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How phosphorus-solubilizing bacteria *Cereibacter sphaeroides* changed the phosphorus uptake, growth, and yield of rice grown in salinized soils under greenhouse conditions

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Abstract

Phosphorus (P) is an important element in crop production. However, under climate change, salinization and acidification limit soil P availability and crop yield, especially rice, while the application of chemical P fertilizer causes an adverse effect on the environment. Thus, the study aimed at assessing the effectiveness of strains of purple nonsulfur bacteria (PNSB) that can solubilize P and tolerate salinity (PNSB-P) in reducing Na^+ in soil and plant and improving P uptake, growth, and yield of rice in salinized soils in Vietnam. An experiment with two factors was arranged in completely randomized blocks and replicated four times under greenhouse conditions. Therein, the first factor was five levels of P fertilizers: 0%, 25%, 50%, 75%, and 100% of the local recommended level. The second factor was the PNSB-P including single strains of *Cereibacter sphaeroides* ST16 and ST26, the mixed strains of both *C. sphaeroides* ST16 and ST26, and the negative control. The results showed that utilizing *C. sphaeroides* ST16 and ST26 decreased plant proline content by 2.46–6.70 μmol g^{-1} and soil Na^+ concentration by 1.47–1.62 meq 100 g^{-1}. Utilizing PNSB-P increased P content by 5.82–29.2% in stem-leaf and 12.1–14.6% in rice grain and decreased 15.1–16.4% of Na content in stem-leaf and 8.00–15.1% in rice grain. Moreover, utilizing PNSB-P improved soluble P content by 4.33–9.07 mg P kg^{-1} and total P uptake by 24.0–46.6% compared with the negative control. The *C. sphaeroides* bacteria not only increased rice yield components such as the number of panicles per pot, the number of rice grains per panicle, and filled rice grain rate but also enhanced 20.7–47.6% of rice grain yield compared with the negative control. Noticeably, utilizing mixed bacterial strains decreased 100% of chemical P fertilizer compared with the recommendation.

1. Introduction

Soil salinization is a threat to sustainable agriculture and global food security (Mukhopadhyay et al., 2021). Over 833 million ha of soil is affected by salinization around the world and farming soil particularly accounts for 10% of salinized soil (FAO, 2021). Besides, rice is one of the most important crops and is directly damaged by saline soil (Coca et al., 2023). The Vietnamese Mekong Delta is a large delta that is the most fertile in South East Asia and has the largest rice farming area in Vietnam (Tho and Umetsu, 2022). Previous studies have been conducted to facilitate farming under salinized conditions, such as improving the yield of salt-tolerant rice variety by utilizing silicon (Khanam et al., 2023) and using biocharcoal (Zhang et al., 2023), fulvic acid (Jesmin et al., 2023), calcium salt (Romano-Armada et al., 2020), and organic fertilizers (Zhang et al., 2021).

Normally, rice uses nitrogen (N), phosphorus (P), and potassium (K) as the major elements (Jiaying et al., 2022). In particular, rice needs N of approximately 120 kg N ha^{-1} (Sharma et al., 2021), P of 50–100 kg P ha^{-1} (George et al., 2016), and K of 45–75 kg K_2O ha^{-1} (Ojha et al., 2020). However, the amount of chemical fertilizer used can be much greater (Basavarajappa et al., 2021) because only a portion of the nutrients can be available for plants (Marschner and Rengel, 2016) due to the effects of high salinity and acidity. Salinity affects the uptake of nutrients by plants (Ehtaiwesh, 2022), while acidity affects the availability of the nutrients in the soil (Barrow and Hartemink, 2023). This is the adverse conditions caused by acid sulfate soil to the rice farming in the Mekong Delta, Vietnam (Morton et al., 2023). Thus, measures should be made. Therefore, a greenhouse experiment imitating the saline acid sulfate soil in rice fields should be conducted to investigate the potency of a biofertilizer in improving this adverse condition. Then, a field trial should be made based on the outcome of the greenhouse study.

On the other hand, phosphorus or phosphate in compound forms is a macronutrient that is vital for the growth and development of crops, and is a component of cell membrane, nucleotide, and metabolisms within the crops (Luo et al., 2024). P accounts for 0.2% of crop biomass (Kayoumu et al., 2023). However, soluble P in the soil is limited, which challenges crop yield under salinization (Kayoumu et al., 2023). Salinity causes reduced soluble P for crops (Shaaban et al., 2023). Thus, using a great amount of chemical P fertilizer over the recommendation to improve soil soluble P for crop demand is a popular approach chosen by farmers (Huo et al., 2023). Nevertheless, about 15–20% of chemical P fertilizer is used by the crops in the first season (Hoque et al., 2024). Most of the P fertilizer is precipitated by soil cations, such as Fe^{2+} and Al^{3+} in acidic soils or Ca^{2+} in alkaline soils (Johan et al., 2021; Zhao et al., 2023). In such cases, bacteria that can solubilize P are candidates for these cases based on their mechanisms to solubilize P such as the production of organic acids, enzymes, and siderophores, to chelate metallic ions and release $P_{soluble}$ for plant uptake and the synthesis of plant growth promoting substances, such as auxin, gibberellin, and cytokinin to assist plants to overcome adverse conditions (Rawat et al., 2020). Thus, utilizing bacteria can lessen the effects of salinization on rice grain yield and exploit immobilized P in the soil.

Therefore, purple nonsulfur bacteria (PNSB) have been studied to provide nutrients via P solubilization (Wang et al., 2021; Khuong et al., 2022, 2023a, 2023b, 2024; Xuan et al., 2024) and applied under saline conditions (Alloul et al., 2021; Sundar et al., 2022; Al Azad et al. 2023; . PNSB can also provide plant growth-promoting substances (Khuong et al., 2022) and improve soil health by decreasing Fe^{2+}, Al^{3+}, and Mn^{2+} toxicities in acidic soils (Khuong et al., 2022, Nguyen et al., 2018) and alkaline soils in rice-shrimp farming systems (Khuong et al., 2022). However, there have been no study investigating the effectiveness of P-solubilizing PNSB in salinized acidic soil. Therefore, the purpose of the current study was to assess the effect of PNSB strains *Cereibacter sphaeroides* ST16 and ST26 that can solubilize P (PNSB-P) on rice growth and rice grain yield in salinized rice-shrimp soil in Chau Thanh District, Tra Vinh Province under greenhouse conditions. In the current study, the mixture of *C. sphaeroides* ST16 and ST26 was combined with different levels of chemical P fertilizer and applied to rice soil in pots to investigate how many levels of chemical fertilizer can be reduced by the bacteria mixture without changing the rice yield. At the same time, soil health was also observed at both the beginning and the end of a season.

2. Materials and methods

2.1. Experimental condition

Via Table 1, pH_{H2O} and pH_{KCl} were 3.10 and 3.09 and EC was 1.23 mS cm^{-1}. The N_{total} was 0,168% while the NH_4^+ concentration was 223 mg kg^{-1}. The P_{total} in the soil was 0.032%, the $P_{soluble}$ was 31.8 mg kg^{-1} and insoluble P (Al-P, Fe-P, and Ca-P) was 219, 84.7, and 56.0 mg P kg^{-1}, respectively. The CEC was 12.7 meq 100 g^{-1}, while Na^+, K^+, Ca^{2+}, and Mg^{2+} concentrations were 10.3, 0.489, 2.97, and 13.5 meq 100 g^{-1}, respectively. The greenhouse conditions: The mean temperature was 39.5°C, and the air moisture content was 61.7%.

2.2. Materials

PNSB-P: The *C. sphaeroides* ST16 and ST26 bacteria were isolated from soil and water in a rice-shrimp system and can solubilize insoluble P compounds, e.g. Al-P, Fe-P, and Ca-P under saline conditions (Dat et al., 2024).

Rice variety *Oryza sativa* cv. OM 5451 had an 88–93-day life cycle, a maximum plant height of 85–95 cm, and a 1,000 rice grains weight of 25–26 g (Hoa et al., 2011).

The surface soil was collected at 0–30 cm depth after rice farming in the rice-shrimp system in Chau Thanh district, Tra Vinh province, Vietnam. The soil was crushed into pieces, dried, and cleaned from plant residues. The pure soil was mixed and weighed for 8 kg pot^{-1}. Each pot was 25 cm wide and 30 cm high. Five liters of water were added to the pot and mixed 2 days later, then 8 rice grains were sowed into each pot.

NPK fertilizers used consisted of Ca Mau Urea (46.3% N), Long Thanh superphosphate (16% P_2O_5), and Ca Mau potassium (61% K_2O).

2.3. Methods

The rice grains were treated with ethanol 70% and NaClO 1% for 10 min, rinsed with distilled water and incubated for 24 h until germination (Khuong et al., 2022). The germinated rice grains were soaked with bacterial solutions of *C. sphaeroides* ST16 and *C. sphaeroides* ST26 (10^8 CFU mL^{-1}) according to the treatments for 1 h in a reciprocal shaker at 60 rpm. The rice grains were dried under the laminar airflow before sowing. Distilled water was used to replace the PNSB-P solution in the negative control. The PNSB-P solution was supplied on days 7, 14, 21, 28, 35, and 42 after sowing at 4 mL pot^{-1}, equivalent to 4 x 10^4 CFU g^{-1} of dry soil.

The NPK fertilizers were supplied according to the following formula: 90N – $60P_2O_5$ – $30K_2O$ or 195.7 kg urea, 375 kg superphosphate, and 50 kg potassium for 2,000,000 kg soil/ha. In other words, the NPK used for each pot was 0.78 g urea, 1.0 g superphosphate, and 0.2 g potassium. 100% P was supplied before sowing. N was supplied at 30, 30, and 40% on days 10, 20, and 45 after sowing, respectively. K was supplied at 50% on days 10 and 45 after sowing. 10 mL of saline water 4 ‰ was supplied into each rice pot on days 20, 40, and 75 after sowing (Khuong et al., 2021). A 3 cm water level was maintained during rice growth

Table 1
Some soil characteristics collected in the surface horizon (0–30 cm) in Chau Thanh – Tra Vinh

Soil traits	Unit	Value	Status	Reference
pH_{H2O}	–	3.10	Very low	Horneck et al., 2011
pH_{KCl}	–	3.09	Very low	Horneck et al., 2011
EC	mS cm^{-1}	1.23	Low – no effect on plants	Horneck et al., 2011
N_{total}	%N	0.032	Very low	Metson, 1961
NH_4^+	mg kg^{-1}	223	–	–
P_{total}	$\%P_2O_5$	0.168	Rich	Cu et al., 2020
$P_{soluble}$	mg kg^{-1}	31.8	Moderate	Horneck et al., 2011
Al-P	mg kg^{-1}	219	–	–
Fe-P	mg kg^{-1}	84.7	–	–
Ca-P	mg kg^{-1}	56.0	–	–
CEC	meq 100 g^{-1}	12.7	Low	Landon, 2014
Na^+	meq 100 g^{-1}	10.3	–	–
K^+	meq 100 g^{-1}	0.489	Moderate	Horneck et al., 2011
Ca^{2+}	meq 100 g^{-1}	2.97	–	–
Mg^{2+}	meq 100 g^{-1}	13.5	High	Horneck et al., 2011

Note: EC: Electrical conductivity. CEC: Cation exchange capacity.

and development. However, on days 0–10 after sowing and before harvesting, the soil was kept at sufficient moisture.

The experiment was performed in the Agricultural Research and Practice Station, College of Agriculture, Can Tho University. The experiment was arranged in completely randomized blocks with two factors and four replications. The first factor was different rates of P fertilization (0, 25, 50, 75, and 100% P compared to the local recommendation). The second factor was PNSB-P (no bacteria, single use of *C. sphaeroides* ST16, single use of *C. sphaeroides* ST26, and mixed use of *C. sphaeroides* ST16 and ST26).

Plant parameters: The growth was measured according to IRRI (1996) and included plant height and panicle length of 6 plants and panicles pot^{-1} at harvesting, respectively. The number of panicles pot^{-1} was counted as the total of panicles in a pot. Ten panicles pot^{-1} were randomly collected to calculate the number of filled and unfilled grains to determine the number of rice grain $panicle^{-1}$ and filled grain percentage. The 1,000 rice grains weight collected in each pot were weighed and converted to the weight at 14% humidity. The actual yield was determined the same but all of the rice grains in the pot were collected.

Stem-leaf and rice grains were dried at 70°C for 72 h. The proline content in stem-leaf was measured according to Bates et al. (1973) by spectrophotometry at 520 nm on day 45 after sowing. The chlorophyll content in the leaf was measured according to Moran (1982) by spectrophotometry at 664 and 647 nm on days 21, 28, 35, and 42 after sowing. The Na and P content were measured according to Houba et al. (1997) by spectrophotometry at 589 nm and by ascorbic acid method and spectrophotometry at 880 nm, respectively. The Na and P uptake was measured according to the content of each element the biomass in each part of a rice plant (stem-leaf and rice grain).

Soil parameters: The soil was analyzed according to Sparks et al. (1996) in parameters such as pH_{H2O}, pH_{KCl}, EC, Na^+, Ca^{2+}, Mg^{2+}, K^+, Fe-P, Ca-P, Al-P, N_{total}, and NH_4^+. The soil sample was broken down by saturated H_2SO_4 and $HClO_4$ and colorized in the form of phosphomolybdate reduced by ascorbic acid. The P_{total} was quantified by spectrophotometry at 880 nm. $P_{soluble}$ was measured according to the Bray II method. The sample was extracted with a 1:7 ratio between soil and the mixture of 0.1 N HCl and 0.03 N NH_4F, reduced by ascorbic acid to form a blue color of phosphomolybdate, and measured by spectrophotometry at 880 nm.

2.3. Statistical analysis

Microsoft Excel 2013 was used to calculate means, standard derivatives, and graphs. The SPSS 13.0 was used to compare means between treatments according to the Duncan test at 5% significance.

3. Results

3.1. Combination of P fertilization and *Cereibacter sphaeroides* ST16 and ST26 changed contents of chlorophyll and proline

3.1.1. Changes in chlorophyll a, b, and a+b in rice leaves

Table 2 indicated that the treatments utilizing PNSB-P had SPAD ranging from 36.8–40.3 which increased significantly compared with the control (35.1–38.7) on days 21, 28, 35, and 42 after sowing in the 2 cropping seasons. This caused increased chlorophyll a + b content (11.6–13.2) compared with the control

Table 2
Influences of P fertilizer and *Cereibacter sphaeroides* on chlorophyll and proline contents

Factor		SPAD				Chlorophyll			Proline
		21 days	28 days	35 days	42 days	a	b	a+b	(μmol g^{-1} DW)
						(μg g^{-1} fresh leaf)			
Season 1									
P level (A) (%)	0	37.6^{b}	39.2^{b}	37.3^{d}	36.3^{b}	9.70	3.25^{a}	13.0^{a}	18.8
	25	37.6^{b}	39.8^{a}	38.2^{c}	36.2^{b}	10.0	2.97^{ab}	12.9^{a}	18.8
	50	37.6^{b}	39.8^{a}	38.1^{c}	37.1^{a}	10.0	2.86^{bc}	12.9^{a}	19.6
	75	38.3^{a}	39.6^{a}	39.1^{a}	36.6^{ab}	9.83	3.11^{ab}	12.9^{a}	17.5
	100	38.2^{ab}	39.8^{a}	38.7^{b}	36.7^{ab}	9.43	2.57^{c}	12.0^{b}	18.0
P bacteria (B)	NB	35.4^{c}	38.7^{c}	36.8^{c}	35.1^{c}	8.70^{b}	3.36^{a}	12.1^{b}	21.9^{a}
	ST16	38.9^{a}	39.9^{b}	39.1^{a}	36.8^{b}	10.2^{a}	2.84^{bc}	13.0^{a}	18.9^{b}
	ST26	38.2^{b}	39.7^{b}	38.2^{b}	37.2^{ab}	10.1^{a}	3.01^{b}	13.2^{a}	18.2^{b}
	MIX	38.9^{a}	40.3^{a}	39.0^{a}	37.3^{a}	10.2^{a}	2.60^{c}	12.8^{a}	15.2^{c}
Significance level (A)		*	*	*	*	ns	*	*	ns
Significance level (B)		*	*	*	*	*	*	*	*
Significance level (A*B)		*	*	*	*	ns	ns	ns	*
CV (%)		2.26	1.40	1.66	2.08	9.08	15.6	8.16	13.6
Season 2									
P level (A) (%)	0	36.5	39.3	39.0	38.0	8.98^{b}	2.28	11.3^{b}	9.67
	25	37.0	39.1	38.6	37.6	9.24^{ab}	2.44	11.7^{ab}	9.89
	50	36.6	39.2	38.4	37.8	9.43^{a}	2.47	11.9^{a}	9.87
	75	36.8	39.0	38.3	37.6	9.36^{a}	2.35	11.7^{a}	9.58
	100	36.5	39.0	38.5	37.3	9.31^{a}	2.25	11.6^{ab}	9.62
P bacteria (B)	NB	35.5^{b}	38.4^{b}	37.6^{b}	36.6^{b}	8.28^{c}	2.37	10.7^{c}	11.8^{a}
	ST16	37.0^{a}	39.0^{a}	39.0^{a}	38.3^{a}	9.27^{b}	2.43	11.7^{b}	9.34^{b}
	ST26	37.1^{a}	39.5^{a}	38.8^{a}	38.0^{a}	9.41^{b}	2.23	11.6^{b}	9.14^{b}
	MIX	37.0^{a}	39.5^{a}	39.0^{a}	37.7^{a}	10.1^{a}	2.40	12.5^{a}	8.58^{c}
Significance level (A)		ns	ns	ns	ns	*	ns	*	ns
Significance level (B)		*	*	*	*	*	ns	*	*
Significance level (A*B)		ns	ns	ns	ns	*	ns	*	*
CV (%)		2.05	2.08	2.85	3.10	4.49	14.9	4.87	5.39

Note: In the same column, numbers followed be different letters are different statistically *: 5% significance; ns: no significance; NB: no bacteria; ST16: *Cereibacter sphaeroides* ST16; ST26: *Cereibacter sphaeroides* ST26; MIX: *Cereibacter sphaeroides* ST16 and *Cereibacter sphaeroides* ST26.

(10.7–12.1) in the treatments utilizing PNSB-P in the 2 cropping seasons. This was because the chlorophyll a content increased, though the chlorophyll b decreased in the first cropping season and remained in the second cropping season. Furthermore, P fertilization varied SPAD and chlorophyll a, b, and a + b contents during the 2 cropping seasons. In particular, the SPAD ranged 36.2–39.8 and increased only in the treatment with 75% P on day 21 after sowing, in the treatments from 25% to 100% P on days 28 and 35 after sowing, and in the treatment with 50% P on day 42 after sowing in the first cropping season. However, the P fertilizer did not change the SPAD in the second cropping season. The chlorophyll a content was 8.98–10.0 μg g^{-1} of fresh leaf, remained between P fertilization levels in the first cropping season, but increased in the second cropping season when fertilizing 50–100% P. The chlorophyll b content was 2.25–3.25 μg g^{-1} of fresh leaf and increased only in the treatment with 100% P in the first cropping season. In the second cropping season, fertilizing 25–100% P resulted in unchanged chlorophyll b. The chlorophyll a + b content was 11.3–13.0 μg g^{-1} of fresh leaf, decreased in the treatment with 100% P in the first cropping season, but remained in the second cropping season. Fertilizing 50% and 75% P did not vary chlorophyll a + b content in the first cropping season but increased that in the second cropping season.

3.1.2. Changes in proline content in rice plants

The proline content in stem-leaf gradually decreased from the control > *C. sphaeroides* ST16 ~ *C. sphaeroides* ST26 > *C. sphaeroides* ST16 + ST26, with 21.9 < 18.9 ~ 18.2 < 15.2 in the first cropping season and 11.8 < 9.34 ~ 9.14 < 8.58 (μmol g^{-1} DW) in the second cropping season, respectively. Furthermore, fertilizing P did not change the proline content in stem-leaf. The interactions between the two factors were significant in the SPAD in the first cropping season, chlorophyll a in the first cropping season, and proline content in the 2 cropping seasons.

3.2. Combination of P fertilization and *Cereibacter sphaeroides* ST16 and ST26 changed the characteristics of saline soil

3.2.1. Changes in soil acidity

In Table 3, pH_{H2O} increased by 7.22% in the first cropping season and by 5.01% in the second cropping season when utilizing PNSB-P. In the meantime, different P fertilizer levels did not affect the pH_{H2O} in the first cropping season, but in the second cropping season, only the treatments with 25 and 100% P increased the pH_{H2O} compared with the control. In addition, pH_{KCl} increased only when utilizing *C. sphaeroides* ST16 + ST26 with 75% P in the first cropping season. Both factors did not affect pH_{KCl} in the second cropping season. Utilizing PNSB-P decreased soil EC by 4.67–24.5%. Therein, the EC in the treatment with *C. sphaeroides* ST26 was equivalent to the mixed use of *C. sphaeroides* ST16 + ST26 and decreased by 5.56% in the first cropping season and 24.5% in the second cropping season. Moreover, fertilizing from 25% to 100% P increased EC (3.00–3.14 and 1.93–2.33 mS cm^{-1}) compared with the control (2.92 and 1.67 mS cm^{-1}) in the 2 cropping seasons, respectively. The interactions between the two factors were significant in the pH_{H2O} and EC in the 2 cropping seasons and pH_{KCl} in the first cropping season (Table 3).

3.2.2. Changes in soil nitrogen and phosphorus

Either P fertilization or utilizing PNSB-P increased soil $P_{soluble}$ and NH_4^+ in the 2 cropping seasons. Particularly, the $P_{soluble}$ among the two factors fluctuated from 24.1 to 57.7 mg kg^{-1} and increased of 4.33 mg kg^{-1} when utilizing PNSB-P in the first cropping season and 9.07 mg kg^{-1} in the second cropping season. Therefore, the $P_{soluble}$ peaked in the treatment with the mixed use of *C. sphaeroides* ST16 + ST26, then the treatments with single uses of *C. sphaeroides* ST26 and ST16. The $P_{soluble}$ and insoluble P increased when utilizing P fertilizers, and peaked in the treatment with 100% P then the treatments with 75% P, 50% P, and 25% P, and bottomed in the treatment with 0% P. Likewise, the NH_4^+ fluctuated from 35.0–72.8 mg kg^{-1} and increased following the treatments with *C. sphaeroides* ST16 < *C. sphaeroides* ST26 < *C. Sphaeroides* ST16 + ST26 or the treatments with 25% P ~ 50% P < 75% P ~ 100% P compared with the control in the 2 cropping seasons. Moreover, the N_{total} and P_{total} were not affected by either PNSB-P or P fertilizer. The contents of NH_4^+, $P_{soluble}$, and insoluble P were influenced by the interactions between the two factors, while the N_{total} and P_{total} did not change via the 2 cropping seasons (Table 3).

3.2.3. Changes in soil cations

The P fertilization and PNSB-P utilization increased soil CEC (12.0–16.9 meq 100 g^{-1}) by 12.5% and 7.26% under PNSB-P and by 10.7% and 9.72% under the P fertilization, respectively in the 2 cropping seasons. This resulted in varied soil cations. For example, utilizing PNSB-P increased Mg^{2+} and Ca^{2+} in the first cropping season but remained in the second cropping season. The K^+ rose only when utilizing mixed use of *C. sphaeroides* ST16 + ST26 in the first cropping season though utilizing single or mixed use increased the parameter in the second cropping season compared with the control. Moreover, utilizing PNSB-P decreased Na^+ in the 2 cropping seasons and valued average at 1.62 meq 100 g^{-1} and 1.47 meq 100 g^{-1}, respectively. The P fertilizer increased K^+ in the 2 cropping seasons and resulted in the greatest in the treatment with 100% P, then 75% P, 50% P, and 25% P, and bottomed in the negative control. Furthermore, in the first cropping season, the Na^+ in the treatments with 100% and 75% P was equivalent (7.81 and 7.68 meq 100 g^{-1}) and was significantly greater than the treatments with 0% and 25% P (7.15%). In addition, the Na^+ was 6.91 > 6.07 ~ 5.93 ~ 5.73 > 5.07 meq 100 g^{-1} in the second cropping season corresponding to the P fertilizer levels at 100% P, 75% P, 50% P, 25% P, and 0% P. Besides, the Mg^{2+} and Ca^{2+} did not change in the treatments with P fertilizer. There were significant interactions between the two factors in CEC and Na^+ in the 2 cropping seasons and Mg^{2+} in the first cropping season (Table 3).

3.3. Combination of P fertilization and *Cereibacter sphaeroides* ST16 and ST26 changed Na and P uptake of rice plant

3.3.1. Changes in rice plant biomass

Stem-leaf biomass in the first cropping season in the treatments with 75% and 100% P reached 29.6–31.8 g pot^{-1}. Particularly, the treatment with 100% P resulted in greater values than the treatments with 0, 25, and 50% P (26.9–28.4 g pot^{-1}). In the second cropping season, biomass in stem-leaf in the treatment with 0% P was 21.3 g pot^{-1} and lower than the treatments with 50% P, 75% P, and 100% P, with corresponding results of 23.2 ~ 23.5 ~ 24.0 g pot^{-1}. The stem-leaf biomass in the treatments utilizing *C. sphaeroides* ST16 and the mixed use of *C. sphaeroides* ST16 and ST26 increased by 2.80–4.50 and 4.30–6.10 g pot^{-1} compared with the control treatment 26.6 and 19.1 g pot^{-1} in the 2 cropping seasons, respectively (Table 4).

Table 3
Influences of P fertilizer and *Cereibacter sphaeroides* on the fertility of saline soil at harvest

Factor		pH_{H2O}	pH_{KCl}	EC	N_{total}	$\mathbf{P_{total}}$	NH_4^+	$P_{soluble}$	Fe-P	Ca-P	Al-P	CEC	Na^+	K^+	Mg^{2+}	Ca^{2+}
		–	–	mS cm^{-1}	%		mg kg^{-1}					meq 100 g^{-1}				
Season 1																
P level (A) (%)	0	3.40	2.84^{bc}	2.92^{c}	0.205	0.036	56.5^{c}	49.7^{d}	107.0^{e}	68.6^{e}	59.6^{e}	12.1^{d}	7.15^{c}	0.411^{d}	11.9	1.72
	25	3.38	2.90^{b}	3.00^{b}	0.184	0.036	64.0^{b}	51.1^{c}	110.1^{d}	70.0^{d}	62.6^{d}	12.5^{c}	7.15^{c}	0.442^{c}	11.8	1.68
	50	3.45	2.89^{b}	3.02^{b}	0.200	0.034	65.8^{b}	53.8^{b}	118.7^{c}	71.9^{c}	64.1^{c}	12.7^{c}	7.55^{b}	0.458^{bc}	12.3	1.65
	75	3.42	2.97^{a}	3.11^{a}	0.184	0.035	69.3^{a}	54.9^{b}	126.9^{b}	73.8^{b}	66.3^{b}	13.8^{b}	7.68^{ab}	0.469^{b}	12.0	1.71
	100	3.38	2.81^{c}	3.14^{a}	0.200	0.033	69.9^{a}	57.5^{a}	134.2^{a}	78.6^{a}	68.1^{a}	14.6^{a}	7.81^{a}	0.504^{a}	12.3	1.70
P bacteria (B)	NB	3.23^{c}	2.86^{b}	3.15^{a}	0.195	0.038	57.6^{d}	46.6^{d}	128.6^{a}	84.2^{a}	69.0^{a}	12.0^{c}	8.68^{a}	0.424^{b}	11.1^{c}	1.49^{c}
	ST16	3.42^{b}	2.84^{b}	3.05^{b}	0.203	0.033	60.8^{c}	53.1^{c}	121.2^{b}	72.1^{b}	65.8^{b}	13.3^{b}	6.72^{d}	0.431^{b}	11.8^{b}	1.74^{b}
	ST26	3.55^{a}	2.89^{ab}	2.98^{c}	0.183	0.033	69.2^{b}	56.2^{b}	115.9^{c}	68.8^{c}	62.5^{c}	14.0^{a}	7.11^{c}	0.441^{b}	12.5^{a}	1.75^{ab}
	MIX	3.42^{b}	2.93^{a}	2.97^{c}	0.196	0.034	72.8^{a}	57.7^{a}	112.0^{d}	65.3^{d}	59.3^{d}	13.2^{b}	7.36^{b}	0.530^{a}	12.7^{a}	1.80^{a}
Significance level (A)		ns	*	*	ns	ns	*	*	*	*	*	*	*	*	ns	ns
Significance level (B)		*	*	*	ns	ns	*	*	*	*	*	*	*	*	*	*
Significance level (A*B)		*	*	*	ns	ns	*	*	*	*	*	*	*	ns	*	ns
CV (%)		2.61	2.93	2.69	15.5	18.2	5.85	3.57	2.61	2.62	2.31	3.36	4.08	7.57	6.28	5.05
Season 2																
P level (A) (%)	0	3.30^{b}	3.02	1.67^{d}	0.163	0.030	37.5^{c}	23.9^{e}	107.3^{e}	34.3^{e}	33.1^{e}	14.4^{e}	5.07^{c}	0.445^{c}	10.9	3.88
	25	3.44^{a}	2.99	1.93^{c}	0.165	0.031	38.4^{b}	25.0^{d}	115.0^{d}	35.5^{d}	37.3^{d}	15.0^{d}	5.73^{b}	0.477^{b}	11.2	3.41
	50	3.35^{ab}	2.99	2.06^{c}	0.169	0.031	38.4^{b}	28.2^{c}	123.9^{c}	39.7^{c}	40.0^{c}	15.4^{c}	5.93^{b}	0.500^{b}	12.4	3.44
	75	3.39^{ab}	3.06	2.20^{b}	0.168	0.029	40.0^{a}	28.9^{b}	132.3^{b}	42.0^{b}	42.8^{b}	15.9^{b}	6.07^{b}	0.532^{a}	10.7	3.82
	100	3.45^{a}	3.07	2.33^{a}	0.158	0.029	40.2^{a}	30.7^{a}	140.1^{a}	47.0^{a}	46.0^{a}	16.9^{a}	6.91^{a}	0.541^{a}	11.2	3.40
P bacteria (B)	NB	3.26^{b}	2.94	2.41^{a}	0.163	0.030	35.0^{d}	24.1^{d}	140.5^{a}	47.7^{a}	50.7^{a}	14.7^{d}	7.04^{a}	0.395^{d}	10.4	3.66
	ST16	3.40^{a}	3.06	2.11^{b}	0.167	0.030	38.5^{c}	27.8^{c}	121.8^{b}	40.5^{b}	41.7^{b}	15.3^{c}	5.69^{b}	0.559^{a}	11.6	3.20
	ST26	3.43^{a}	3.03	1.83^{c}	0.164	0.031	39.3^{b}	28.5^{b}	119.2^{c}	36.1^{c}	35.5^{c}	15.9^{b}	5.95^{b}	0.507^{b}	11.9	3.87
	MIX	3.44^{a}	3.07	1.81^{c}	0.163	0.030	42.8^{a}	29.0^{a}	113.3^{d}	34.4^{d}	31.5^{d}	16.1^{a}	5.08^{c}	0.536^{c}	11.4	3.63
Significance level (A)		*	ns	*	ns	ns	*	*	*	*	*	*	*	*	ns	ns
Significance level (B)		*	ns	*	ns	ns	*	*	*	*	*	*	*	*	ns	ns
Significance level (A*B)		*	ns	*	ns	ns	*	*	*	*	*	*	*	ns	ns	ns
CV (%)		4.51	6.44	8.49	9.11	7.32	0.86	2.80	2.81	3.87	4.81	2.02	7.68	7.25	16.4	30.5

Note: In the same column, numbers followed be different letters are different statistically *: 5% significance; ns: no significance; NB: no bacteria; ST16: *Cereibacter sphaeroides* ST16; ST26: *Cereibacter sphaeroides* ST26; MIX: *Cereibacter sphaeroides* ST16 and *Cereibacter sphaeroides* ST26.

Table 4
Influences of P fertilizer and *Cereibacter sphaeroides* on dry biomass and uptake of Na and P in rice plants

Factor		Biomass		Na content		Na uptake		Total Na uptake	P content		P uptake		Total P uptake
		Stem-leaf g pot^{-1}	Grain	Stem-leaf %	Grain	Stem-leaf mg Na pot^{-1}	Grain		Stem-leaf %	Grain	Stem-leaf mg P pot^{-1}	Grain	
Season 1													
P level (A) (%)	0	26.9^{c}	19.1^{c}	4.15^{d}	3.48^{d}	0.779^{c}	0.665^{c}	1.33^{c}	0.222^{e}	0.220^{c}	0.060^{d}	0.042^{c}	0.102^{c}
	25	28.0^{bc}	18.6^{c}	4.44^{c}	3.62^{c}	0.815^{c}	0.672^{c}	1.34^{c}	0.242^{d}	0.225^{c}	0.068^{c}	0.043^{c}	0.110^{c}
	50	28.4^{bc}	22.1^{b}	4.64^{b}	3.84^{b}	1.012^{b}	0.840^{b}	1.68^{b}	0.248^{c}	0.242^{b}	0.070^{bc}	0.054^{b}	0.124^{b}
	75	29.6^{ab}	23.1^{ab}	4.71^{b}	3.98^{a}	1.074^{b}	0.913^{b}	1.83^{b}	0.253^{b}	0.243^{b}	0.075^{b}	0.056^{b}	0.131^{b}
	100	31.8^{a}	25.3^{a}	4.95^{a}	4.07^{a}	1.238^{a}	1.018^{a}	2.04^{a}	0.261^{a}	0.258^{a}	0.083^{a}	0.066^{a}	0.149^{a}
P bacteria (B)	NB	26.6^{c}	16.9^{b}	5.22^{a}	4.04^{a}	0.885^{b}	0.690^{b}	1.38^{b}	0.235^{c}	0.218^{c}	0.062^{c}	0.037^{d}	0.100^{c}
	ST16	29.4^{ab}	22.5^{a}	4.67^{b}	3.86^{b}	1.058^{a}	0.875^{a}	1.75^{a}	0.242^{b}	0.252^{a}	0.071^{b}	0.057^{c}	0.128^{b}
	ST26	28.7^{bc}	22.4^{a}	4.34^{c}	3.75^{c}	0.973^{ab}	0.844^{a}	1.69^{a}	0.251^{a}	0.227^{b}	0.072^{b}	0.051^{b}	0.124^{b}
	MIX	31.1^{a}	24.7^{a}	4.08^{d}	3.54^{d}	1.018^{a}	0.878^{a}	1.76^{a}	0.253^{a}	0.254^{a}	0.079^{a}	0.063^{a}	0.142^{a}
Significance level (A)		*	*	*	*	*	*	*	*	*	*	*	*
Significance level (B)		*	*	*	*	*	*	*	*	*	*	*	*
Significance level (A*B)		ns	*	*	*	ns	*	*	*	ns	ns	*	ns
CV (%)		11.8	16.2	5.52	4.06	17.0	16.8	16.7	2.19	5.34	11.8	15.8	10.2
Season 2													
P level (A) (%)	0	21.3^{c}	24.4^{e}	4.74^{b}	3.54^{d}	1.02^{c}	0.843^{e}	1.86^{d}	0.428^{e}	0.528^{b}	0.093^{d}	0.130^{d}	0.224^{d}
	25	22.2^{bc}	25.5^{d}	4.84^{b}	3.66^{cd}	1.12^{bc}	0.908^{d}	2.02^{c}	0.470^{d}	0.547^{ab}	0.106^{c}	0.140^{c}	0.244^{c}
	50	23.2^{ab}	26.2^{c}	5.02^{a}	3.78^{bc}	1.14^{bc}	0.966^{c}	2.10^{bc}	0.523^{c}	0.567^{a}	0.122^{b}	0.151^{b}	0.268^{b}
	75	23.5^{ab}	26.7^{b}	5.05^{a}	3.89^{ab}	1.20^{ab}	1.014^{b}	2.21^{b}	0.552^{b}	0.581^{a}	0.131^{a}	0.156^{b}	0.283^{ab}
	100	24.0^{a}	28.5^{a}	5.09^{a}	3.99^{a}	1.27^{a}	1.112^{a}	2.39^{a}	0.574^{a}	0.577^{a}	0.139^{a}	0.167^{a}	0.297^{a}
P bacteria (B)	NB	19.1^{c}	19.3^{d}	5.58^{a}	4.74^{a}	1.23^{a}	0.915^{c}	2.14^{ab}	0.418^{c}	0.505^{c}	0.080^{c}	0.097^{c}	0.208^{d}
	ST16	23.7^{b}	27.6^{c}	5.24^{b}	3.79^{b}	1.21^{a}	1.048^{a}	2.26^{a}	0.509^{b}	0.565^{b}	0.121^{b}	0.157^{b}	0.261^{c}
	ST26	23.4^{b}	28.1^{b}	4.54^{c}	3.42^{c}	1.03^{b}	0.960^{b}	1.99^{c}	0.508^{b}	0.565^{b}	0.119^{b}	0.159^{b}	0.279^{b}
	MIX	25.2^{a}	30.1^{a}	4.43^{c}	3.13^{d}	1.13^{ab}	0.951^{b}	2.08^{bc}	0.603^{a}	0.606^{a}	0.152^{a}	0.182^{a}	0.305^{a}
Significance level (A)		*	*	*	*	*	*	*	*	*	*	*	*
Significance level (B)		*	*	*	*	*	*	*	*	*	*	*	*
Significance level (A*B)		ns	*	*	*	ns	*	ns	*	*	ns	*	*
CV (%)		8.37	1.15	4.98	5.35	15.4	5.34	9.14	6.23	8.56	10.2	9.10	10.1

Note: In the same column, numbers followed be different letters are different statistically *: 5% significance; ns: no significance; NB: no bacteria; ST16: *Cereibacter sphaeroides* ST16; ST26: *Cereibacter sphaeroides* ST26; MIX: *Cereibacter sphaeroides* ST16 and *Cereibacter sphaeroides* ST26.

According to Table 4, the rice grain biomass in the control and the treatment with 25% P was equivalent (19.1 and 18.6 g pot^{-1}, respectively) and lower than the treatments with 50–100% P (22.1–25.3 g pot^{-1}) in the first cropping season. In the second cropping season, the rice grain biomass between P fertilizing treatments was 24.4 < 25.5 < 26.2 < 26.7 < 28.5 g pot^{-1} corresponding to 0, 25, 50, 75, and 100% P. The rice grain biomass in the treatments utilizing a single use of *C. sphaeroides* ST16 or ST26 or the mixed use of them was equivalent, with 22.5 ~ 22.4 ~ 24.7 g pot^{-1}, which increased by 5.50–7.80 g pot^{-1} compared with the negative control (16.9 g pot^{-1}) in the first cropping season. In the meantime, in the second cropping season, utilizing PNSB-P improved rice grain biomass (27.6–30.1 g pot^{-1}) compared with the control (19.3 g pot^{-1}).

3.3.2. Changes in rice Na content and uptake

The Na content in stem-leaf and rice grain fluctuated 4.08–5.58 and 3.13–4.74%, respectively. Particularly, utilizing PNSB-P decreased the Na content in stem-leaf (0.550–1.14% and 0.340–1.150%) and in rice grain (0.180–0.500% and 0.950–1.610%) in the 2 cropping seasons, respectively. In addition, fertilizing 25%, 50%, 75%, and 100% P all increased Na content in stem-leaf and rice grain with 4.44 > 4.64 ~ 4.71 > 4.95% and 3.62 > 3.84 > 3.98 > 4.07% compared with 4.15 and 3.48% in the control in the first cropping season. In the second cropping season, the control and the treatment with 25% P had equivalent Na contents in stem-leaf and rice grain with 4.74 ~ 4.84 and 3.54 ~ 3.66%, respectively. Moreover, the treatments with 50%, 75%, and 100% P had greater Na contents in stem-leaf (5.02 ~ 5.05 ~ 5.09%) and rice grain (3.78 ~ 3.89 ~ 3.99%) than the control.

The total Na uptake in stem-leaf and rice grain varied among treatments utilizing PNSB-P or P fertilization (1.33–2.39 mg Na pot^{-1}). Particularly, when utilizing PNSB-P, the total Na uptake increased from 1.38 to 1.69–1.76 mg Na pot^{-1} in the first cropping season. However, in the second cropping season, only the treatment with *C. sphaeroides* ST26 reduced the total Na uptake while the other treatments had equivalent results to the control. Moreover, P fertilizer rates from 50% to 100% P increased the total Na uptake in the 2 cropping seasons. Although the treatment with 25% P had equivalent total Na uptake to the control in the first cropping season, it increased in the second cropping season (Table 4).

3.3.3. Changes in rice P content and uptake

Fig. 1 shows that the total P uptake in rice peaked in the treatment with 100% P in the 2 cropping seasons, while those in the treatments with 0%, 25%, and 50% P were equivalent, i.e. 50% ~ 75% P in the first cropping season and 0% ~ 25% ~ 50% ~ 75% P in the second cropping season.

According to Table 4, fertilizing from 25% to 100% P or utilizing PNSB-P increased P uptake in stem-leaf and rice grain and total P uptake. In particular, the P content in stem-leaf and rice grain ranged from 0.222–0.603 and 0.218–0.606 mg P pot^{-1}. When utilizing PNSB-P increased the P contents in stem-leaf (0.007%–0.018% and 0.090%–0.185%) and in rice grain (0.009%–0.036% and 0.060%–0.101%) in treatments with P fertilizers, in the 2 cropping seasons. The total P uptake in rice increased by 24.0%–42.0% in the first cropping season and 25.5%–46.6% in the second cropping season when utilizing PNSB-P. When fertilizing P, the increases were by 7.8–46.1% in

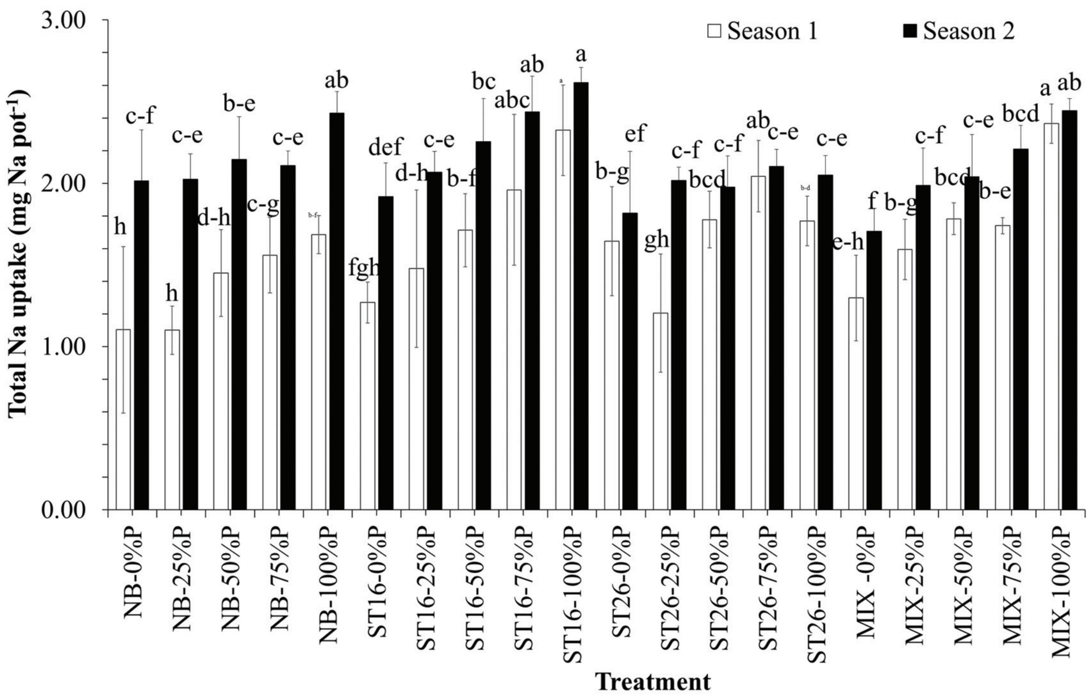

Fig. 1. Influences of P fertilizer and *Cereibacter sphaeroides* on the total Na uptake in two rice cropping seasons

*Note: NB: no bacteria; ST16: *Cereibacter sphaeroides* ST16; ST26: *Cereibacter sphaeroides* ST26; MIX: *Cereibacter sphaeroides* ST16 and *Cereibacter sphaeroides* ST26; 0, 25, 50, 75, 100: fertilizer rates. For the bars with the same color, different letters indicate significant difference at 5%.

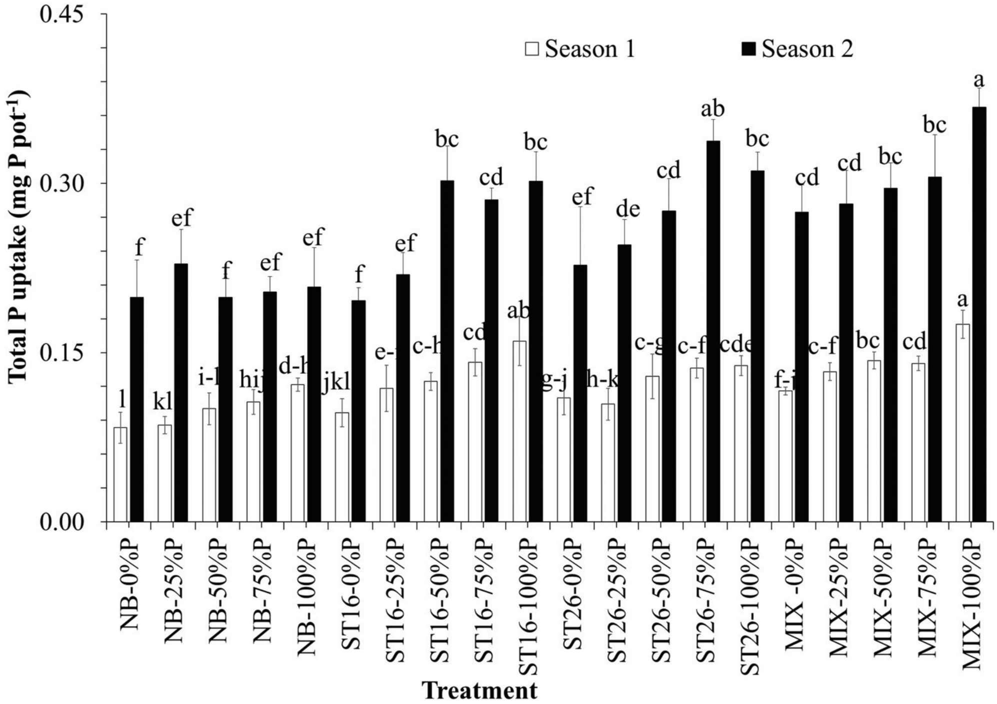

Fig. 2. Influences of P fertilizer and *Cereibacter sphaeroides* on the total P uptake in two rice cropping seasons

*Note: NB: no bacteria; ST16: *Cereibacter sphaeroides* ST16; ST26: *Cereibacter sphaeroides* ST26; MIX: *Cereibacter sphaeroides* ST16 and *Cereibacter sphaeroides* ST26; 0, 25, 50, 75, 100: fertilizer rates. For the bars with the same color, different letters indicate significant difference at 5%.

the first cropping season and 8.93–32.6% in the second cropping season.

Via Table 4 and Fig. 2, *C. sphaeroides* and P fertilizer improved the total P uptake in the 2 cropping seasons. The total P uptake influenced by the P fertilizer increased gradually in the 2 cropping seasons. The treatments with both *C. sphaeroides* ST16 and 100% P, *C. sphaeroides* ST16 + ST26 and 50% P or 100% P had greater total P uptake than the treatment with 100% P in the first cropping season. Utilizing *C. sphaeroides* ST16 or ST26 with 50%, 75%, and 100% all had greater total P uptake than the treatment with only 100% P. Notably, utilizing mixed use of *C. sphaeroides* ST16 and ST26 with P fertilizer from 0% to 100% P had greater total P uptake than the treatment with only 100% P.

3.4. Combination of P fertilization and *Cereibacter sphaeroides* ST16 and ST26 changed growth, yield components, and rice grain yield

3.4.1. Changes in rice growth

Plant height and panicle length increased when utilizing PNSB-P. The treatments utilizing a single use or the mixed use of *C. sphaeroides* ST16 and ST26 had taller plant height than the control in the 2 cropping seasons. The panicle length peaked in the treatment with the mixed use of 2 strains *C. sphaeroides* ST16 and ST26, then the single use of *C. sphaeroides* ST16 or ST26 in the first cropping season. In the second cropping season, the panicle length rose according to the following order: control < mixed use of *C. sphaeroides* ST16 and ST26 < *C. sphaeroides* ST26 ~ *C. sphaeroides* ST16. Moreover, plant height and panicle length varied in the 2 cropping seasons, with increased plant height in the treatments with 75% and 100% P and unchanged in the treatments with 25% and 50% P in the first cropping season. All of the P-fertilized treatments had increased plant height compared with the control in the second cropping season. The panicle length proportionally increased according to the P fertilizer rates from 0%, 25%, 50%, 75% to 100% P in the first cropping season, but remained in the second cropping season (Table 5).

3.4.2. Changes in rice yield traits

Utilizing PNSB-P or P fertilizer increased rice grain yield significantly compared with the control in the 2 cropping seasons because the yield components, including the number of panicles pot^{-1}, the number of rice grains panicle^{-1}, and the filled rice grain rate, increased. In particular, the rice grain was the greatest when utilizing the mixed use of 2 *C. sphaeroides* ST16 and ST26 (33.7 g pot^{-1}), then the single use of *C. sphaeroides* ST26 (32.2 g pot^{-1}), and the single use of ST16 (30.8 g pot^{-1}). The lowest was in negative control (23.5 g pot^{-1}) in the first cropping season. In the second cropping season, the yield was superior in the treatment with the mixed use of *C. sphaeroides* ST16 and ST26 (30.7 g pot^{-1}), then the single use of each of *C. sphaeroides* ST16 ▯ ST26 with 25.8 and 25.1 g pot^{-1}, respectively. The lowest one was still the negative control. Besides, the yield gradually increased according to the P fertilizer rates from 0% to 100% P in the 2 cropping seasons (Table 5).

Table 5
Influences of P fertilizer and *Cereibacter sphaeroides* on growth, yield components, and rice grain yield

Factor		Plant height	Panicle length	The number of panicles pot^{-1}	The number of grains $panicle^{-1}$	1,000-grain weight	Filled grain rate	Rice grain yield
		cm	cm	panicles	grains	g	%	g pot^{-1}
Season 1								
P level (A) (%)	0	101^{c}	19.0^{e}	19.0^{d}	73.3^{d}	20.7	79.0^{c}	27.1^{e}
	25	102^{c}	19.6^{d}	20.5^{c}	75.8^{c}	20.6	80.7^{b}	28.9^{d}
	50	103^{bc}	20.3^{c}	21.1^{c}	80.9^{b}	21.0	81.4^{b}	31.1^{c}
	75	104^{ab}	20.8^{b}	23.0^{b}	82.3^{b}	20.9	82.6^{a}	31.4^{b}
	100	105^{a}	21.6^{a}	26.4^{a}	89.2^{a}	21.0	83.3^{a}	31.7^{a}
P bacteria (B)	NB	94.6^{b}	18.9^{c}	20.3^{c}	66.4^{c}	20.7	79.7^{c}	23.5^{d}
	ST16	105.6^{a}	20.5^{b}	22.4^{b}	83.4^{b}	21.0	81.9^{b}	30.8^{c}
	ST26	105.5^{a}	20.4^{b}	22.0^{b}	85.6^{a}	20.7	80.1^{c}	32.2^{b}
	MIX	106.1^{a}	21.2^{a}	23.3^{a}	85.8^{a}	21.0	83.9^{a}	33.7^{a}
Significance level (A)		*	*	*	*	ns	*	*
Significance level (B)		*	*	*	*	ns	*	*
Significance level (A*B)		ns	*	*	*	ns	ns	*
CV (%)		2.38	2.44	6.54	3.58	2.92	2.01	6.54
Season 2								
P level (A) (%)	0	88.4^{c}	18.6	18.7^{d}	66.0^{e}	23.0	87.4^{d}	23.4^{c}
	25	90.0^{b}	18.7	21.0^{c}	69.4^{d}	23.2	89.8^{c}	24.7^{b}
	50	90.8^{ab}	18.5	21.1^{c}	70.7^{c}	23.5	90.7^{b}	25.2^{b}
	75	91.8^{a}	18.5	21.9^{b}	72.8^{b}	23.5	91.8^{a}	26.9^{a}
	100	90.8^{ab}	18.8	23.0^{a}	74.8^{a}	23.2	92.0^{a}	27.7^{a}
P bacteria (B)	NB	84.9^{c}	18.1^{c}	18.6^{c}	64.6^{c}	23.2	88.2^{c}	20.8^{c}
	ST16	90.7^{b}	19.0^{a}	21.6^{b}	72.3^{b}	23.2	91.2^{a}	25.8^{b}
	ST26	93.1^{a}	18.8^{ab}	21.7^{b}	73.7^{a}	23.2	90.4^{b}	25.1^{b}
	MIX	92.7^{a}	18.6^{b}	22.7^{a}	72.3^{b}	23.5	91.6^{a}	30.7^{a}
Significance level (A)		*	ns	*	*	ns	*	*
Significance level (B)		*	*	*	*	ns	*	*
Significance level (A*B)		*	ns	*	*	ns	*	*
CV (%)		1.66	3.15	3.90	2.30	3.02	1.27	4.47

Note: In the same column, numbers followed be different letters are different statistically *: 5% significance; ns: no significance; NB: no bacteria; ST16: *Cereibacter sphaeroides* ST16; ST26: *Cereibacter sphaeroides* ST26; MIX: *Cereibacter sphaeroides* ST16 and *Cereibacter sphaeroides* ST26.

3.4.3. Changes in rice grain yield

The Fig. 3 illustrates that the rice grain yield increased according to the increase in the fertilizer rate from 0% to 100% P without utilizing PNSB-P in the 2 cropping seasons. When utilizing *C. sphaeroides* ST16 without P fertilizer, the yield was equivalent to that in the treatment with only 75% P in the negative control in the first cropping season and that in the treatment with only 100% P in the second cropping season. Furthermore, utilizing *C. sphaeroides* ST16 with P fertilizer from 25% to 100% P and utilizing *C. sphaeroides* ST26 or *C. sphaeroides* ST16 + ST26 with P fertilizer from 0% to 100% P resulted in greater yield than the treatment with only 100% P in the 2 cropping seasons.

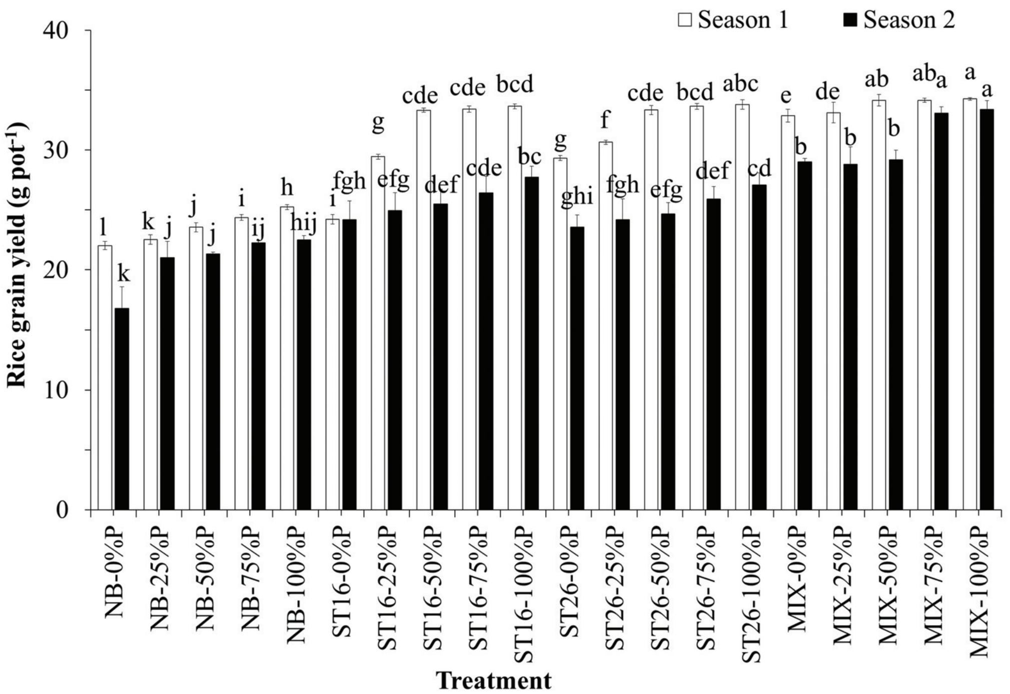

Fig. 3. Influences of P fertilizer and *Cereibacter sphaeroides* on the rice grain yield in two rice cropping seasons

*Note: NB: no bacteria; ST16: *Cereibacter sphaeroides* ST16; ST26: *Cereibacter sphaeroides* ST26; MIX: *Cereibacter sphaeroides* ST16 and *Cereibacter sphaeroides* ST26; 0, 25, 50, 75, 100: fertilizer rates. For the bars with the same color, different letters indicate significant difference at 5%.

4. Discussion

As classified by Cu et al. (2000), the P_{total} content in the soil was rich, while and the $P_{soluble}$ was moderate (Horneck et al., 2011). This means a great amount of insoluble P. These P, if solubilized, would be a great source for plant use. On the other hand, the total N content was very low (Metson, 1961), indicating a poorly fertile soil. Furthermore, both the pH_{H2O} and pH_{KCl} were very low, limiting plant growth (Horneck et al., 2011). Moreover, EC was also low and insignificantly affected crops according to Horneck et al. (2011). In addition, regarding soil cations, the CEC was low according to Landon (2014), while the K^+ and Mg^{2+} were moderate and high (Horneck et al., 2011).

The SPAD from days 21 to 42 after sowing and the chlorophyll a and a + b contents increased in the 2 cropping seasons when utilizing *C. sphaeroides*. Moreover, the proline content in rice was lower in the treatments utilizing PNSB-P (Table 2). The 5-aminolevulinic acid (ALA) participated in improving plants' tolerance against non-biotic stresses, such as salinization (Jiao et al., 2021). In addition, salinity is the cause of the remarkable reductions in chlorophyll content (Alagoz et al., 2023). As per Nunkaew et al. (2015), ALA can be produced by salt tolerant PNSB strains. Based on the ability to immobilize soil Na^+, EPS produced by PNSB can lessen the influences of salinity on plants (Khuong et al., 2022). Moreover, ALA is an essential precursor to produce porphyrin which can recover the chlorophyll content (Jiao et al., 2021). Treating 30 mg L^{-1} ALA on *Taxus chinensis* resulted in greater chlorophyll content and photosynthesis rate (Wu et al., 2023). Additionally, PNSB can also provide available N for plants based on their ability to fix N (Morey-Yagi et al., 2024), resulting in increased chlorophyll content (Fiorentini et al., 2019, Xuan et al., 2024). Furthermore, since the proline is known as an indicator of saline stress, while PNSB produced EPS to fix soil Na^+, the proline content in rice dropped (Khuong et al., 2021, 2022; Giannelli et al., 2023).

The values of pH_{H2O}, NH_4^+ and $P_{soluble}$, CEC, K^+, Mg^{2+}, and Ca^{2+} were improved and m EC and Na^+ were decreased in the treatments utilizing *C. sphaeroides* ST16 and ST26 (Table 3). pH directly affects the soil nutrient availability and nutrients are the most available when the soil pH fluctuates from 6.0 to 7.0 (Faizullah et al., 2024). In particular, in acidic or alkaline soils, P complexifies with metal oxides of Fe, Al, and Ca and forms corresponding insoluble P compounds, e.g. Fe-P and Al-P in acidic soils and Ca-P in alkaline soils (Zhao et al., 2023; Faizullah et al., 2024). PNSB play a role as plant growth-promoting bacteria because they can secrete ALA, EPS, IAA, and siderophores to assist plants in overcoming non-biotic stresses such as salinity (Lee et al., 2021) by reducing the exchangeability of cation Na^+, soil EC (Khuong et al., 2021), and toxicities of H^+, Al^{3+}, Fe^{2+}, and Mn^{2+} in saline acidic soils in the Mekong Delta Vietnam (Khuong et al., 2022). The pH rose when utilizing *Luteovulum sphaeroides* W11 and W03 due to the linkage between EPS and H^+ (Khuong et al., 2021). The soil pH increased by 0.13 when using mixed *L. sphaeroides* EPS18, EPS37, and EPS54 (Khuong et al., 2024). Moreover, PNSB are known as biofertilizers (Sabki et al. (2021) because they can make use of insoluble P compounds in the soil and turn them into $P_{soluble}$ for plants to use, along with the N fixing and K dissolving functions (Sundar and Chao, 2022). In addition, PNSB can be considered safe to the environment because in the study by Wang et al. (2021), a 5-year use of PNSB promote the soil fertility without harms.

Table 4 and Fig. 1 reveal that the Na content in stem-leaf and rice grain was lower than the control not utilizing PNSB-P, though the total Na uptake varied in the 2 cropping seasons. Interestingly, utilizing *C. sphaeroides* ST26 with 100% P had equivalent total Na uptake to the treatment with only 75% P. The mixed use of 3 the PNSB *L. sphaeroides* EPS18, EPS37, and EPS54 also reduced Na uptake in rice by 9.50 mg Na pot^{-1} (Khuong et al., 202b, 2024).

In Table 4 and Fig. 2, the total P uptake rose when utilizing *C. sphaeroides* ST16 and ST26. The mixed use of *R. palustris* VNW64, VNS89, TLS06, and VNS02 combined with 50% P of chemical fertilizer increased the soluble P content 41.4% and had equivalent total P uptake to fertilizing 100% P according to the recommended fertilizer rate for sesame (Khuong et al., 2023b). Using *Rhodopseudomonas palustris* PSB32 enhance rice growth, yield, and tolerance (Sundar et al., 2024). As per Shan et al. (2022), foliar application of PNSB can also improve rice growth and yield. In peanut, PNSB inoculants also show positive results (Wang et al. 2021).

Growth traits, such as plant height and panicle length, yield components, such as the number of panicles pot^{-1}, the number of rice grains panicle^{-1}, and filled rice grain rate, and yield increased under the presence of *C. sphaeroides* ST16 and ST26 (Table 4; Fig. 3). PNSB can solubilize P and provide it in the available form for plants to use (Dat et al., 2024). Moreover, PNSB can also fix N, dissolve K, and provide PGPS to facilitate plants under adverse conditions (Lee et al., 2021; Maeda, 2021), leading to improved plant height, panicle length, yield components, and rice grain yield (Khuong et al., 2021, 2022, 2024). Moreover, gene expressions of rice can also be influence by PNSB (Iwai et al. 2023). Thus, *C. sphaeroides* ST16 and ST26 are potent in applications in cultivations under harsh conditions, such as saline acidic conditions common in the Mekong Delta to ameliorate soil traits, cut off fertilizer cost, and plant growth and yield.

5. Conclusions

By the application of *C. sphaeroides* ST16 and ST26, the acidity and salinity of the salinized acidic soil were alleviated. Moreover, the soluble P content increased, while the insoluble P, e.g. Fe-P, Al-P, and Ca-P decreased under the application of the P-solubilizing strains. From the improvement in soil fertility, the salt stress of the rice was lessened via the reduced proline content by and total Na uptake. Furthermore, from the solubilized P content by the ST16 and ST26 strains, the total P uptake in plants increased by 24.0 to 46.6% compared with the negative control. Consequently, the rice yield components, including the number of panicle pot^{-1}, rice grains panicle^{-1}, and the filled rice grain rate and rice grain yield were improved by 24.0–46.6% compared with the negative control in saline soil. Ultimately, utilizing mixed use of *C. sphaeroides* ST16 and ST26 reduced 100% of chemical P fertilizer. Thus, it should be further applied on the field practice.

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Conflict of interest

The authors declare no conflict of interest. The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. This research did not involve human or animal subjects.

Author contribution

All authors participated in conceptualization and approval of the final version of the manuscript. Le Tien Dat wrote the first draft of the manuscript. Nguyen Quoc Khuong, Tran Trong Khoi Nguyen, Ha Ngoc Thu, Nguyen Duc Trong, and Le Thi My Thu involved to the methodology. Do Thi Xuan, Ly Ngoc Thanh Xuan, Tran Chi Nhan, and Le Thanh Quang conducted formal analysis and investigation. Nguyen Quoc Khuong and Le Thanh Quang edited and revised the final manuscript.

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