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Potential Biofertilizers for Alkaline Soil: Bacteria Isolated from the Rhizosphere of Potatoes

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Abstract: Root-associated microorganisms, which can be recruited specially by plants to cope with environmental stress under extreme conditions, are one of the major mediators of nutrient exchange between plants and the environment. To obtain more crop-beneficial microbes, rhizosphere bacteria of Désirée potatoes cultivated in poor and alkaline soil have been studied. The screening of 83 strains with incomplete identical 16S rDNA sequences showed that 47 strains produced indole acetic acid (IAA), with contents ranging from 0.2 to 42 mg/L, and seven strains were phosphorus-solubilizing, among which six strains significantly increased the growth rate of potato plants. Thirty-seven strains produced siderophore and four strains were zinc-solubilizing, among which three strains significantly alleviated the chlorosis of potato plants. In all of the isolates, the species *Variovorax soli* (ST98) and *Cellulomonas biazotea* (ST118) were first found to possess an IAA-secreting ability; the species *Leifsonia aquatica* (ST172) and *Leifsonia naganoensis* (ST177) and the genus *Sutcliffiella* (ST11) were first discovered to be capable of phosphorus solubilization; the species *Chryseobacterium daecheongense* (ST32) was the first reported to be capable of zinc solubilization; and the species *V. soli* (ST98), *C. biazotea* (ST118) and *L. naganoensis* (ST177) were first found to be capable of plant growth promotion. The discovery of multiple functional bacteria enriched the resources of plant growth-promoting bacteria and provided a foundation for biofertilizer production to improve soil conditions and crop production.

Keywords: potato; rhizosphere microbes; plant–microbe interaction; siderophores; phosphorus solubilization; biofertilizer

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1. Introduction

The potato is the fourth most important staple food crop. It is a food security crop and a possibly decisive weapon in the fight against starvation because of its high yield and great nutritive value, and it is rich in starch, protein and microelements [1]. China, as a major potato-planting country, has consistently ranked first in terms of potato-planting area and production volume worldwide [2]. Unfortunately, quality and production are under great threat because of the soil environment, pests and diseases. The application of large amounts of chemical fertilizers and pesticides will cause environmental degradation and affect the sustainable development of agriculture.

Plants growing in natural ecosystems live in close association with a multitude of microorganisms [3]. As the second genome of plants, the rhizosphere microbiome plays an important role in promoting plant growth and disease resistance [4]. In particular, plant growth-promoting rhizobacteria (PGPR), which can benefit plants by producing plant growth hormones [5], convert many plant-unavailable essential nutrients, such as nitrogen, phosphorous, zinc and iron, into available forms, synthesize antibiotics or enhance induced systemic resistance (ISR) to help plants against pathogenic bacteria and fungi [6].

In potatoes, the function of rhizosphere microorganisms is mainly concentrated on the resistance of pathogenic bacteria. Only a few studies have shown that arbuscular fungi, such as *Rhizophagus irregularis*, *Funneliformis mosseae* and *Claroideoglomus etunicatum*, and some bacteria, such as *Enterobacter cloacae*, *Bacillus thuringiensis* and *Pseudomonas pseudoalcaligenes*, can improve increase both the yield and nutritional quality of potatoes [7].

Plant rhizosphere microbial composition is affected by hosts and environment [8]. Plants shape rhizosphere microbes by modifying the amount and composition of root exudates to acquire belowground resources in nutrient-limited soil, which is consistent with the "cry for help" hypothesis in disease resistance [9]. Plants may shape rhizosphere flora by secreting phenolic substances and recruit related flora to improve the iron solubility in the rhizosphere when planted in iron-deficient soil [10,11], and the result was similar when it experienced phosphorus deficiencies [12]. In view of the above research, we hypothesized that when potatoes are grown in poor alkaline soil, special beneficial strains will be recruited to facilitate nutrient absorption. Yunnan is a major province for potato cultivation, but some of the major cultivation areas for potatoes have alkaline soils with extremely low nutrient availability. This is particularly true for Dayao, a small city located in the northwestern part of Yunnan Province. To exploit more microbial biofertilizer to assist the green potato industry development in Yunnan, the rhizosphere bacteria of potatoes cultivated in Dayao were studied.

2. Materials and Methods

2.1. Soil Sample Collection and Physicochemical Parameter Determination

Soil samples were collected from four major production areas of potatoes in Yunnan Province of China, including Dayao (25.85° N, 101.25° E), Xundian (25.63° N, 102.96° E), Dehong (24.02° N, 97.85° E) and the planting base on campus (24.86° N, 102.84° E). The pH of the soils was measured using a pH meter. Plant-available iron and zinc were measured using chelator diethylenetriaminepentaacetic acid (DTPA) extraction [13]. Briefly, 10 g of air-dried soil was shaken for 2 h with 20 mL of extracting solution (0.005 M DTPA, 0.1 M triethanolamine and 0.01 M $CaCl_2$, pH 7.3). The leachate was centrifuged and filtered through a 0.22 μm membrane. The iron and zinc contents in the leachate were measured using an atomic spectrophotometer. Plant-available phosphorus was measured using $NaHCO_3$ extraction—the molybdenum antimony resistance colorimetric method [14].

2.2. Isolation and Purification of Potato Rhizosphere Bacteria

Samples were collected from the growing region of potato plants that grow in Dayao, Yunnan, China (25.85° N, 101.25° E). The whole root system was carefully collected using tweezers, and large soil aggregates and debris were removed by gently shaking. Roots were placed in a 15 mL centrifuge tube and transferred to a laboratory being kept on ice. Isolation of bacteria was carried out through the serial dilution method. Ten grams of root tissues were homogenized using a grinding mill and dissolved in 100 mL of saline solution (0.9% NaCl). One milliliter of suspension was added to a test tube containing 9 mL of saline solution to obtain a suspension with a 10^{-2} dilution level. Dilution was performed in the same manner until a 10^{-6} suspension was obtained. Subsequently, 0.1 mL of the suspension was grown on Tryptone Soy Agar (TSA) medium in a Petri dish at 30 °C. Single colonies were picked and grown to reisolate and make pure cultures [15].

2.3. Sequencing and Phylogenetic Analysis

To confirm the taxonomic status of bacterial isolates, 16S ribosomal Deoxyribo Nucleic Acid(16S rDNA) with a length of 1.5 kb was amplified and sequenced with the primers 8F/1492R (8F, AGAGTTTGATCCTGGCTCAG; 1492R, GGTTACCTTGTTACGACTT) [16]. The sequences of the selected strains were compared and aligned with those of other strains from GenBank using BLAST (http://www.ncbi.nlm.nih.gov/blast, accessed on 4 May 2023). A phylogenetic tree was constructed using the neighbor joining method with MEGA.

2.4. Indole Acetic Acid (IAA) Production

Each bacterial strain was grown in TSB solution under shaking at 180 rpm at 30 °C for 3 days, and supernatants were collected to determine the auxin IAA. The production of IAA by bacteria was tested using Salkowski reagent (1.2% $FeCl_3$ and 37% H_2SO_4) and measured at 530 nm wavelength using a spectrophotometer. The concentration of IAA was calculated using a standard curve of known concentrations of synthetic IAA [17].

2.5. Siderophore Production

Siderophore production by the bacterial isolates was detected using the universal chrome azurol 'S' (CAS) agar plate assay. A single colony of isolated bacteria was cultured in TSB solution overnight at 30 °C, and then 10 µL of bacterial solution was inoculated on CAS plates and incubated at 30 °C for 72 h [18]. The diameters of the colony and orange halo were detected, and the solubilization index (SI) was calculated as follows:

$$\mathrm{SI} = \text{Halozone Diameter(mm)} \ / \text{Colony Diameter(mm)} \quad (1)$$

2.6. Phosphate Solubilization

Ten microliters of bacterial solution cultured in TSB overnight were inoculated on insoluble inorganic phosphorus medium (glucose 10 g, $Ca_3(PO_4)_2$ 5 g, $(NH_4)_2SO_4$ 0.5 g, NaCl 0.3 g, $CaCl_2$ 0.3 g, MgSO2084·7H2082O 0.3 g, FeSO2084·7H2082O 0.03 g, $MnSO_4 \cdot H_2O$ 0.03 g, agar powder 18 g, distilled water 1 L, pH 7.0 to 7.2) and incubated at 30 °C for 3–5 days. The plates were observed for clear phosphate solubilization around colonies, and the solubilization index (SI) was calculated as follows:

$$\mathrm{SI} = \text{Clearance zone Diameter(mm)} / \text{Colony Diameter(mm)} \quad (2)$$

2.7. Zinc Solubilization

A 10 µL volume of bacterial solution cultured in TSB overnight was inoculated on insoluble zinc medium (10 g glucose, 5 g ZnO, 0.5 g $(NH_4)_2SO_4$, 0.3 g NaCl, 0.3 g $CaCl_2$, 0.3 g MgSO2084·7H2082O, 0.3 g FeSO2084·7H2082O, 0.03 g $MnSO_4 \cdot H_2O$ 0.03 g, agar powder 18 g, distilled water 1 L, pH 7.0 to 7.2) and incubated at 30 °C for 7–10 days. The plates were observed for clear ZnO solubilization around colonies, and the solubilization index (SI) was calculated as above [19].

2.8. Plant–Bacteria Interaction

To investigate the effect of the strains on plant growth under greenhouse conditions, the strains were cultured overnight, washed and resuspended in 0.9% NaCl. Three-week-old potato plants grown in 1/2 Hoagland medium were inoculated with a cell suspension of strains at a final concentration of 5×10^7 CFU mL^{-1}. To further verify whether related strains can promote mineral element absorption in plants, potato plants were grown in 1/2 Fe/P/Zn-deficient Hoagland medium with insoluble $FeCl_3$ (pH 7.3)/$Ca_3(PO_4)_2$/ZnO. The plant height and root length were measured every week to calculate the growth rate. The relative growth rates (RGRs) were calculated as follows:

$$\mathrm{RGR} = \frac{\text{height on the 7th/14th/21st day(mm)} - \text{height on the 1st day(mm)}}{\text{height on the 1st day(mm)}} \quad (3)$$

2.9. Detection of Chlorophyll and Mineral Elements in Plants

Chlorophyll extraction and quantification were adapted from reference [20]. Samples were prepared by a hole puncher from 10 mm^2 of leaf tissue. Chlorophyll was extracted by adding 1 mL Dimethyl sulfoxide (DMSO) and incubating samples at 65 °C with shaking for 45–60 min until plant tissue was transparent and chlorophyll was completely extracted. The absorbance of the tissue-free chlorophyll extract was measured at 652 nm on a spectrophotometer (NanoDrop One, Thermo Scientific, Waltham, MA, USA). The youngest fully

expanded leaves were collected for drying and digestion by a microwave digestion system, and the content of mineral elements was measured by an atomic spectrophotometer.

2.10. Data Analysis

Statistical analysis of the data was carried out by GraphPad Prism 6 software. When the normality and homogeneity of variance hypotheses were satisfied, a one-way analysis of variance (ANOVA) was used to compare the effect of these bacterial isolates on potato growth performance. A posteriori multiple comparisons were carried out using Tukey's range tests at $p \leq 0.05$. All results are the means of three to five independent replicates, as specified above.

2.11. Nucleotide Sequence Accession Number

The GenBank accession numbers for the 16S rDNA gene sequence of all the strains are attached in Table S1.

3. Results

3.1. Physicochemical Parameters of Soils

The pH and available iron, zinc and phosphorus of soil samples collected from four areas of potato crops in Yunnan Province were measured. All the soil samples were neutral (6.5 < pH < 7.5) or alkaline (7.5 < pH < 8.5). The soil of Dehong contained high contents of iron and phosphorus, followed by Xundian and the planting base in campus. The soil of Dayao contained the lowest iron and phosphorus contents, possibly because of its higher pH (Figure 1).

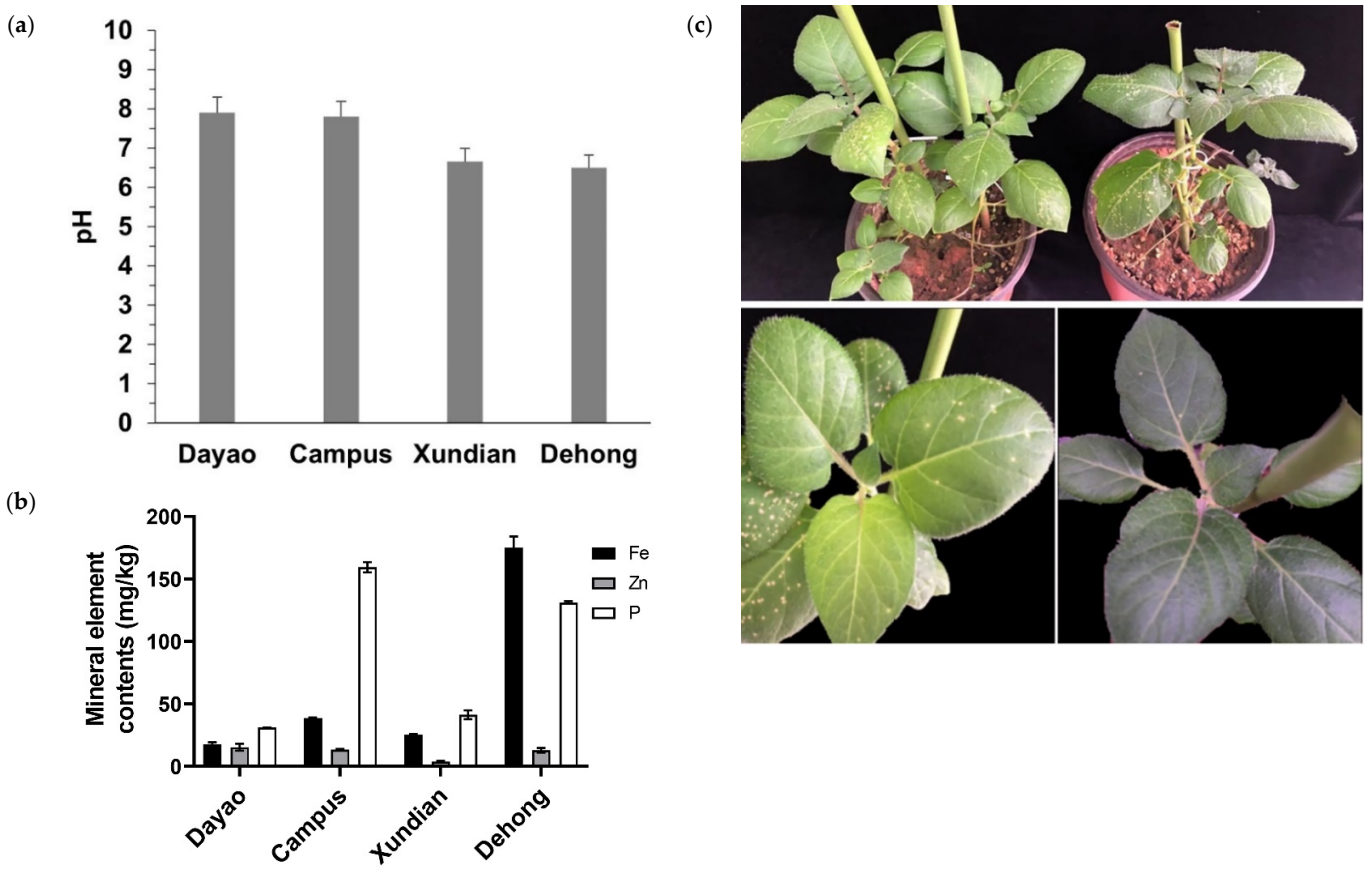

Figure 1. The pH and available mineral element contents of soil from different areas of Yunnan Province: (**a**) pH of soil from different areas of Yunnan Province; (**b**) available mineral element contents of soil from different areas of Yunnan Province; and (**c**) potato plants cultivated in Dayao (left) and Dehong soil (right).

3.2. Identification and Phylogenetic Analysis of Bacteria Isolated from the Potato Rhizosphere

One hundred and fifty-three strains were isolated and identified from the roots (mixed with six plants) of cultivated potato cultivated in Dayao and named following ST (*Solanum tuberosum*). Based on the sequencing results of the 16S rDNA gene, the nucleotide sequences displayed with high query coverage and sequence similarity (to 98%) were assigned to the same species. These bacterial isolates belonged to four phyla (Actinomycetota, Bacillota, Bacteroidota and Pseudomonadota), six classes (Actinomycetes, Bacilli, Flavobacteriia, Betaproteobacteria, Alphaproteobacteria and Gammaproteobacteria), 10 orders (Micrococcales, Mycobacteriales, Kitasatosporales, Bacillales, Flavobacteriales, Burkholderiales, Hyphomicrobiales, Xanthomonadales, Pseudomonadales and Sphingomonadales), 19 families (Microbacteriaceae, Cellulomonadaceae, Promicromonosporaceae, Streptomycetaceae, Bacillaceae, Paenibacillaceae, Weeksellaceae, Alcaligenaceae, Rhizobiaceae, Boseaceae, Burkholderiaceae, Devosiaceae, Rhizobiaceae, Xanthomonadaceae, Sphaerotilaceae, Pseudomonadaceae, Xanthomonadaceae, Sphingomonadaceae and Comamonadaceae) and 32 genera (Table S1). *Microbacterium*, which belongs to Actinomycetota, was determined to be the dominant genus among them (Figure 2).

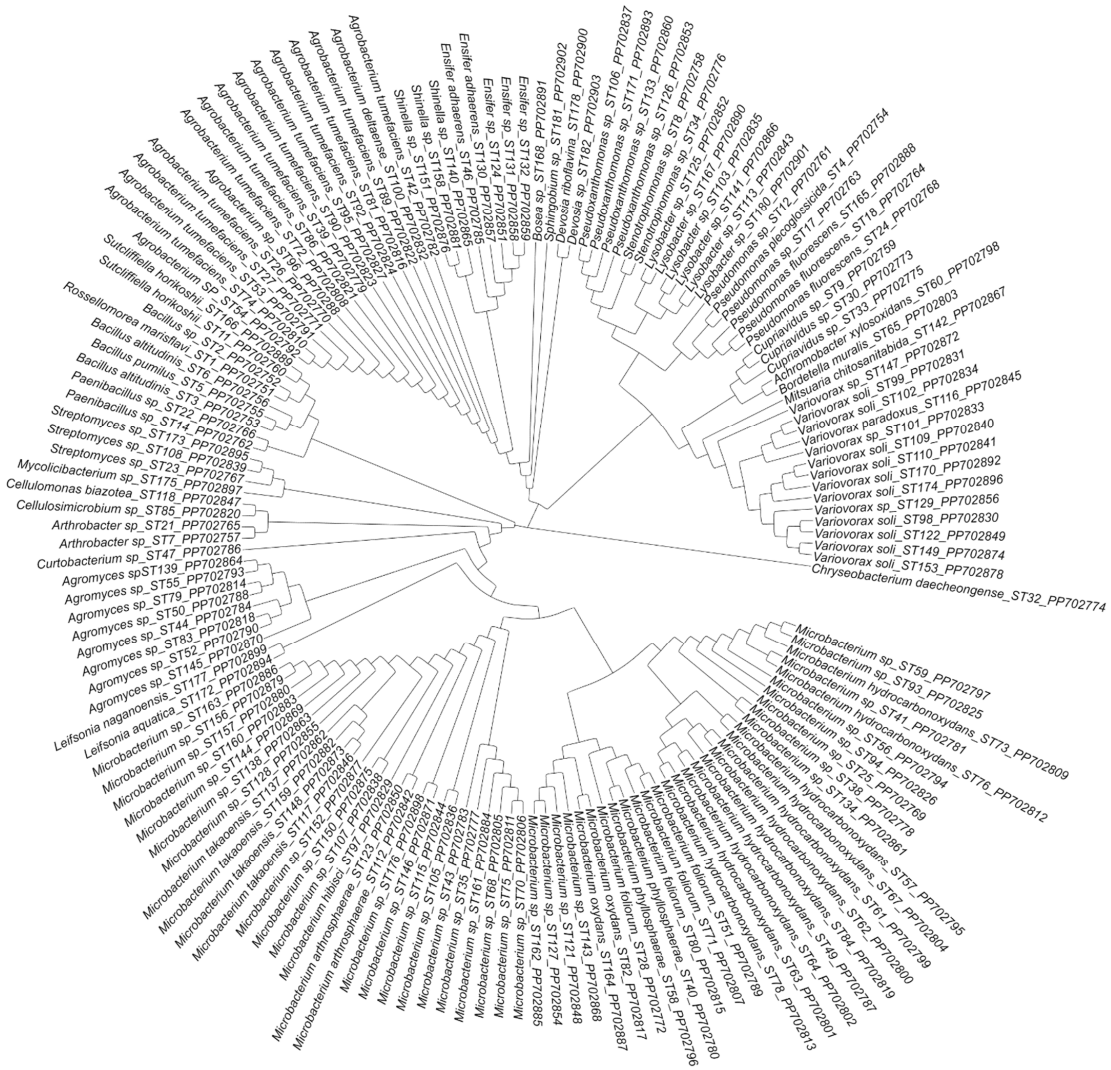

Figure 2. Phylogenetic tree of strains isolated from potato rhizosphere.

3.3. Rhizosphere Bacterial Strains Promote Plant Growth by Producing IAA

IAA is one of the most physiologically active auxins in plants and can regulate the growth of stems, buds and roots. Forty-seven isolates could produce IAA, among

which seven strains had concentrations greater than 10 mg/L, nine strains had concentrations between 5 and 10 mg/L and 18 strains had concentrations ranging from 1 to 5 mg/L (Table 1). Twenty strains that were highly IAA-producing strains were inoculated into three-week-old potato plant roots. The results showed that the growth rates of plants inoculated with strains, *V. soli* ST98, *Agromyces* sp. ST139, *C. biazotea* ST118, *Cupriavidus* sp. ST9 and *Cellulosimicrobium* sp. ST85 were significantly increased on the 21st day (Figure 3a,b). We also observed the growth of roots. Interestingly, plants whose above-ground growth was promoted had a decrease in the amount of root (Figure 3c), which may be related to the availability of nutrition, because root morphology and growth are regulated by environmental nutrition, and in an environment with adequate nutrition, not too many roots are needed for nutrient acquisition [21,22].

Table 1. IAA production by strains.

Strains	IAA Contents (mg/L)	Strains	IAA Contents (mg/L)
ST32	43.16 ± 0.5894	ST146	1.69 ± 0.0192
ST25	23.57 ± 0.7434	ST112	1.67 ± 0.1761
ST49	23.47 ± 0.235	ST50	1.41 ± 0.0419
ST7	14.18 ± 0.4438	ST4	1.37 ± 0.3029
ST98	9.81 ± 0.8337	ST1	1.15 ± 0.0679
ST139	9.6 ± 0.3101	ST128	1.14 ± 0.2128
ST118	7.79 ± 0.2416	ST130	1.05 ± 0.0712
ST9	7.5 ± 0.3165	ST176	0.96 ± 0.0546
ST85	6.13 ± 0.1182	ST22	0.96 ± 0.0726
ST46	6.05 ± 0.1425	ST55	0.93 ± 0.0144
ST21	5.93 ± 0.1774	ST68	0.92 ± 0.0173
ST140	5.88 ± 0.2822	ST14	0.84 ± 0.0127
ST144	5.67 ± 0.319	ST145	0.71 ± 0.1446
ST43	5.56 ± 0.0459	ST107	0.69 ± 0.1248
ST28	4.38 ± 0.166	ST121	0.69 ± 0.1357
ST124	3.89 ± 0.2196	ST26	0.49 ± 0.0474
ST82	3.84 ± 0.0679	ST70	0.48 ± 0.1639
ST132	3.16 ± 0.1692	ST17	0.34 ± 0.1901
ST173	2.43 ± 0.0804	ST51	0.31 ± 0.0694
ST35	2.34 ± 0.2021	ST12	0.23 ± 0.0614
ST116	2.09 ± 0.0939	ST100	0.18 ± 0.0139
ST172	2.03 ± 0.5157	ST175	0.16 ± 0.0948
ST73	1.94 ± 0.141	ST97	0.15 ± 0.036
ST40	1.92 ± 0.0756		

(**a**)

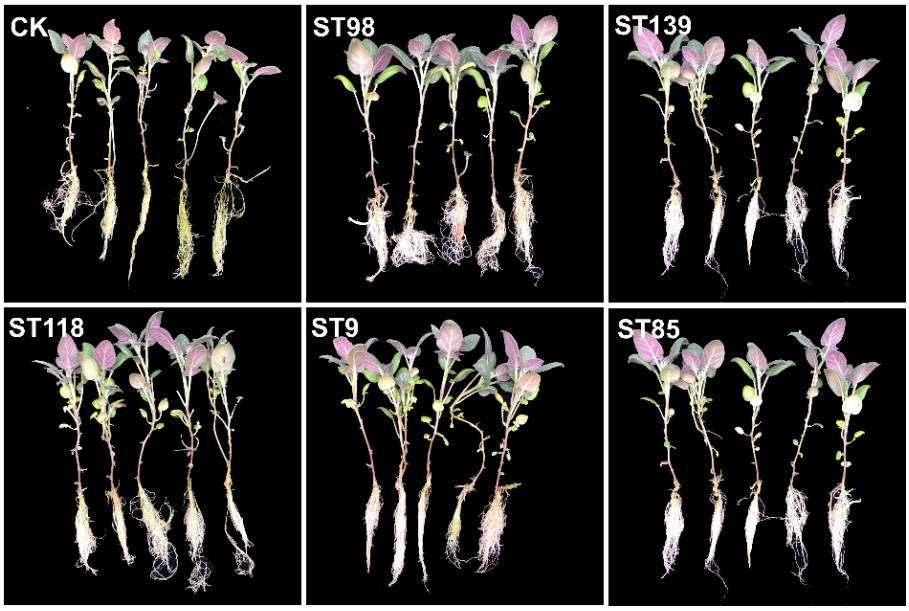

Figure 3. *Cont.*

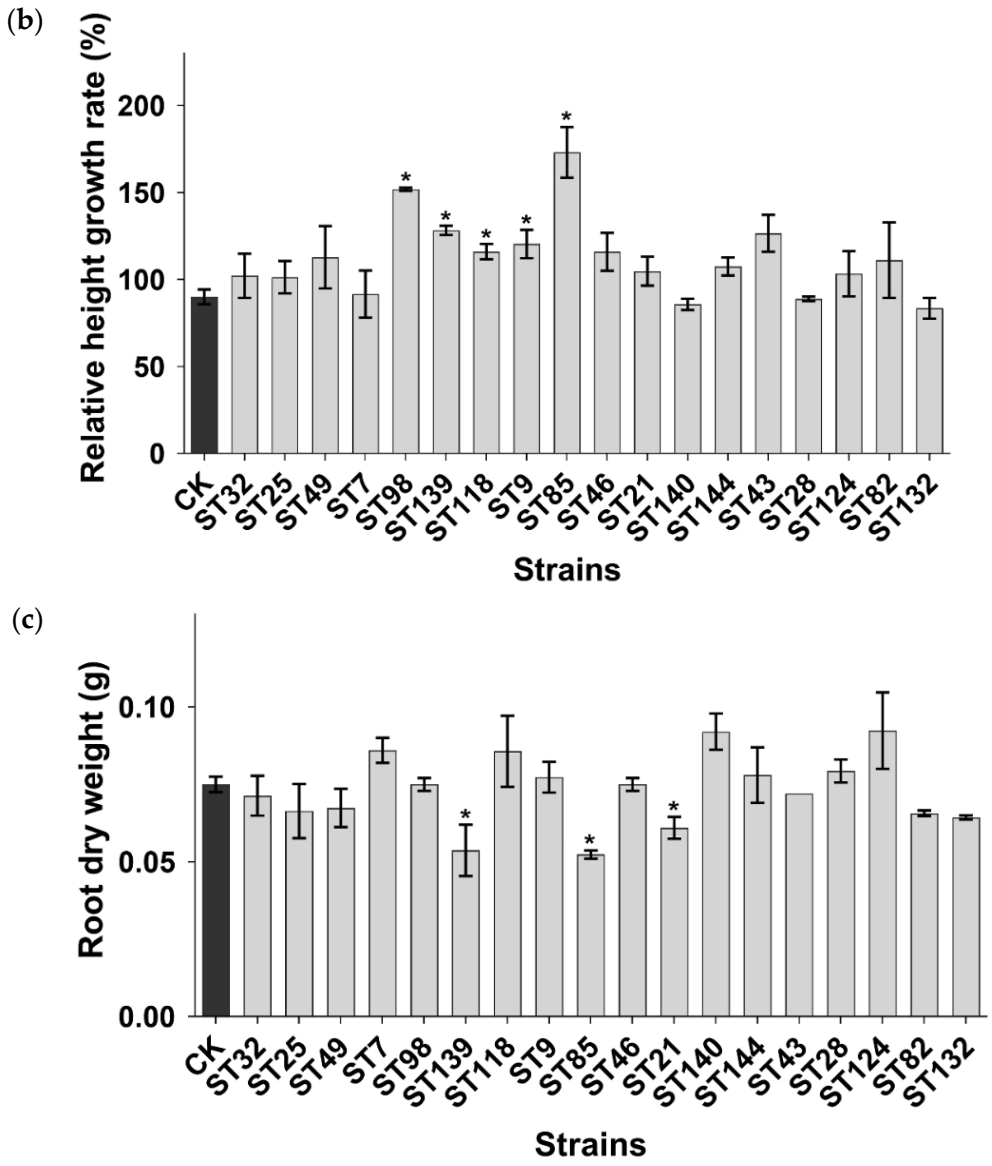

Figure 3. Growth promotion by IAA-producing strains: (**a**) partial plant growth state on the 21st day; (**b**) relative height growth rate on the 21st day; and (**c**) root dry weight on the 21st day. * $p \leq 0.05$ (Student's *t* test).

3.4. Rhizosphere Bacterial Strains Promote Plant Iron Absorption by Siderophore Production

Siderophores production were tested using a chrome azurol 'S' (CAS) agar plate. Nearly one-third of the isolates could produce siderophores, among which nine strains, including *Microbacterium foliorum* ST51, *Microbacterium phyllosphaerae* ST40, *Microbacterium* sp. ST35, *Pseudomonas fluorescens* ST18, *Microbacterium hydrocarbonoxydans* ST49, *Agrobacterium tumefaciens* ST81, *Cellulosimicrobium* sp. ST85, *Microbacterium* sp. ST43 and *Pseudoxanthomonas* sp. ST106, had a high solubilization index greater than 1.7 and were inoculated into plant roots (Figure 4a, Table 2). The results showed that plants inoculated with *M. phyllosphaerae* ST40 and *Microbacterium* sp. ST35 had higher chlorophyll in young leaves when cultured in Fe-deficient Hoagland medium with $FeCl_3$ (pH = 7.3) (Figure 4b,c).

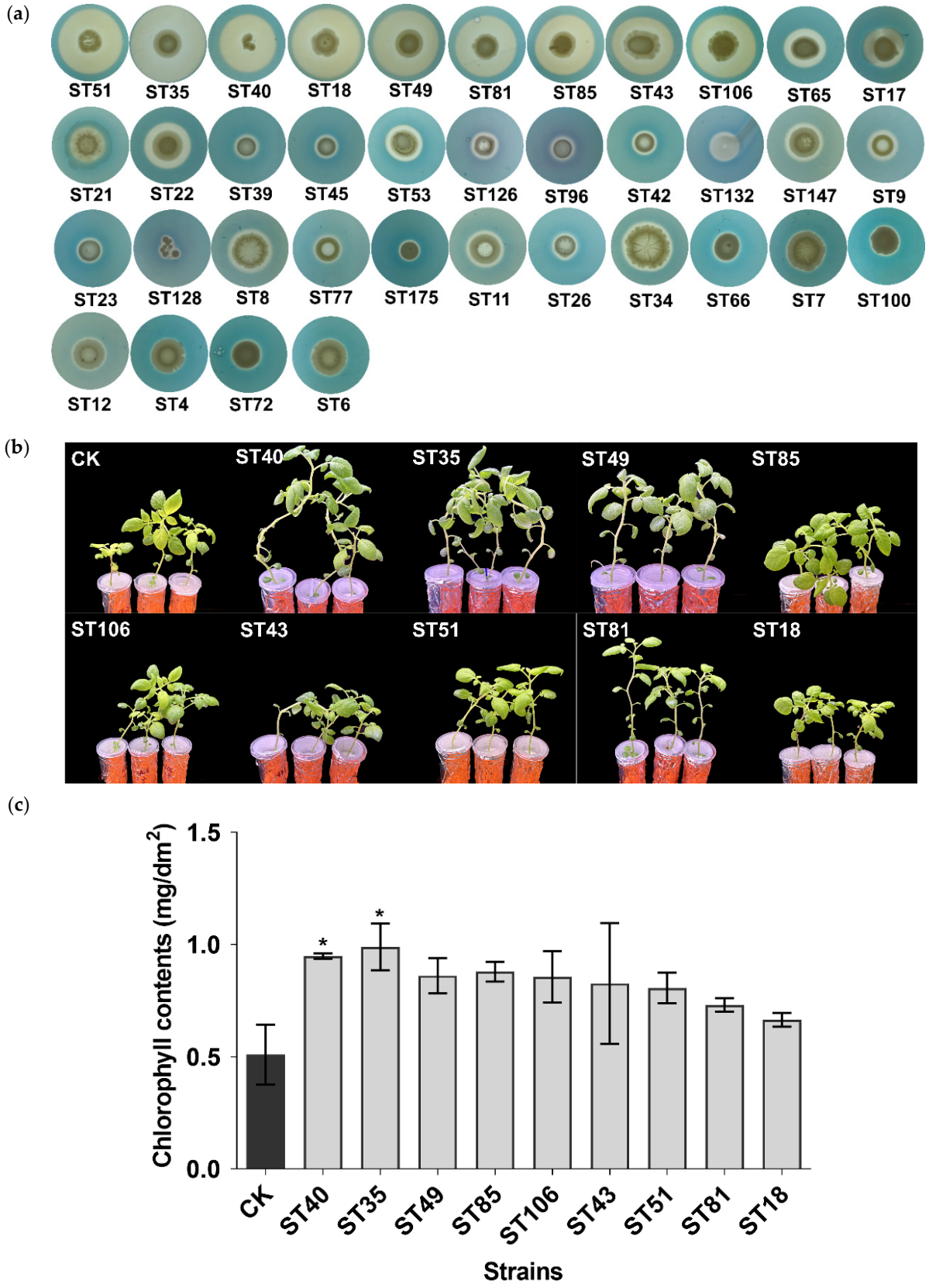

Figure 4. Production of siderophores in strains: (**a**) halo presented on CAS; (**b**) plant growth state cultured in Fe-deficient Hoagland medium with $FeCl_3$ (pH = 7.3); and (**c**) chlorophyll contents of plants. * $p \leq 0.05$ (Student's *t* test).

Table 2. Solubilization index of siderophores produced by strains.

Strains	Solubilization Index (SI)	Strains	Solubilization Index (SI)
ST51	2.72 ± 0.0473	ST132	1.25 ± 0.0056
ST35	2.57 ± 0.0552	ST147	1.25 ± 0.0029
ST40	2.66 ± 0.1117	ST23	1.18 ± 0.0025
ST18	2.29 ± 0.0072	ST8	1.17 ± 0.0085
ST49	2.08 ± 0.0087	ST128	1.18 ± 0.0101
ST81	2.02 ± 0.015	ST77	1.15 ± 0.0214
ST85	1.92 ± 0.0532	ST9	1.19 ± 0.0391
ST43	1.77 ± 0.025	ST175	1.12 ± 0.0028
ST106	1.73 ± 0.018	ST26	1.1 ± 0.012
ST17	1.54 ± 0.019	ST11	1.11 ± 0.0074
ST39	1.45 ± 0.0262	ST66	1.08 ± 0.0016
ST22	1.47 ± 0.0336	ST12	1.05 ± 0.0225
ST65	1.5 ± 0.054	ST7	1.08 ± 0.0036
ST21	1.42 ± 0.0836	ST34	1.07 ± 0.0148
ST45	1.31 ± 0.0207	ST6	1.05 ± 0.0195
ST53	1.29 ± 0.0067	ST100	1.07 ± 0.0186
ST126	1.27 ± 0.0177	ST4	1.05 ± 0.0093
ST96	1.27 ± 0.0057	ST72	1.02 ± 0.0097
ST42	1.26 ± 0.0056		

3.5. Rhizosphere Bacterial Strains Promote Plant Phosphorus Absorption by Phosphorus Solubilization

Phosphorus (P) availability limits crop productivity in many agricultural soils [23]. Phosphate-solubilizing microorganisms (PSM) are often reported to positively affect crop productivity through enhanced phosphorus (P) nutrition [24]. Seven isolates could improve the solubility of insoluble phosphorus. The strains were identified as *L. naganoensis* ST177, *Curtobacterium* sp. ST47, *P. fluorescens* ST18, *L. aquatica* ST172, *Paenibacillus* sp. ST22, *Pseudomonas plecoglossicida* ST4 and *Sutcliffiella horikoshii* ST11. *L. naganoensis* ST177 showed a prominent growth-promoting effect on potato plants when planted in P-deficient Hoagland medium with $Ca_3(PO_4)_2$ (Figure 5, Table 3).

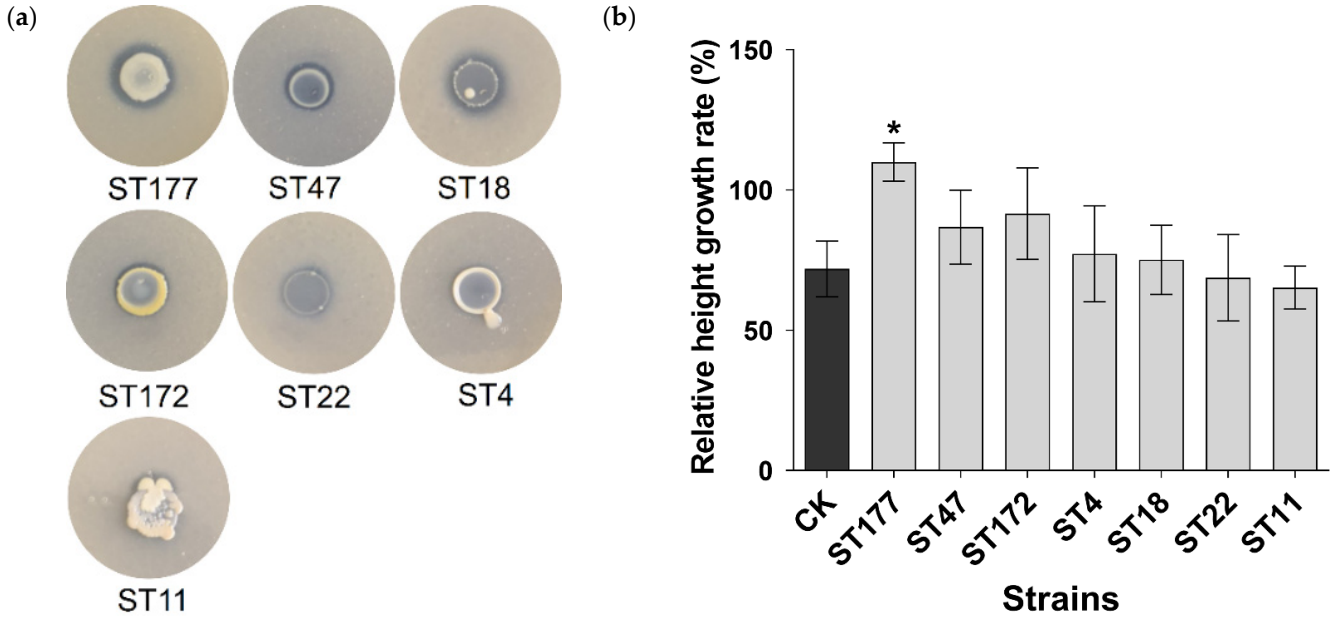

Figure 5. *Cont.*

(**c**)

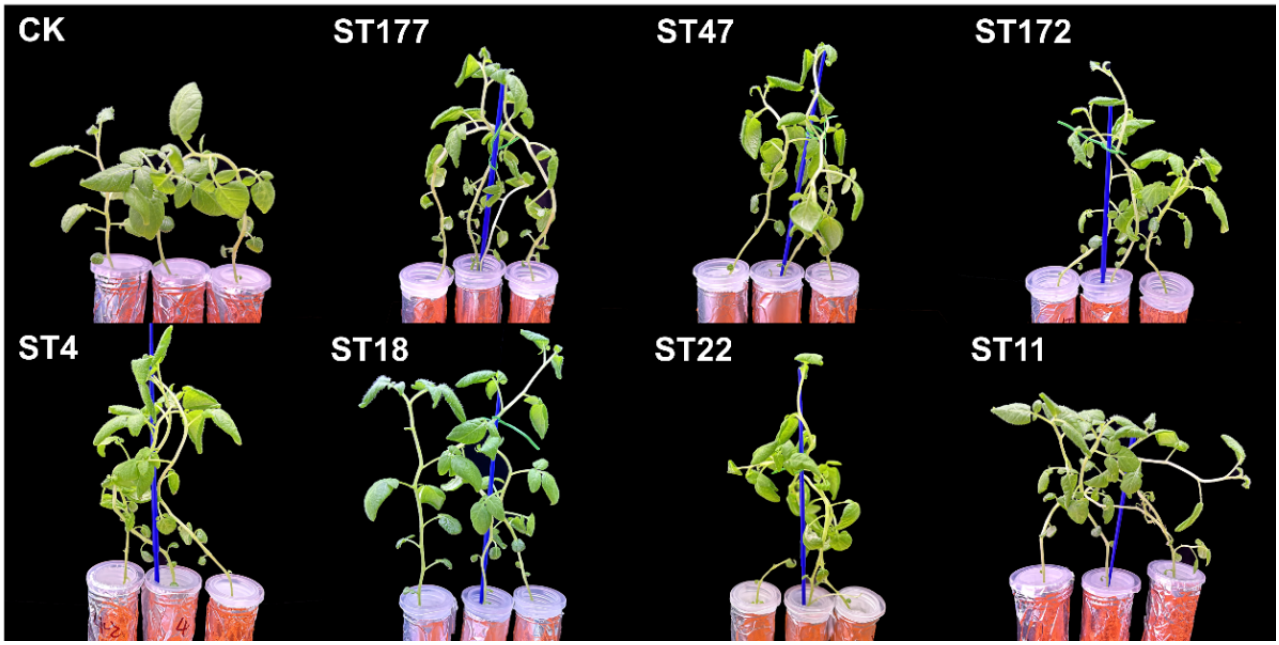

Figure 5. Solubilization of phosphorus: (**a**) clearance zone presented on medium with insoluble $Ca_3(PO_4)_2$; (**b**) relative height growth rate of plants; and (**c**) plant growth state cultured in P-deficient Hoagland medium with $Ca_3(PO_4)_2$. * $p \leq 0.05$ (Student's *t* test).

Table 3. Solubilization index of strains on phosphorus.

Strains	Solubilization Index (SI)
ST177	1.35 ± 0.2046
ST47	1.27 ± 0.0433
ST172	1.23 ± 0.0396
ST18	1.27 ± 0.0584
ST22	1.15 ± 0.0496
ST4	1.07 ± 0.0278
ST11	1.06 ± 0.0014

3.6. Rhizosphere Bacterial Strains Promote Plant Zinc Absorption by Zinc Solubilization

Four isolates, *Lysobacter* sp. ST103, *C. daecheongense* ST32, *Stenotrophomonas* sp. ST34 and *Cellulosimicrobium* sp. ST85, could improve the solubility of insoluble zinc. ST103 showed significant solubilizing capacity, and large clearance rings with diameters greater than two appeared around the colony (Figure 6a, Table 4). Plants inoculated with *Lysobacter* sp. ST103 and *Stenotrophomonas* sp. ST34 had higher chlorophyll in leaves when planted in Zn-deficient Hoagland medium with ZnO (Figure 6b,c).

Table 4. Solubilization index of strains on zinc.

Strains	Solubilization Index (SI)
ST103	2.4 ± 0.0111
ST32	1.47 ± 0.0384
ST34	1.16 ± 0.0411
ST85	1.08 ± 0.0072

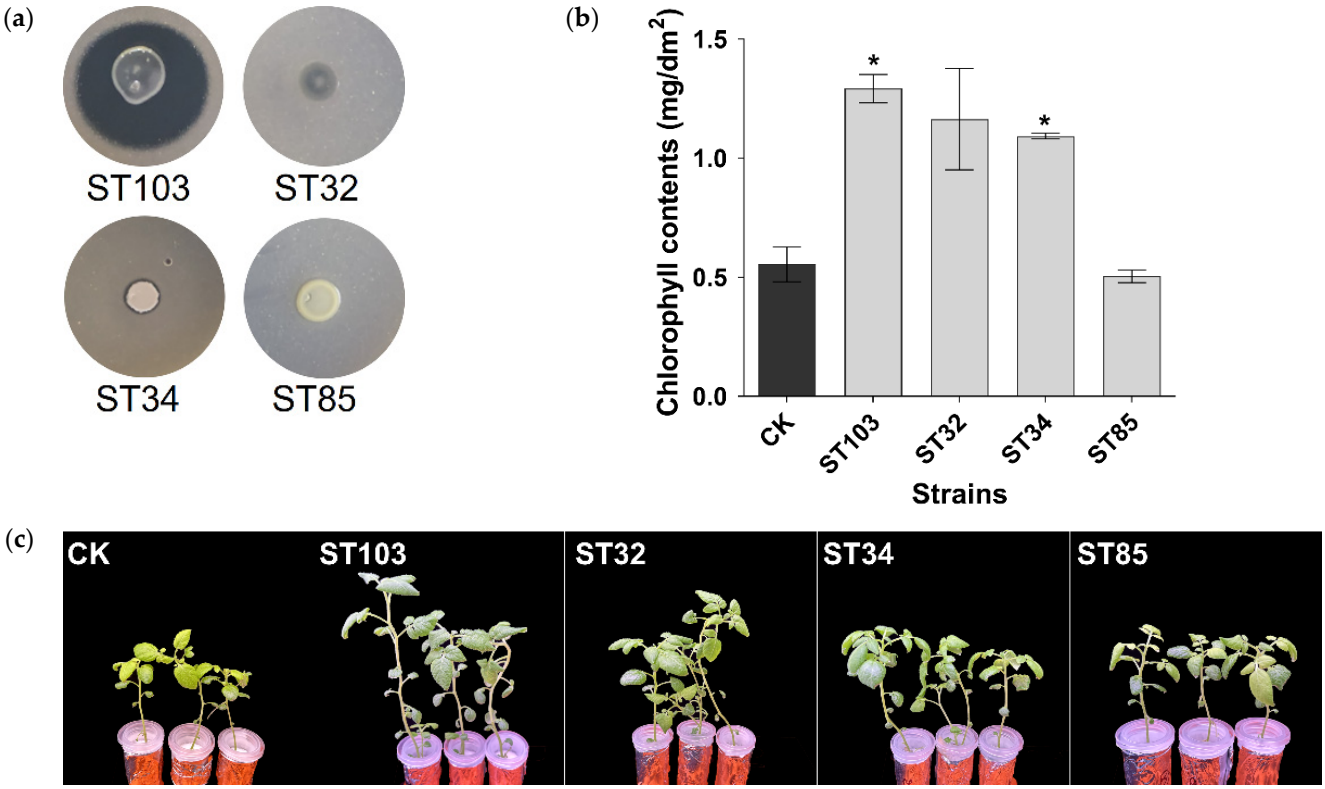

Figure 6. Solubilization of zinc: (**a**) clearance zone presented on medium with insoluble ZnO; (**b**) chlorophyll contents of plans; and (**c**) plant growth state cultured in Zn-deficient Hoagland medium with ZnO. * $p \leq 0.05$ (Student's *t* test).

4. Discussion

Plant growth and health are closely related to rhizosphere microorganisms. Plants regulate rhizosphere microbiota through exudate secretion to shape and utilize specific microbial communities to help them respond to external stressors by secreting hormones, siderophores, organic acid antibiotics, lytic enzymes, volatile organic compounds and so on [9]. Our object was to isolate and screen more plant-promoting bacteria from potato rhizosphere soils with low iron, phosphorus and zinc. Our research showed that *Microbacterium*, which is one of the most common PGPR, was determined to be the dominant genus [6]. Bacteria in this genus promoted plant growth in a variety of ways, such as auxin, salicylic acid and gibberellin secretion [25], siderophore production [26], phosphorus solubilization [26], volatile substances production [27], nitrogen fixation [28] and zinc solubilization [29].

PGPR can promote plant growth by directly secreting plant hormones or by influencing the hormone synthesis process of plants [5]. The production of IAA has been recognized as an important factor in direct plant growth-promoting abilities of rhizosphere bacteria. They stimulate the proliferation of lateral roots that increase nutrient-absorbing surfaces and result in the better assimilation of water and nutrients from the soil [30]. In our study, more than 50% of strains produced IAA, among which *Chryseobacterium* sp. ST32 reached the highest with a yield of 43.16 mg/L under natural culture conditions. The genus of *Chryseobacterium* has been widely reported for IAA production and a growth-promoting effect on crops, and most of them were tryptophan-dependent [5,31]. In addition, the genera of *Microbacterium* (ST25, ST49, ST144, ST43) [25], *Arthrobacter* (ST7, S21) [32], *Variovorax* (ST98) [33], *Agromyces* (ST139) [34], *Cellulomonas* (ST118) [35], *Cupriavidus* (ST9) [36], *Cellulosimicrobium* (ST85) [37] and *Ensifer* (ST46) [38] were also reported to possess the ability to secrete IAA, while the species *V. soli* (ST98) and *C. biazotea* (ST118) were first found to be capable of that in the present study.

Siderophores are common microbial secondary metabolites that can chelate metal ions such as iron and zinc from the environment and transport them into cells through specific receptors [39], and the bacterial siderophore–Fe complex can be utilized by plants with higher efficiency than EDTA-Fe [40]. Studies have shown that, in addition to serving as a medium to chelate iron, siderophores can also act as signaling molecules [41]. Siderophores produced by some bacteria can induce other strains to produce homologous iron carriers, thereby enhancing the use of iron in the soil. In addition, some strains can secrete siderophores to deplete limited iron in the environment, thereby inhibiting the growth of pathogenic bacteria from the same ecological niche [42] or inducing other genera of bacteria to produce many antibacterial substances to resist invasion by plant pathogens [43]. According to our research, half of the isolates from potato roots planted in Dayao were siderophore producers, which may be involved in the low iron property of the soil. Most of the strains identified as high-siderophore-producing strains belong to *Microbacterium* (ST51, ST35, ST40, ST49, ST43), and the species *M. foliorum* (ST51) [44], *M. phyllosphaerae* (ST40) [45] and *M. hydrocarbonoxydans* (ST49) [46] have been reported to produce a high amount of siderophores and promote plant growth. Siderophores produced by *P. fluorescens* (ST18) have been extensively studied and demonstrated to play roles in growth promotion, biocontrol and pheromones [47]. The kinds and biosynthetic gene clusters of siderophores produced by *A. tumefaciens* (ST81) have also been identified [48]. In addition to these common species, the genera *Cellulosimicrobium* (ST85) [29], *Pseudoxanthomonas* (ST106) [49] and *Bordetella* (ST65) [50] have also been reported to produce siderophores.

Phosphorus and zinc solubilization are also approaches through which PGPR promote nutrient absorption. Among our seven strains of phosphorus-solubilizing bacteria, *Leifsonia* (ST172, ST177) [51], *Curtobacterium* (ST47) [52], *Pseudomonas* (ST4, ST18) [53] and *Paenibacillu* (ST22) [54] have been reported to be related to phosphorus solubilization, while the species *L. aquatica* (ST172) and *L. naganoensis* (ST177) and the genus *Sutcliffiella* (ST11) were the first-discovered to have this capability. Four isolates possessing a zinc-solubilizing ability were screened, and the genera *Lysobacter* (ST103) [55], *Chryseobacterium* (ST32) [56], *Stenotrophomonas* (ST34) [57] and *Cellulosimicrobium* (ST85) [37] have been reported to be zinc-solubilizing, but the species *C. daecheongense* (ST32) was the first reported to have this ability.

According to relevant reports, appropriate amounts of IAA can promote plant growth, and P is an essential element for plant growth, so the relative growth rate was selected as the target for the function verification of IAA-producing and phosphorus-solubilizing strains. Most strains isolated from potato roots could produce a certain concentration of IAA, but only strains with IAA concentrations ranging from 5 to 15 mg/L could promote the root growth of potato plants. This indicated that the promotive effect of IAA on plants was limited to a certain concentration range, which was consistent with reports [58]. Among the screened strains, the species *V. soli* (ST98), *C. biazotea* (ST118) and *L. naganoensis* (ST177) were first found in the present study to promote plant growth. Both iron and zinc are directly related to chlorophyll synthesis, and the chlorosis of leaves is an obvious symptom of iron and zinc deficiency [59]. Therefore, chlorophyll content was selected as the functional target of iron- and zinc-solubilizing strains. Only two isolates with a high siderophores yield and one isolate with a zinc-solubilizing function could improve the chlorosis of plants significantly, which may be related to the colonization ability of the strains.

According to our research, none of these strains can dissolve iron, phosphorus and zinc simultaneously, indicating that a single strain is unlikely to possess multiple functions. Only multiple strains that coexist and collaborate can help plants achieve a balanced nutrient absorption and resist pathogen invasion in complex soil environments. Therefore, research on and the preparation of synthetic microbial communities (SynComs) that contain carefully chosen microbial species to produce the desired microbiome function has become the trend. In recent years, more and more studies have focused on the use of SynComs to improve plant nutrient efficiency and health [60,61]. In contrast to selecting microbes

based on single microbial in vitro activities or taxonomy, SynComs development considers multiple attributes, including microbes associated with desirable plant phenotypes and microbial traits, such as the production of metabolites, robust biofilm formation and the ability to chemically trigger plant defense mechanisms that will make microbes fit to persist in different environments and to colonize plants.

5. Conclusions

In this study, 153 bacterial strains were isolated and identified from potato roots cultured in alkaline soil. Among the 83 bacterial strains with incompletely identical 16S rDNA sequences, 47 isolates produced different concentrations of IAA, 37 isolates produced siderophores and seven and four isolates produced phosphate and zinc solubilizers, respectively. Five isolates significantly increased the growth rate of potato plants and four isolates significantly alleviated the chlorosis of leaves. Among all strains, the species *V. soli* (ST98) and *C. biazotea* (ST118) were first found to possess the ability to secrete IAA; the species *L. aquatica* (ST172) and *L. naganoensis* (ST177) and the genus *Sutcliffiella* (ST11) were first discovered to be phosphorus-solubilizing; the species *C. daecheongense* (ST32) was first reported to be zinc-solubilizing; and the species *V. soli* (ST98), *C. biazotea* (ST118) and *L. naganoensis* (ST177) were first found to be plant growth-promoting. Although the isolates represented only part of large plant rhizosphere bacteria population, the new functions discovered in some strains has enriched the resources of plant growth-promoting bacteria. The validation of growth-promoting functions under hydroponic conditions is the initial step for biofertilizer production for field applications. Future research on colonization mechanisms and optimization conditions, and competition with other soil microbial communities for exploiting multifunctional microbial fertilizers (i.e., SynComs) are needed.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agronomy14061241/s1.

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