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Effect of *Streptomyces* Inoculation on *Ipomoea aquatica* and *Pachyrhizus erosus* Grown Under Salinity and Low Water Irrigation Conditions

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ABSTRACT

The distribution of salty areas and drought conditions caused by climate change can limit successful crop production. The co-occurrence of salinity and drought gives a unique challenge for plant growth-promoting bacteria (PGPB) in agricultural purposes. In this study, the effect of irrigation and salinity on the abilities of isolates of plant growth-promoting bacteria (*Streptomyces* sp. St1 and St8) to promote the growth of *Ipomoea aquatica* and *Pachyrhizus erosus* was investigated. Both plants were planted in pots with combinations of salinity (non-saline or saline soil), different irrigation levels, and different bacterial inoculations. The results showed that the salinity decreased the root dry weight of *I. aquatica* and decreased the shoot and root dry weight of *P. erosus*. Salinity also decreased the tuber formation and root efficiency of *P. erosus*. Low irrigation and bacterial species did not affect either plant's shoot or root growth. However, the chlorophyll content in the leaves of both plants decreased in the inoculated plants compared to the non-inoculated plants. Among the three factors in this study, salinity was the most influential factor, and irrigation was the least effective factor on plant growth for both parts. Soil salinity may concern plant growth-promoting bacteria, and salt-tolerant strains may be an interesting choice for use in combination with saline and low water conditions.

Keywords: Drought stress, economic crop, plant growth-promoting bacteria, salt stress, *Streptomyces*

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INTRODUCTION

Using plant growth-promoting bacteria (PGPB) is a promising environmentally friendly method to increase the growth of several plants for both agricultural and environmental purposes. However, salinity and drought can affect the growth of both plants and bacteria. Chloride ions are toxic to bacteria via induction of acidification in the cytoplasm (Rivera-Araya et al., 2020). A lack of available water and exposure to a high concentration of salt results in bacterial cells encountering hyperosmotic stress. This stress decreases microbial growth and inhibits many essential cellular functions (Guan et al., 2017). Soil salinity causes decreases in crop growth and yield. The germination rate, shoot length, root length, and biomass of many plant species that have received saline wastewater decrease with an increase in the salinity (Calheiros et al., 2012). In addition, plants exposed to salinity led to an increased sodium ion (Na^+) content in the tissue and induced oxidation stress in the plant (A. Kumar et al., 2021). Soluble salt accumulation in the root zone may disrupt plant water uptake and essential nutrient absorption (Leogrande & Vitti, 2018). In addition, drought stress increased the oxidation stress, chloroplast damage, and destruction of chlorophyll in plants (Munné-Bosch et al., 2001).

Several semi-arid and arid areas in Asia encounter drought and salinity problems, and they are distributed in South Asia, Central Asia, and North Africa (Aryal et al., 2020; Kilroy, 2015). In Thailand, there are around 2.3 million hectares of salt-affected soil, and more than three-quarters of this is in the north-eastern part of the country (Somsri & Pongwichian, 2015). The slight to moderate levels of saline soil in these areas are normally used to cultivate many crops in Thailand, including rice (Somsri & Pongwichian, 2015). In addition to the problems of salt-affected soil, climate change induces prolonged drought, which is an important issue because this decreases agricultural productivity (Aryal et al., 2020; Marks, 2011). Salt and drought stress expose plants to osmotic stress, nutrient deficiency, and ion imbalance in soil (Hussian et al., 2018; Shankar & Evelin, 2019), which results in subsequent decreases in their productivity.

There are several mechanisms in PGPB that can stimulate plant growth under drought and salt stresses. For example, ACC deaminase production could decrease the ethylene level in plants, indole-3-acetic acid (IAA) production increases the root surface area, which subsequently increases the water and nutrient uptake, exopolysaccharide production increases the soil water holding capacity, and phosphate solubilizing activity increases the phosphate uptake in plants (Ilangumaran & Smith, 2017; Ojuederie et al., 2019). Several PGPB has been used to stimulate plant growth under salt or drought stresses (Ansari et al., 2019; Batool et al., 2020; Bharti et al., 2016).

Among several PGPB species, successful use of the bacteria in genus *Streptomyces* has been reported to promote crop growth under drought or salt stress conditions. For example, *Streptomyces* sp. isolate IT25, which can produce ACC deaminase, could prevent yield losses in

tomatoes cultivated under drought stress (Abbasi et al., 2020). Actinobacteria's cell-free extract produced phytohormones and siderophores and induced plant reactive oxygen species scavengers and osmoprotectants, improved corn growth under normal and drought conditions (Warrad et al., 2020). *Streptomyces* strain C-2012 could increase the chlorophyll and carotenoid levels and reduce the Na^+ content in wheat cultivars Zarin and Gonbad, and this helped alleviate the negative effect of salt stress (Akbari et al., 2020). Most research studies have focused on only one stress, either salt or drought, but when using PGPB to stimulate the growth of plants under a combination of stresses, there is little work. It would be interesting for cultivation in drought and saline areas. In addition, different physiologies of plants may respond to a combination of these stresses and the inoculant strain in different ways.

Thus, this study was carried out to investigate the effect of irrigation, salinity, and isolates of PGPB on their ability to promote the growth of *I. aquatica* and *P. erosus*. *Streptomyces* sp. St1 and *Streptomyces* sp. St8, the selected isolates, were PGPB with the ability to produce indole-3-acetic acid (IAA) and phosphate solubilization (Somtrakoon et al., 2019). *Ipomoea aquatica* and *P. erosus* were the selected plant species with different habitats. *Ipomoea aquatica* is an herbaceous plant and has been reported to survive in saline soil, while *P. erosus* is a tuber plant and can grow in several parts of Thailand. These results will be useful for selecting potential PGPB to be used as biofertilizers in agricultural areas facing drought and salt stress in the future.

MATERIALS AND METHODS

Preparation of Immobilized Cells + Spores of *Streptomyces* St1 and St8

Streptomyces sp. St1 and *Streptomyces* sp. St8 was isolated from soil planted with mango trees in Kosumphisai District, Maha Sarakham Province, and Kalasin Province, respectively, by A. Sangdee. The morphology of the colonies and spore chains of these bacteria are shown in Figure 1. The immobilization of both isolates were done according to the method described in Somtrakoon et al. (2021). Briefly, *Streptomyces* sp. St1 and St8 were cultured in a half formulation of potato dextrose agar (PDA) (Himedia, India, pH 5.2–5.3) for 16 days. Then, the cells + spore suspensions of *Streptomyces* sp. St1 and St8 were scrapped and transferred into 0.85 % sodium chloride (NaCl). Coconut husk was autoclaved at 121 ºC for 15 min before use. Then the autoclaved coconut husk was soaked in the cells + spore suspensions of *Streptomyces* sp. St1 and St8 for 3 h. The cell numbers of *Streptomyces* sp. St1 and St8 in the coconut husk after the immobilization process were counted by the spread plate method with a half formulation of potato dextrose agar. Initially, both bacterial isolates were around 10^4 cell/g of coconut husk. Then, 7 g of coconut husk with immobilized cells of *Streptomyces* sp. St1 or St8 were used in the experimental pots—autoclaved coconut husk without cells of *Streptomyces* sp. St1 and St8 were used in the control pots.

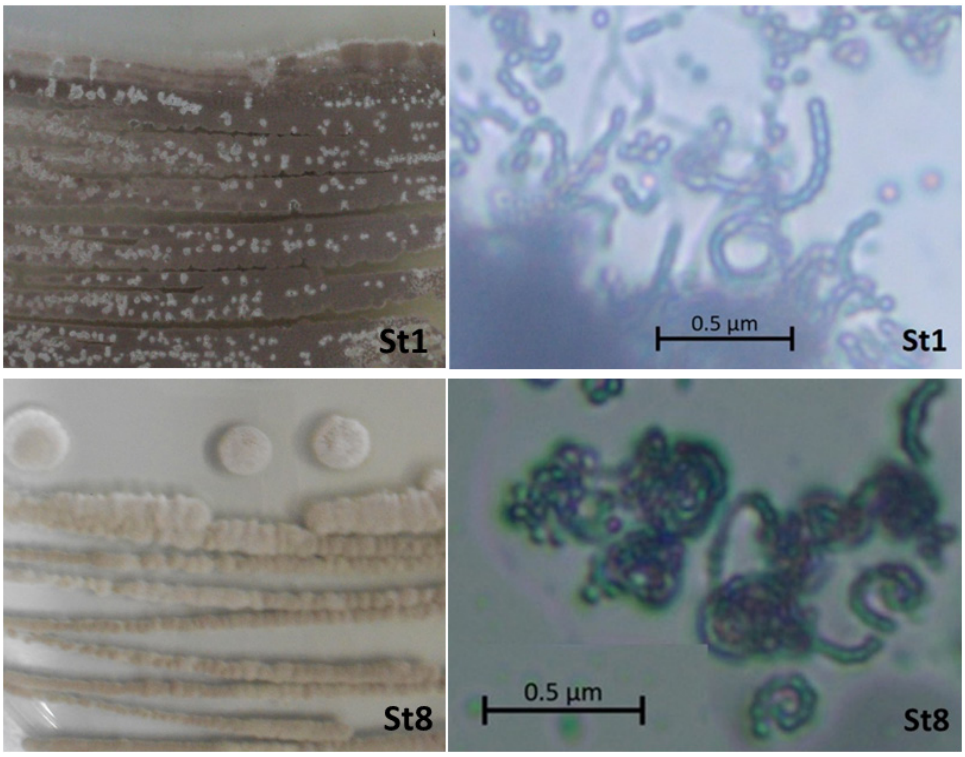

Figure 1. Morphology of colonies and spore chains of *Streptomyces* sp. St1 and *Streptomyces* sp. St8 growing on half formula of PDA for 14 days

Soil Preparation and Experimental Design

The soil was collected from Takhianluan Sub-district, Muang District, Nakhon Sawan Province, Thailand, and sent for character analysis at the Central Laboratory (Thailand) Company Limited, Khonkaen Province, Thailand. Saline soil was prepared by adding 0.4 % w/w of NaCl to the soil before sending it for analysis. Soil without NaCl addition was used as the non-saline soil. The soil characteristics analyzed in this study were soil texture, pH, cation-exchange capacity, organic matter, available phosphorus, total nitrogen, and total potassium. The physical and chemical characteristics of these soils are listed in Table 1. The experiment was laid out in a 2x2x3 factorial completely randomized design (CRD). The details of each factor for each plant are shown in Table 2. Each treatment was performed in seven replicates.

Stimulation of Growth of Crops Under Low Water Irrigation

According to a previous study, the pot experiment was done with some adaptation (Somtrakoon et al., 2022). The seeds of

I. aquatica and *P. erosus*, which were commercial seeds from Nakhon Ratchasima Province, Thailand, were soaked in distilled water for 5 h before sowing in each pot containing 2 kg soil/pot. After thinning the five-day-old, germinated seedlings to one plant per pot, the inoculation of immobilized bacteria in coconut husk was done. It was the first day of the experiment. The irrigation levels of *I. aquatica* and *P. erosus* were different. For *I. aquatica*, 20 mL of distilled water was watered every day in normal irrigation, and 20 mL of distilled water was used every other day in low irrigation. For *P. erosus*, 20 mL of distilled water was watered every other day in normal irrigation, and 20 mL of distilled water was used every other day in low irrigation. The experiment ended 45 days after germination for both plants—the total levels of *Streptomyces* sp. St1, St8, and other bacteria in the soil from each treatment were counted on a half formulation of PDA on the last day of the experiment. Each plant's shoot and root growth were determined, including length, dry weight, chlorophyll content, and leaf number. The chlorophyll content was determined according to the method described in Huang et al. (2004). Briefly, 200 mg of small leaves were incubated in 80% acetone at 4 ºC for 24 h in the dark. The absorbance of the acetone solution was measured with a spectrophotometer at 645 and 663 nm and the chlorophyll concentrations (mg/mL) were calculated using the following equations:

$$[\text{Chl } a] = [12.7 \times A663] - [2.69 \times A645]$$

$$[\text{Chl } b] = [22.9 \times A645] - [4.68 \times A663]$$

$$[\text{Total Chl}] = [8.02 \times A663] + [20.2 \times A645]$$

where,
Chl *a* = Chlorophyll *a* content
Chl *b* = Chlorophyll *b* content
Total Chl = Total chlorophyll content
A645 = Absorbance at a wavelength of 645 nm
A663 = Absorbance at a wavelength of 663 nm

Statistical Analysis

One-way, two-way, and three-way analyses of variance tests were used for the main effects at $P \leq 0.05$. In addition, pairwise comparisons of mean treatment of parameters for the significant effect were carried out using the least square difference test (LSD test) at $P \leq 0.05$.

RESULTS AND DISCUSSION

Shoot and Root Growth of *Ipomoea aquatica*

Bacterial inoculation, salinity, and irrigation did not affect the shoot growth of *I. aquatica*. On the other hand, these factors affected the root growth of *I. aquatica* (Table 3). Salinity decreased the root dry weight significantly while low irrigation increased the root length of *I. aquatica*. Following inoculation with *Streptomyces* sp. St8, the root dry weight of *I. aquatica* in treatment 6 was increased compared to treatment 12.

Table 1

Characteristics of soil used in this study

Characteristic	Non-saline soil	Saline soil	Method
Soil texture	Sandy loam	Sandy loam	Mechanical analysis, pipette method
% sand	67.46 %	65.27 %	
% silt	22.76 %	18.66 %	
% clay	9.78 %	16.07 %	
Electrical conductivity	1.33	2.61 ds/m	A handbook of soil analysis (Chemical and physical method) 1/2553
pH	7.80	7.94	A handbook of soil analysis (Chemical and physical method) 1/2553
Organic matter	0.13 %	0.17 %	A handbook of soil analysis (Chemical and physical method) 1/2553
Available phosphorus	237.80 mg/kg	243.43 mg/kg	A handbook of soil analysis (Chemical and physical method) 1/2553
Total nitrogen	0.20 %	0.27 %	A handbook of soil analysis (Chemical and physical method) 1/2553
Total potassium (Total K_2O)	0.54 %	0.54 %	Manual of fertilizer analysis, APSRDO, DOA; 4/2551

Note. Commercial analysis at Central Laboratory (Thailand) Company Limited, Khonkaen Province, Thailand

Table 2

Details of each treatment in this experiment

Treatment no.	Factor 1soil	Factor 2 irrigation	Factor 3 bacterial isolates
1	Non-saline soil	Normal irrigation	Non-inoculation
2			*Streptomyces* sp. St1
3			*Streptomyces* sp. St8
4		Low irrigation	Non-inoculation
5			*Streptomyces* sp. St1
6			*Streptomyces* sp. St8

Table 2 *(Continue)*

Treatment no.	Factor 1 soil	Factor 2 irrigation	Factor 3 bacterial isolates
7	Saline soil	Normal irrigation	Non-inoculation
8			*Streptomyces* sp. St1
9			*Streptomyces* sp. St8
10		Low irrigation	Non-inoculation
11			*Streptomyces* sp. St1
12			*Streptomyces* sp. St8

In addition, *Streptomyces* sp. St1 inoculation tended to decrease the root length of *I. aquatica* compared with the *Streptomyces* sp. St8 inoculation. *Streptomyces* sp. St8 inoculation to *I. aquatica* growing in treatment 3 decreased the root length, shorter than those growing in treatment 6 (Table 4).

Inoculation with *Streptomyces* sp. St1 and St8 tended to increase the specific root length of *I. aquatica* in treatments 8-9 and 11–12 compared with treatments 2–3 and 5–6. The root to shoot ratio of *I. aquatica* tended to increase in treatments 4 and 10, but the root to shoot ratio of *I. aquatica* inoculated with *Streptomyces* sp. St1 and St8 tended to increase in treatments 5–6 only, but not observed in treatments 11–12. This result showed that low irrigation to *I. aquatica* tended to decrease the root efficiency to produce shoot biomass in both soils. *Streptomyces* inoculation to *I. aquatica* receiving low irrigation could resemble the root efficiency of those receiving normal irrigation in saline soil, but it is still deceased in non-saline soil (Table 4).

All factors, salinity, irrigation, and bacterial inoculation affected the chlorophyll content in *I. aquatica* in several ways. Salinity significantly increased the chlorophyll content, while *Streptomyces* inoculation decreased. In addition, low irrigation decreased the leaf size (Figure 2) and the chlorophyll *a* and total chlorophyll contents significantly. However, when considered for each soil separately, the inoculation of *Streptomyces* sp. St8 to *I. aquatica* in treatment 6 increased the chlorophyll a and total chlorophyll contents, which were 2.40 and 3.90 mg/mL respectively, and 4.68 and 7.72 mg/mL respectively in treatment 12 when compared with *I. aquatica* in treatments 3 and 9 (1.86 and 2.92 mg/mL in non-saline soil and 2.24 and 6.49 mg/mL in saline soil, respectively), as shown in Table 5.

Decreases in length and biomass are often found in plants exposed to salt or drought stresses. Increased oxidation stress, chloroplast damage, and destruction of chlorophyll followed by the plant senescence process were observed to start (Munné-Bosch et al., 2001). Maintaining the chlorophyll content under salt stress

Table 3

Effect of soil, irrigation, and bacterial isolate on Ipomoea aquatica *growth traits*

	Number of leaves	Shoot length (cm)	Shoot dry weight (g)	Root length (cm)	Root dry weight (g)	Chlorophyll *a* (mg/ml)	Chlorophyll *b* (mg/ml)	Total chlorophyll (mg/ml)
Soil (factor 1)								
Non-saline soil	3.0b	18.0	0.04	5.5	0.022a	3.22b	1.91b	5.13b
Saline soil	3.9a	16.0	0.03	4.9	0.013b	3.25a	4.27a	7.53a
F-test	*	ns	ns	ns	**	**	**	**
Irrigation (factor 2)								
Normal irrigation	3.8	15.7	0.04	4.4b	0.015	3.28a	2.93b	6.20b
Low irrigation	3.2	18.2	0.03	6.0a	0.020	3.19b	3.26a	6.45a
F-test	ns	ns	ns	**	ns	**	**	**
Bacterial isolate (factor 3)								
Control	3.5	17.3	0.03	4.9ab	0.015	4.10a	4.23a	8.33a
St1	3.0	15.6	0.03	4.7b	0.016	2.81b	2.58b	5.40b
St8	3.9	18.0	0.04	6.0a	0.022	2.80b	2.46b	5.26c
F-test	ns	ns	ns	*	ns	**	**	**
F-test								
Soil x irrigation	ns	ns	ns	ns	**	**	**	**
Soil x bacterial isolate	ns	ns	ns	ns	ns	**	**	**
Irrigation x bacterial isolate	ns	ns	ns	ns	ns	**	**	**
Soil x irrigation x bacterial isolate	ns	ns	ns	*	ns	**	**	**

Note. Different lower-case letters show significant differences within each factor by LSD test at $P \leq 0.05$; Abbreviations: ns, *, ** denote non-significance ($P \geq 0.05$), statistical significance ($P \leq 0.05$), and high statistical significance ($P \leq 0.01$), respectively.

Table 4

Growth of Ipomoea aquatica *in presence or absence of* Streptomyces *sp. when cultivated under non-saline soil and saline conditions for 45 days (Mean ± Standard Error)*

		Shoot		
		Leaf number	Length (cm)	Dry weight (g)
Non-inoculation				
Non-saline soil	Normal irrigation (T1)	3.7 ± 0.98Aa	16.7 ± 0.72Aa	0.030 ± 0.003Aa
	Low irrigation (T4)	2.8 ± 0.41Aa	19.3 ± 2.28Aa	0.042 ± 0.006Aa
Saline soil	Normal irrigation (T7)	4.8 ± 0.74Aa	18.1 ± 1.38Aa	0.046 ± 0.008Aa
	Low irrigation (T10)	3.0 ± 0.47Aa	15.1 ± 2.79Aa	0.162 ± 0.020Aa
***Streptomyces* sp. St1**				
Non-saline soil	Normal irrigation (T2)	3.4 ± 0.46Aa	18.5 ± 4.59Aa	0.041 ± 0.011Aa
	Low irrigation (T5)	2.0 ± 0.40Aa	16.4 ± 4.41Aa	0.036 ± 0.010Aa
Saline soil	Normal irrigation (T8)	3.0 ± 0.61Aa	11.0 ± 1.91Aa	0.024 ± 0.004Aa
	Low irrigation (T11)	3.8 ± 0.96Aa	16.6 ± 1.06Aa	0.173 ± 0.025Aa
***Streptomyces* sp. St8**				
Non-saline soil	Normal irrigation (T3)	3.4 ± 0.46Aa	13.4 ± 2.91Aa	0.037 ± 0.010Aa
	Low irrigation (T6)	3.0 ± 0.35Aa	23.5 ± 0.93Aa	0.043 ± 0.003Aa
Saline soil	Normal irrigation (T9)	4.5 ± 0.75Aa	16.8 ± 3.43Aa	0.049 ± 0.011Aa
	Low irrigation (T12)	4.7 ± 0.77Aa	18.4 ± 1.85Aa	0.204 ± 0.019Aa

Table 4 *(Continue)*

		Root			
		Length (cm)	Dry weight (g)	Specific root length (m/g)	Root to shoot ratio
Non-inoculation					
Non-saline soil	Normal irrigation (T1)	5.3 ± 1.31Aa	0.011 ± 0.003Aa	5.02	0.358
	Low irrigation (T4)	4.9 ± 0.51Aa	0.021 ± 0.004Aa	2.36	0.498
Saline soil	Normal irrigation (T7)	4.2 ± 0.35Aa	0.016 ± 0.004Aa	2.55	0.354
	Low irrigation (T10)	5.3 ± 0.17Aa	0.012 ± 0.004Aa	4.52	0.604
***Streptomyces* sp. St1**					
Non-saline soil	Normal irrigation (T2)	4.3 ± 0.78Aa	0.016 ± 0.004Aa	2.70	0.389
	Low irrigation (T5)	6.8 ± 0.79Aa	0.030 ± 0.007Aa	2.23	0.849
Saline soil	Normal irrigation (T8)	3.5 ± 0.28Aa	0.009 ± 0.003Aa	3.71	0.394
	Low irrigation (T11)	4.2 ± 0.72Aa	0.010 ± 0.002Ba	4.14	0.374
***Streptomyces* sp. St8**					
Non-saline soil	Normal irrigation (T3)	3.4 ± 0.53Ab	0.018 ± 0.005Aa	1.90	0.478
	Low irrigation (T6)	8.6 ± 0.56Aa	0.036 ± 0.003Aa	2.38	0.838
Saline soil	Normal irrigation (T9)	5.7 ± 0.73Aa	0.020 ± 0.003Aa	2.82	0.410
	Low irrigation (T12)	6.4 ± 0.71Aa	0.013 ± 0.002Ba	5.08	0.390

Note. Different lower-case letters show significant differences between different irrigation treatments for the same soil at each bacterial inoculation by LSD test at $P \leq 0.05$; Different capital letters show significant differences between different soils for the same irrigation treatment at each bacterial inoculation by LSD test at $P \leq 0.05$

Table 5

Chlorophyll content in leaves of Ipomoea aquatica *and* Pachyrhizus erosus *in presence or absence of* Streptomyces *sp. when cultivated under non-saline soil and saline conditions for 45 days (Mean ± Standard Error)*

		Ipomoea aquatica		
		Chlorophyll *a* content (mg/ml)	Chlorophyll *b* content (mg/ml)	Total chlorophyll content (mg/ml)
Non-Saline Soil				
Normal irrigation	Non-inoculation (T1)	5.75 ± 0.01Aa	3.34 ± 0.02Aa	9.08 ± 0.02Aa
	Streptomyces sp. St1 (T2)	3.51 ± 0.01Ab	2.25 ± 0.01Ab	5.77 ± 0.01Ab
	Streptomyces sp. St8 (T3)	1.86 ± 0.01Bc	1.06 ± 0.01Bc	2.92 ± 0.01Bc
Low irrigation	Non-inoculation (T4)	3.33 ± 0.01Ba	1.74 ± 0.01Ba	5.07 ± 0.01Ba
	Streptomyces sp. St1 (T5)	2.44 ± 0.01Bb	1.58 ± 0.01Bb	4.03 ± 0.00Bb
	Streptomyces sp. St8 (T6)	2.40 ± 0.01Ac	1.50 ± 0.02Ac	3.90 ± 0.00Ac
Saline Soil				
Normal irrigation	Non-inoculation (T7)	3.46 ± 0.03Ba	4.69 ± 0.20Ba	8.16 ± 0.18Ba
	Streptomyces sp. St1 (T8)	2.86 ± 0.01Ab	1.96 ± 0.03Bb	4.82 ± 0.02Bc
	Streptomyces sp. St8 (T9)	2.24 ± 0.01Bc	4.25 ± 0.02Aa	6.49 ± 0.01Bb
Low irrigation	Non-inoculation (T10)	3.87 ± 0.01Ab	7.16 ± 0.07Aa	11.03 ± 0.05Aa
	Streptomyces sp. St1 (T11)	2.43 ± 0.03Bc	4.53 ± 0.18Ab	6.96 ± 0.15Ac
	Streptomyces sp. St8 (T12)	4.68 ± 0.01Aa	3.04 ± 0.04Bc	7.72 ± 0.03Ab

Table 5 *(Continue)*

		Pachyrhizus erosus		
		Chlorophyll *a* content (mg/ml)	Chlorophyll *b* content (mg/ml)	Total chlorophyll content (mg/ml)
Non-Saline Soil				
Normal irrigation	Non-inoculation (T1)	3.21 ± 0.06A	3.83 ± 0.35A	7.04±0.28A
	Streptomyces sp. St1 (T2)	B.D.	B.D.	B.D.
	Streptomyces sp. St8 (T3)	B.D.	B.D.	B.D.
Low irrigation	Non-inoculation (T4)	1.29 ± 0.13Ba	1.77 ± 0.12Bb	3.06 ± 0.07Bb
	Streptomyces sp. St1 (T5)	1.88 ± 0.17a	3.19 ± 0.33a	5.07 ± 0.39a
	Streptomyces sp. St8 (T6)	1.28 ± 0.13a	2.05 ± 0.20b	3.33 ± 0.33b
Saline Soil				
Normal irrigation	Non-inoculation (T7)	3.43 ± 0.01A	3.87 ± 0.20A	7.30 ± 0.19A
	Streptomyces sp. St1 (T8)	B.D.	B.D.	B.D.
	Streptomyces sp. St8 (T9)	B.D.	B.D.	B.D.
Low irrigation	Non-inoculation (T10)	1.45 ± 0.29Ba	2.04 ± 0.30Aa	3.49 ± 0.59Ba
	Streptomyces sp. St1 (T11)	B.D.	B.D.	B.D.
	Streptomyces sp. St8 (T12)	1.44 ± 0.34a	1.38 ± 0.46a	2.82 ± 0.19a

Note. Different lower-case letters show significant differences between different inoculations for the same irrigation treatment at each soil by LSD test at $P \leq 0.05$; Different capital letters show significant differences between different irrigation treatments for the same inoculation at each soil by LSD test at $P \leq 0.05$; B.D. means that all leaves were brown and dry

indicated plant tolerance. The chlorophyll content decreased in gac (*Momordica cochinchinensis*) leaves related to an increase in the electrolyte leakage and antioxidant enzymes (Jumpa et al., 2017). Drought stress also decreased the total chlorophyll content in finger millet leaves, but inoculation with some drought-tolerant bacteria could increase the chlorophyll content (Chandra et al., 2018). However, only the root dry weight of *I. aquatica* was decreased by salinity, and only chlorophyll content was decreased by low irrigation when inoculation with *Streptomyces* sp. St1 or non-inoculation. Inoculation with *Streptomyces* sp. St8 seemed helpful for the root length and chlorophyll content of *I. aquatica* growing in low irrigation and non-saline soil.

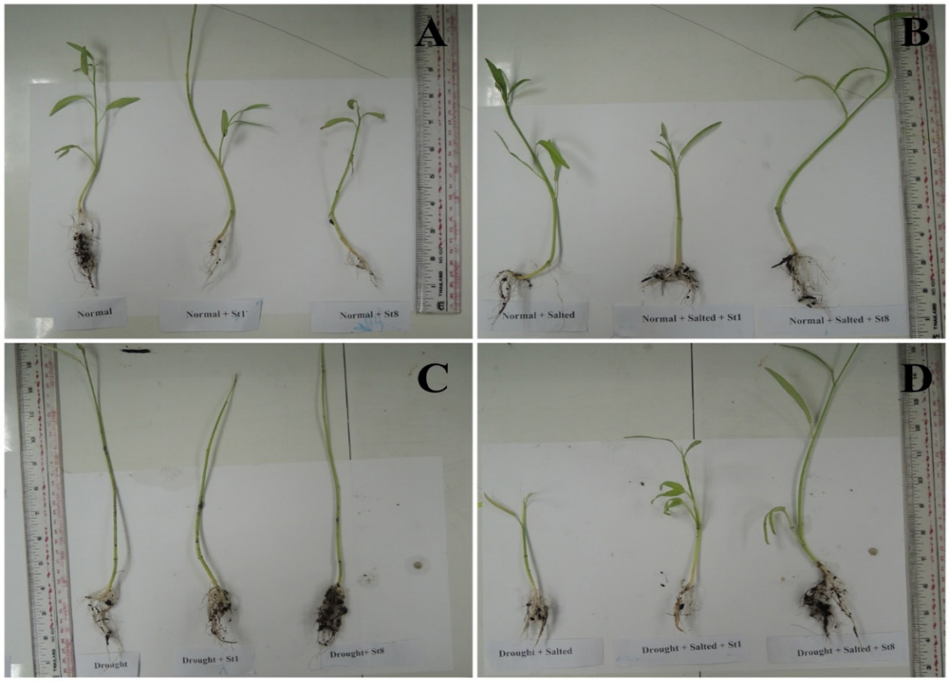

Figure 2. Characteristics of shoot and root of *Ipomoea aquatica* grown under non-saline soil + normal irrigation (A), saline soil + normal irrigation (B), non-saline soil + low water (C), and saline soil + low water conditions (D)

Shoot and Root Growth of *Pachyrhizus erosus*

Only salinity decreased the shoot and root dry weight of *P. erosus* significantly. At the same time, irrigation and bacterial inoculation did not affect the shoot and root growth of *P. erosus* but affected the chlorophyll content in the plant (Table 6). The interaction of drought and salinity stress affected the leaf area and relative water in canola leaves (Sharif et al., 2018). An additive effect of water deficit and salinity

was found on the chlorophyll fluorescence in tomato leaves (Kautz et al., 2014). However, an interaction of soil salinity and irrigation was found clearly on the root dry weight and chlorophyll content in leaves of *I. aqutica*, but it was not seen for *P. erosus*. Only irrigation affected the chlorophyll content in the leaves of *P. erosus*.

Salinity decreased the dry shoot weight of *P. erosus* when receiving normal irrigation and inoculation with *Streptomyces* sp. St1 or non-inoculation. On the other hand, salinity decreased the root dry weight of *P. erosus* when receiving normal irrigation and non-inoculation only (Table 7). The specific root length of *P. erosus* tended to increase in saline soil compared with non-saline soil under all irrigation and bacterial inoculation treatments. For example, the specific root length of *P. erosus* growing in treatment 7 was 2.55 when it was 1.89 in treatment 1 (Table 7). The root to shoot ratio of *P. erosus* tended to decrease in treatments 10-12 (0.085–0.127) compared with that grown in treatments 7–9 (0.112–0.199). The result revealed that low irrigation to *P. erosus* in saline soil tended to increase the efficiency of the root to produce shoot biomass. Tuber formation of *P. erosus* decreased when planted in saline soil with normal irrigation and bacterial inoculation (Table 7).

The leaves of *P. erosus* in some *Streptomyces* inoculation treatments (all *Streptomyces* inoculations for normal irrigation in both soils and *Streptomyces* St8 for low irrigation in saline soil) turned yellow and white after day 30 of the experiment (Figure 3). On day 45 of the experiment, these white leaves turned brown and dry. The chlorophyll content was not measured for these treatments. Low irrigation decreased the chlorophyll content of *P. erosus* leaves, while salinity did not affect the chlorophyll in these leaves. For example, the total chlorophyll content in *P. erosus* leaves grown in treatment 1 was 7.04 mg/ml while they were 3.06–5.07 mg/mL for treatments 4-6. In addition, the total chlorophyll contents in the leaves of *P. erosus* grown in treatments 1 and 4–6 were 3.06–7.04 mg/mL while they were 2.82–7.30 mg/mL in treatments 7, 10, and 12 (Table 5). The chlorophyll content in the leaves of *P. erosus* significantly decreased when grown with low irrigation both in saline and non-saline soil. *Streptomyces* inoculation did not alleviate this effect on the chlorophyll content in *P. erosus* leaves.

Among these factors, salinity affected both plants' growth more than the other factors. Normally, the responses of plants to salinity and drought are similar, which are hyperosmotic and oxidative stress (Jumpa et al., 2017). However, salinity could enhance the Na^+ accumulation, disrupting plant cells ion homeostasis (A. Kumar et al., 2021). In addition, salinity did not decrease the plant health of *I. aquatica*. It may be due to the concentration of sodium chloride used in this study as it was in the range that *I. aquatica* could tolerate (Cha-um et al., 2007). The low irrigation in this experiment may not have stressed both plants enough. Generally, drought stress induces premature leaf senescence via reduced photosynthesis

Table 6

Effect of soil, irrigation, and bacterial isolate on Pachyrhizus erosus *growth traits*

	Number of leaves	Shoot length (cm)	Shoot dry weight (g)	Root length (cm)	Root dry weight (g)	Chlorophyll *a* (mg/ml)	Chlorophyll *b* (mg/ml)	Total chlorophyll (mg/ml)
Soil (factor 1)								
Non-saline soil	3.0	46.2	0.20a	5.2	0.024a	1.92	2.71	4.63
Saline soil	2.7	44.3	0.15b	4.8	0.015b	2.11	2.43	4.54
F-test	ns	ns	**	ns	*	ns	ns	ns
Irrigation (factor 2)								
Normal irrigation	3.2	43.7	0.18	4.8	0.021	3.32a	3.85a	7.17a
Low irrigation	2.5	46.8	0.17	5.2	0.017	1.47b	2.09b	3.56b
F-test	ns	ns	ns	ns	ns	**	**	**
Bacterial isolate (factor 3)								
Control	2.8	44.4	0.16	5.2	0.023	2.35	2.88a	5.22a
St1	3.3	44.1	0.19	5.0	0.018	1.88	3.19a	5.07a
St8	2.5	47.2	0.17	4.8	0.017	1.36	1.72b	3.08b
F-test	ns	ns	ns	ns	ns	ns	*	**
F-test								
Soil x irrigation	ns	ns	ns	ns	ns	ns	ns	ns
Soil x bacterial isolate	ns	ns	ns	ns	ns	ns	ns	ns
Irrigation x bacterial Isolate	ns	ns	ns	ns	ns	-	-	-
Soil x irrigation x Bacterial isolate	ns	ns	ns	ns	ns	-	-	-

Note. Different lower-case letters show significant differences within each factor by LSD test at $P \leq 0.05$; Abbreviations: ns, *, ** denote non-significance ($P \geq 0.05$), statistical significance ($P \leq 0.05$), and high statistical significance ($P \leq 0.01$), respectively

Table 7

Growth of Pachyrhizus erosus *in presence or absence of* Streptomyces *sp. when cultivated under non-saline soil and saline conditions for 45 days (Mean ± Standard Error)*

		Shoot		
		Leaf number	Length (cm)	Dry weight (g)
Normal irrigation				
Non-inoculation	Non-Saline Soil (T1)	3.2 ± 0.52Aa	48.7 ± 3.08Aa	0.220 ± 0.016Aa
	Saline Soil (T7)	3.2 ± 0.52Aa	40.8 ± 4.00Aa	0.161 ± 0.026Ab
Streptomyces sp. St1	Non-Saline Soil (T2)	3.8 ± 0.22Aa	44.0 ± 4.14Aa	0.226 ± 0.015Aa
	Saline Soil (T8)	4.0 ± 0.28Aa	44.2 ± 4.79Aa	0.188 ± 0.017Ab
Streptomyces sp. St8	Non-Saline Soil (T3)	3.0 ± 0.61Aa	45.9 ± 3.24Aa	0.209 ± 0.042Aa
	Saline Soil (T9)	2.0 ± 0.00Aa	38.6 ± 4.63Aa	0.086 ± 0.021Aa
Low irrigation				
Non-inoculation	Non-Saline Soil (T4)	2.7 ± 0.38Aa	51.4 ± 4.09Aa	0.162 ± 0.020Aa
	Saline Soil (T10)	2.0 ± 0.71Aa	36.6 ± 3.11Aa	0.109 ± 0.037Aa
Streptomyces sp. St1	Non-Saline Soil (T5)	2.9 ± 0.24Aa	40.8 ± 4.32Aa	0.173 ± 0.025Aa
	Saline Soil (T11)	2.5 ± 1.06Aa	47.5 ± 8.84Aa	0.188 ± 0.006Aa
Streptomyces sp. St8	Non-Saline Soil (T6)	2.6 ± 0.49Aa	46.6 ± 2.86Aa	0.204 ± 0.019Aa
	Saline Soil (T12)	2.6 ± 0.36Aa	58.0 ± 9.22Aa	0.175 ± 0.018Aa

Table 7 *(Continue)*

		Root				
		Length (cm)	Dry weight (g)	Specific root length (m/g)	Root to shoot ratio	% Tuber formation
Normal irrigation						
Non-inoculation	Non-Saline Soil (T1)	5.9 ± 0.26Aa	0.031 ± 0.007Aa	1.89	0.142	71.4 %
	Saline Soil (T7)	4.5 ± 0 .39Aa	0.018 ± 0.004Ab	2.55	0.108	57.1 %
Streptomyces sp. St1	Non-Saline Soil (T2)	5.3 ± 0.12Aa	0.022 ± 0.003Aa	2.40	0.097	14.3 %
	Saline Soil (T8)	4.7 ± 1.00Aa	0.013 ± 0.002Aa	3.65	0.069	28.6 %
Streptomyces sp. St8	Non-Saline Soil (T3)	3.9 ± 0.25Aa	0.012 ± 0.001Aa	3.40	0.055	14.3 %
	Saline Soil (T9)	4.8 ± 1.91Aa	0.008 ± 0.003Aa	5.65	0.099	0.0 %
Low irrigation						
Non-inoculation	Non-Saline Soil (T4)	5.2 ± 0.25Aa	0.032 ± 0.005Aa	1.62	0.199	100 %
	Saline Soil (T10)	5.2 ± 0.71Aa	0.010 ± 0.001Aa	5.25	0.091	0.0 %
Streptomyces sp. St1	Non-Saline Soil (T5)	6.1 ± 0.48Aa	0.020 ± 0.007Aa	3.14	0.112	57.1 %
	Saline Soil (T11)	4.2 ± 0.11Aa	0.016 ± 0.005Aa	2.58	0.085	28.6 %
Streptomyces sp. St8	Non-Saline Soil (T6)	5.1 ± 0.24Aa	0.027 ± 0.006Aa	1.92	0.131	71.4 %
	Saline Soil (T12)	5.3 ± 0.57Aa	0.022 ± 0.003Aa	2.40	0.127	28.6 %

Note. Different lower-case letters show significant differences between different soils for the same inoculation at each irrigation treatment by LSD test at $P \leq 0.05$; Different capital letters show significant differences between different inoculations for the same soil at each irrigation treatment by LSD test at $P \leq 0.05$

Figure 3. Characteristics of shoot and root of *Pachyrhizus erosus* grown under non-saline soil + normal irrigation (A), saline soil + normal irrigation (B), non-saline soil + low irrigation (C), and saline soil + low irrigation (D)

and affects the membrane integrity (Ergo et al., 2021), leading to a decreasing leaf number, but the leaf numbers of both plants in this experiment were not affected by low irrigation.

Bacterial inoculation had negative effects on the chlorophyll content of both plants and only *Streptomyces* sp. St8 increased the root length of *I. aquatica*. Despite *Streptomyces* sp. St1 and St8 having been reported to produce IAA and solubilize phosphate at the laboratory scale (Somtrakoon et al., 2019), both activities of these bacterial isolates did not support the growth of *I. aquatica* and *P. erosus* in the pot experiment in this study. It might be due to several reasons, including the initial number of bacterial cells used being too low (10^4 cfu/g of coconut husk) and the low number of microbial inoculants that might not have the ability to compete with the indigenous bacteria in the soil. Colonies of both isolates were not detected after enumeration from the soil on half formulations of PDA from each treatment at the end of the experiment. The colonies of other bacteria overgrew the agar plates of half formulation PDA. Moreover, the organic matter, total nitrogen, and total potassium in the soil used in this study were low (Table 1), which may not favor the growth and survival of *Streptomyces* sp. St1 and St8 after introduction to the soil. *Streptomyces* sp. St1 and St8 could not be adapted to growth under low water irrigation

or saline soil in this study. Indigenous bacteria isolated from drought or saline soils have been suggested as a source for biofertilizers (B. L. Kumar & Gopal, 2015).

Normally, plant growth-promoting bacteria used under salt stress should be tolerant to salt stress—for example, inoculation of *Pseudomonas* sp. Strain UW4, wildtype or mutant OxtreS that tolerated 0.2 M NaCl could protect tomato plant growth from salt stress when irrigated with 0.2 M NaCl (Orozco-Mosqueda et al., 2019). In the laboratory, *Streptomyces* sp. St1 and St8 could conserve their phosphate solubilization and IAA production abilities when exposed to NaCl. Within 35 days, the IAA production of *Streptomyces* sp. St1 in PDA + 3.4% NaCl did not decrease while the phosphate solubilization decreased 9% in PDA + 2.55% NaCl compared with those grown on PDA without NaCl. In addition, IAA production by *Streptomyces* sp. St8 in PDA + 1.7 % NaCl decreased 9%, and phosphate solubilization decreased 39% in PDA + 4.25% NaCl compared with those grown on PDA without NaCl (Pukmak et al., 2020), but both isolates did not enhance plant growth when introduced to the soil. In summary, the salinity of the soil might be more of a concern for PGPB used under a combination of drought and salinity. Developing *Streptomyces* sp. St1 and St8 as biofertilizers might not be appropriate because the plant growth-promoting activities of both bacterial isolates did not boost and promote the growth of the tested plants.

CONCLUSION

Salinity affected the success of plant growth-promoting bacteria used in *Ipomoea aquatica* and *Pachyrhizus erosus* cropping more than the water-limited effect. Based on the shoot and root growth, there were significant interactions between salinity and irrigation on root dry weight of *I. aquatica* only. All factors had significant interactions with the chlorophyll content of *I. aquatica*. Salinity was the most effective factor, and irrigation was the least influential factor on both plants' growth. The importance of considering the plant growth-promoting bacterial strain for use under salt and drought conditions is the salt tolerance of these bacteria.

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