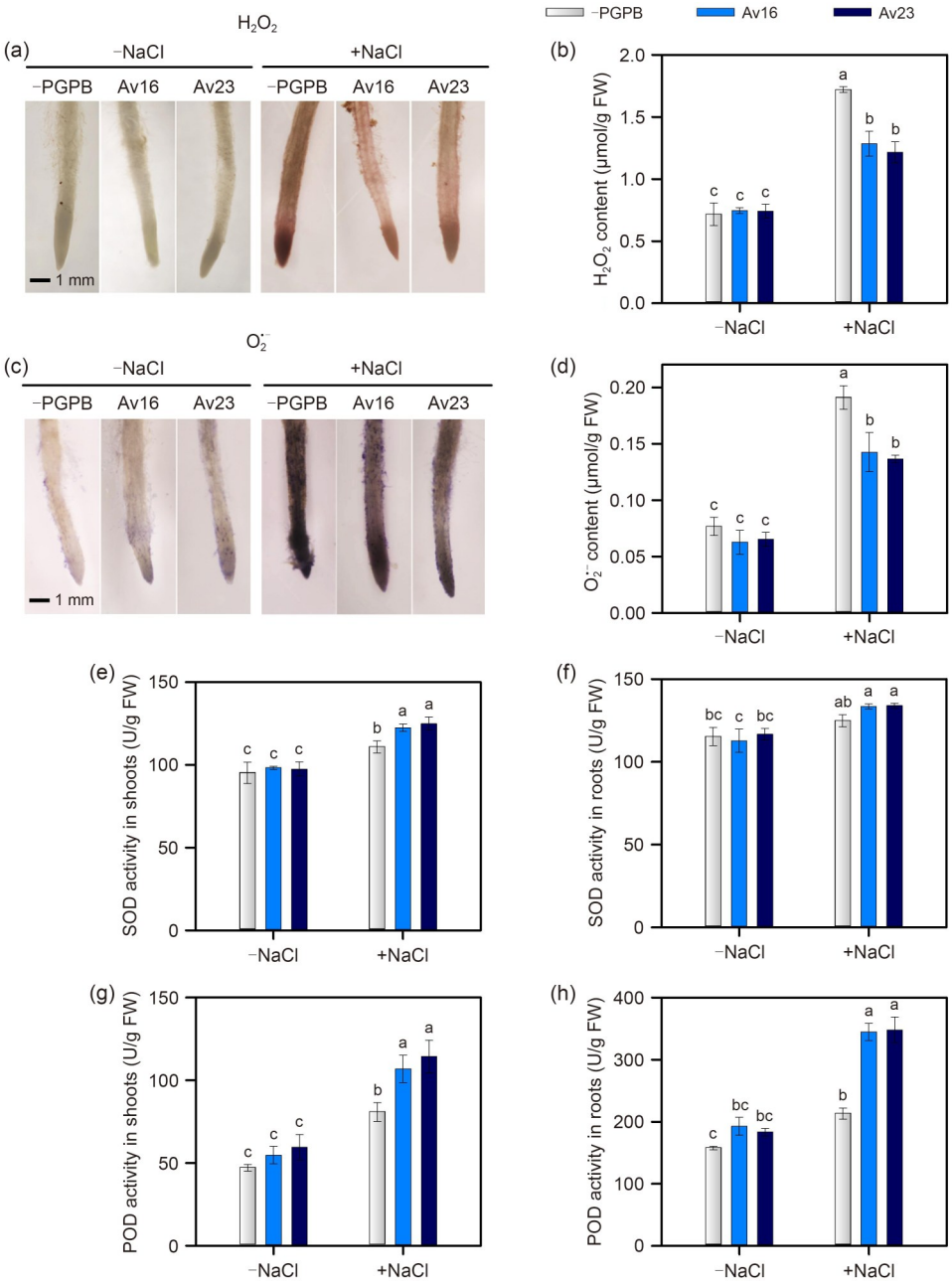

Fig. 7 Effects of plant growth-promoting bacteria (PGPB) on the localization and contents of hydrogen peroxide (H_2O_2) and superoxide ($O_2^{\cdot-}$), and the activities of superoxide dismutase (SOD) and peroxidase (POD) in *Apocynum pictum* seedlings. (a) 3,3'-Diaminobenzidine (DAB) staining of H_2O_2; (b) H_2O_2 content; (c) Nitroblue tetrazolium (NBT) staining of $O_2^{\cdot-}$; (d) $O_2^{\cdot-}$ content; (e, f) SOD activities in shoots (e) and roots (f); (g, h) POD activities in shoots (g) and roots (h). Data are expressed as mean±standard deviation (SD) (n=3). Different letters indicate significant differences between treatments (P<0.05). FW: fresh weight; Av16: *Enterobacter* sp. Av16; Av23: *Acinetobacter* sp. Av23.

An increase in leaf area is another manifestation of plant growth promotion by PGPB. Taj et al. (2024) reported that *Staphylococcus sciuri* ET101 increased the length and width of tomato leaves by 8.4%–19.3% and 17.5%–27.6%, respectively, under saline conditions. A similar observation was found in the present study, where inoculation of Av16 or Av23 resulted in significant increases in leaf length, width, and area by 29.1%–45.6%, 31.6%–42.3%, and 65.0%–106.6%, respectively (Fig. 4). The improvement of plant growth by PGPB is closely related to their ability to alleviate the inhibitory effects of salt stress on photosynthesis.

Inoculation with PGPB mitigates both stomatal and non-stomatal limitations of photosynthesis under saline conditions by increasing the osmotic adjustment substances, photosynthetic pigment levels, density of RCs, and electron transfer in photosystems (Chauhan et al., 2019; Guo et al., 2024; Taj et al., 2024). The degree of stomatal opening regulates photosynthesis, as stomata control the influx of carbon dioxide (CO_2) into leaves (Lawson et al., 2018; van den Berg et al., 2025). The present results showed that *A. pictum* seedlings inoculated with either *Enterobacter* sp. Av16 or *Acinetobacter* sp. Av23 exhibited significantly higher values of C_i, T_r, pigment contents, RC/CS_m, δR_o, and ΦR_o, as well as lower values of ΔW_K and ΔW_J compared to non-inoculated seedlings under salt stress (Figs. 4–6). These results show that a larger degree of stomatal opening was associated with higher activity of PSII in PGPB-inoculated seedlings. This, in turn, improves the overall photosynthetic parameters and plant growth. These findings align with the results on tomato reported by Taj et al. (2024), who observed that PGPB-enhanced stomatal opening facilitated greater CO_2 uptake and improved photosynthetic efficiency.

In the chloroplast, photosynthetic pigments, in combination with photosynthetic proteins, play roles in harvesting light energy and facilitating the photochemical reaction of PSII, which affects subsequent photosynthesis electron transport on thylakoid membranes (Fig. 6) (Chen et al., 2021; Wang et al., 2022). Salt stress causes a significant decline in photosynthetic pigments, including chlorophyll and carotenoids, by both inhibiting their synthesis and accelerating their degradation (Fig. 4) (Zhu et al., 2019; Tian et al., 2025). Several studies have reported that bacteria can markedly increase chlorophyll and carotenoid contents by 8.9%–28.2% in various plants under 100–240 mmol/L NaCl conditions (Kang et al., 2023; Ning et al., 2024; Azeem et al., 2025). Beneficial effects of PGPB on photosynthetic pigments were also observed in this study. The results showed that chlorophyll and carotenoid contents in *A. pictum* seedlings inoculated with PGPB were 13.4%–24.3% higher than those in non-inoculated seedlings (Fig. 4). Alterations in photosynthetic pigment levels are largely responsible for changes in individual photosynthetic rates under adverse conditions (Fig. 4) (Ma et al., 2020). Resultingly, similar trends were observed in photosynthetic pigment levels, photosynthetic rates, and chlorophyll fluorescence parameters, including F_m, ΦP_o, ΦE_o, δR_o, ΦR_o, RC/CS_m, ET_o/CS_m, PI_{abs}, and PI_{total} in *A. pictum* seedlings under salt stress and PGPB treatments (Figs. 4–6).

Salt stress disrupts electron transfer in PSII and PSI, resulting in excess accumulation of ROS, such as H_2O_2 and $O_2^{\cdot-}$, within chloroplasts (Jiang et al., 2020; Stefanov et al., 2024). This overproduction of ROS causes significant damage to photosynthetic pigments and the thylakoid membrane, impairing photosystem complexes and/or inactivating photosynthetic enzymes, leading to a decline in PI_{abs}, PI_{total}, and P_n under salt stress (Figs. 4–6) (Chen et al., 2021; Hameed et al., 2021). The PGPB *Enterobacter* sp. Av16 and *Acinetobacter* sp. Av23 activated antioxidant enzymes such as SOD and POD, which subsequently reduced ROS accumulation in plant tissues under salt stress (Fig. 7). The decline in ROS levels may have mitigated damage to photosynthetic pigments, membranes, and enzymes, thereby promoting the recovery of photosynthesis in *A. pictum*, which in turn enhanced plant growth (Figs. 5 and 7) (Tolba et al., 2019). Similarly, Guo et al. (2024) and Taj et al. (2024) reported that PGPB maintained steady-state ROS levels by activating the synthesis and activity of antioxidant enzymes, thereby alleviating salt-induced reduction in photosynthesis. This consistency across studies underscores the potential of the use of PGPB as a universal strategy to mitigate salt stress and improve plant productivity.

5 Conclusions

Two PGPB, *Enterobacter* sp. Av16 and *Acinetobacter* sp. Av23, were screened out for their ability to promote the growth of *A. pictum* seedlings. Both strains could secrete IAA, solubilize phosphate, fix nitrogen, and produce siderophore. Av16 and Av23 significantly enhanced both seed germination and seedling growth of *A. pictum*. The PGPB improved the ROS scavenging ability and alleviated the reduction of the photosynthetic pigments, RC density, electron transfer in photosystems, and stomatal gas exchange caused by salt stress, thereby enhancing the photosynthesis of *A. pictum* under saline conditions.

Data availability statement

The data that support the findings of this study are not openly available due to reasons of sensitivity and are available from the corresponding author upon reasonable request.

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Author contributions

Xue WANG contributed to the study design, conducted the experimental research, and performed data analysis. Li JIANG contributed to the study design, conducted the experimental research, and secured funding for the project. Yao GE performed the experimental research. Yiping ZOU performed data analysis, and wrote and edited the manuscript. Qingsheng CAI and Yan XIA wrote and edited the manuscript. Laiqing LOU contributed to the study design, data analysis, supervision, and funding acquisition, and wrote and edited the manuscript. All authors have read and approved the final manuscript, and therefore, have full access to all the data in the study and take responsibility for the integrity and security of the data.

Compliance with ethics guidelines

Xue WANG, Li JIANG, Yao GE, Yiping ZOU, Qingsheng CAI, Yan XIA, and Laiqing LOU declare that they have no conflicts of interest.

This article does not contain any studies with human or animal subjects performed by any of the authors.

Declaration on the use of generative AI tools

During the preparation of this manuscript, the authors used DeepSeek-V3 to improve language and readability in March 2025, when we revised the manuscript according to the reviewers' comments. After using this tool, the authors carefully reviewed and edited the related content as needed and take full responsibility for the content of the published article.

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Supplementary information

Figs. S1–S5; Tables S1–S6; Materials and methods