Effects of growth-promoting rhizobacteria on blueberry growth and rhizosphere soil microenvironment

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Background. PGPR have specific symbiotic relationships with plants and rhizosphere soil. The purpose of this study was to evaluate the effects of PGPR to the growth of blueberry plant, rhizospheric soil nutrients and rhizospheric soil microbial community. **Methods.** In this study nine PGPR strains were selected to be added in the soil in which blueberry cuttings were planted. All physiological indexes of the cutting-seedlings and all rhizospheric soil element contents were determined at day 6 after the end of quartic root irrigation experiments. The microbial diversity in the soil was determined by high-throughput amplicon sequencing technology. The correlations between phosphorus solubilizing and auxin production of PGPR strains with rhizosphere microenvironmental factors and physiological indexes of blueberry plants and the correlations between rhizospheric microbial diversity and soil element contents were determined by using the Pearson's correlation, Kendall's tau correlation and Spearman's rank correlation analysis methods. **Results.** Results showed that, the number of branches, leaf number, chlorophyll content in theleaves and plant height of the blueberry plants treated by the PGPR significantly higher than the blueberry in control group. The rhizospheric soil element contents also increased after the PGPR root irrigation. The rhizospheric microbial community structure changed significantly under the PGPR of root irrigation. The dominant phyla except Actinomycetota in the soil samples had the greatest correlation with phosphorus solubilizing and auxin production of PGPR strains. The branch number, leaf number, and chlorophyll content had positive correlation with the phosphorus solubilizing and auxin production of PGPR strains and soil element contents. In conclusion, plant growth could be promoted by the root irrigation of PGPR to improve rhizospheric soil nutrients and microenvironment with the modification of rhizospheric soil microbial community. **Discussion.** This work revealed that, plant growth could be promoted by the root irrigation of PGPR to improve rhizospheric soil nutrients and microenvironment with

the modification of rhizospheric soil microbial community. These data may help us to better understand the improvement of PGPR on blueberry growth and rhizosphere soil microenvironment, and also provide the research basis for the subsequent development of rhizosphere promoting microbial fertilizer of blueberry plant.

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Abstract

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Methods. In this study nine PGPR strains were selected to be added in the soil in which blueberry cuttings were planted. All physiological indexes of the cutting-seedlings and all rhizospheric soil element contents were determined at day 6 after the end of quartic root irrigation experiments. The microbial diversity in the soil was determined by high-throughput amplicon sequencing technology. The correlations between phosphorus solubilizing and auxin production of PGPR strains with rhizosphere microenvironmental factors and physiological indexes of blueberry plants and the correlations between rhizospheric microbial diversity and soil element contents were determined by using the Pearson's correlation, Kendall's tau correlation and Spearman's rank correlation analysis methods.

Results. Results showed that, the number of branches, leaf number, chlorophyll content in the leaves and plant height of the blueberry plants treated by the PGPR significantly higher than the blueberry in control group. The rhizospheric soil element contents also increased after the PGPR root irrigation. The rhizospheric microbial community structure changed significantly under the PGPR of root irrigation. The dominant phyla except Actinomycetota in the soil samples had the greatest correlation with phosphorus solubilizing and auxin production of PGPR strains. The branch number, leaf number, and chlorophyll content had positive correlation with the phosphorus solubilizing and auxin production of PGPR strains and soil element contents. In

conclusion, plant growth could be promoted by the root irrigation of PGPR to improve rhizospheric soil nutrients and microenvironment with the modification of rhizospheric soil microbial community.

Discussion. This work revealed that, plant growth could be promoted by the root irrigation of PGPR to improve rhizospheric soil nutrients and microenvironment with the modification of rhizospheric soil microbial community. These data may help us to better understand the improvement of PGPR on blueberry growth and rhizosphere soil microenvironment, and also provide the research basis for the subsequent development of rhizosphere promoting microbial fertilizer of blueberry plant.

Keywords: Rhizosphere, Soil, Plant growth promoting bacteria, Soil elements, Plant growth

Introduction

Blueberries are a popular fruit with health benefits of the prevention of common chronic diseases (Tobar-Bolaños et al., 2021). As most plants, the growth of blueberry was profoundly influenced by the environmental factors in rhizosphere soil, such as nutritional elements, rhizospheric microorganism, etc. (Yurgel et al., 2019). The Improvement of rhizospheric microecological environment has positive effects on crop productivity and sustainable development (Ren et al., 2021). The plant growth-promoting rhizobacteria (PGPR), as an important part of rhizospheric microorganism, play a critical role in promoting plant health and regulating soil microecological environment (Santoyo et al., 2021).

PGPR have specific symbiotic relationships with plants and positively affect plant life cycles in direct and indirect manners (Singh et al., 2015). They directly promote plant growth by enhancing acquisition of soil nutrients, nitrogen fixation and mobilization of key nutrients (phosphorus, potassium and iron) (Rashid et al., 2016). The PGPR inhabit the rhizosphere and develop nodules on legumes and endophytes that can colonize the interior tissues of plants (Meena et al., 2020). As biocontrol agents, PGPR are cheap and easily available and less adverse effects from various stresses that plants encounter (Hafez et al., 2021). Thus, they can be an efficient economical tool for increasing the productivity of important agriculture crops (Calvo et al., 2014). Not only that, application of PGPR has the potential of regulating the microecological environment in rhizosphere through elicitation of several physiological and molecular mechanisms (Shi et al., 2022).

78 They also improve root systems, including antioxidant capability, production of
79 exopolysaccharides (EPS) and siderophores, modulation of phytohormones, synthesis of
80 osmolytes, uptake of minerals and control of phytopathogens (Shahzad et al., 2017; Arora
81 et al., 2018). Several PGPR strains have been reported to increase soil organic matter,
82 improve soil structure and water retention capacity as bioinoculants (Arora et al., 2020).
83 Our previous study found that a poor soil ecosystem could be restored by a
84 bioremediation method through intervening soil bacterial diversity and stability using
85 PGPR (Wang et al., 2019a).

86 In this study, nine PGPRs were applied to the blueberry plants via root irrigation.
87 Physiological indexes of the blueberry plants at day 6 after the end of quartic root irrigation
88 experiments were evaluated. The soil element contents and microbial diversity in
89 rhizosphere were measured. The correlations between physiological indexes of
90 the blueberry plants with rhizospheric microenvironmental factors, soil element contents
91 and microbial diversity were determined. This study could be an initial step of developing
92 efficient and environmentally friendly PGPR fertilizer to promote the blueberry plant
93 growth.

94

95 ## Materials & Methods

96 ### 2.1. Plant root irrigation

97 Nine PGPR strains selected in the article Wang et al. (2022) were choosen for root
98 irrigation because of high phosphorus and silicate solubilizing, auxin production and

nitrogen fixation capabilities. The capabilities of phosphorus- and silicate-solubilizing, auxin production and nitrogen fixation, and the classified information for nine PGPR strains were shown in appendix table 1.

Blueberry cutting-seedlings with five leaves and 10 cm of height were chosen for root irrigation. The experiment used 18-cm-height pots with soil samples collectes from a blueberry field. All the PGPR strains were incubated in 5 ml of liquid beef extract peptone medium individually and incubated at 28 °C for 3 days. Every liquid beef extract peptone medium was diluted by using sterilized water to a final 50 ml volume. Twenty cutting-seedlings were irrigated every 6d with prepared liquid beef extract peptone medium. As a control group (CK), another 5 ml of sterilized liquid beef extract peptone medium was diluted by using sterilized water to a final 50 ml volume. And the 50 ml diluted sterilized liquid beef extract peptone medium were irrigated to other twenty cutting-seedlings every 6d. All plants were grown at 25 °C under continuous illumination (~ 1500 lx). Rhizosphere soil samples were collected from the roots of the cutting-seedlings at day 6 after the end of quartic root irrigation experiments.

2.2. Determination of physiological indexes of the blueberry plants and Collection of soil sample

All physiological indexes of the cutting-seedlings were determined at day 6 after the end of quartic root irrigation experiments. The eighth leaf of every cutting-seedling was harvested, weighed, and finely ground in liquid N_2. Total chlorophyll (Chl) was extracted with 95% ethanol, and chlorophyll concentrations were calculated according to the

120 method of Lichtenthaler (1987). After the number of branches and leaf number were
121 counted, the rhizosphere soil samples were collected by the method described in previous
122 study (Fujii et al., 2004). Soil samples collected in each treatment were fully mixed and
123 stored at 4 °C before use. Then all cutting-seedlings were carefully removed from soil and
124 washed in distilled water until there was no excess soil attached to the roots. Primary root
125 length was evaluated on images of plants using Image J software (NIH) (Kohanová et al.
126 2018). Plant height was measured as distance from the base of plant till the tip of main
127 shoot (Kaur et al., 2021).

128 **2.3. Determination of soil element contents and Analysis of DNA sequences of**
129 **microbes in soil sample**

130 Organic carbon content (OCC), total nitrogen content (TNC), total phosphorous
131 content (TPHC), total potassium content (TPOC), hydrolysable nitrogen content (HNC),
132 available phosphorous content (APHC), and available potassium content (APOC) of all
133 soil samples were determined using the methods can be found in Wang et al. (2021).

134 The genome of microbes in soil samples were extracted using a DNA extraction kit
135 (Fast DNA Spin Kit for Soil, MP Biomedicals, Santa Ana, CA, USA). These Hiseq
136 sequencing results in double-ended sequence data (pairwise. Fastq files) were submitted
137 to the Sequence Read Archive (https://submit.ncbi.nlm.nih.gov/subs/sra/), and the
138 submission number was obtained. Then all the analysis, including the amplification and
139 purification of 16S rRNA genes and ITS genes, library preparation and sequencing, and
140 data analysis, were carried out by the same method described in Wang et al. (2022).

141 **2.4. Data analysis**

142 All experiments were repeated in triplicates. The physiological indexes of the cutting-
143 seedlings, and soil element contents were expressed by mean with standard derivation.
144 They were tested for statistical distribution before ANOVA analysis with a significant
145 difference between two data at $p < 0.05$ or $p < 0.01$, and bars with different letters indicate
146 a significant difference between the data. The distribution of microorganism with relative
147 abundance greater than or equal to 1% in blueberry cutting-seedlings rhizospheres were
148 expressed by mean value of three parallel experiments.The significant differences
149 between different species were determined by linear discriminant analysis (LDA) effect
150 size (LEfSe) (https://github.com/biobakery/lefse) with 2 as the default setting filter value
151 for LDA score. Pearson's correlation coefficient, Kendall's tau correlation coefficient and
152 Spearman's rank correlation coefficient were analyzed by multivariate process of the GLM
153 in SPSS (Statistical Product and Service Solutions) software to identify and to quantify
154 the nature of the link between phosphorus solubilizing ability and auxin production ability
155 of PGPR strains with rhizosphere soil microbial diversity, soil element content and plant
156 growth status. The correlations between physiological indexes of the blueberry plants
157 with rhizosphere microenvironmental factors, the correlations between rhizosphere
158 microbial diversity and rhizosphere soil element contents were analyzed by multivariate
159 process of the GLM in SPSS software as well (Cornbleet and Shea, 1978; Mangena 2021;
160 Wang et al. 2021).

Results

3.1. Effects of PGPR strains on blueberry plant growth and elements content of blueberry rhizosphere soil

Physiological indexes of the blueberry plants in control and treatment groups are shown in Fig. 1. The PGPR treatment groups significantly enhanced the number of branches and plant height of cutting-seedlings (Fig 1A, D). All the strain treatments except B5 and B7 had higher leaf number compared with the control (Fig 1B). Among them, the number of leaves was the highest in the cutting-seedlings treated by strain B8 that was 32.5% more than the control (Fig 1B). Strain B2, B3, B6 and B9 significantly increased the Chl concentration of eighth leaf of blueberry cutting-seedlings by 20.0%, 43.4%, 36.1% and 37.2%, respectively (Fig 1C). The root lengths in treatment B3, B6, and B9 were 13.3 cm,11.9 cm and 11.0 cm, while it was 9.5 cm in the control group (Fig 1D).

The concentrations of major environmental elements, OCC, TNC, HNC, TPHC, APHC, TPOC and APOC were 433.03 - 583.50 g/kg, 21.50 - 29.26 g/kg, 5.75 - 10.73 g/kg, 224.32 - 445.13 mg/kg, 129.35 - 174.12 mg/kg, 1.21 – 4.58 g/kg, and 0.45 - 0.23 g/kg, respectively (Fig 2). Inoculation with the strains significantly increased OCC in rhizosphere soil compared with the control (Fig 2A). All the strain isolates except B7 increased the TNC in rhizosphere soil, while strain B1, B2, B3, B6 and B7 significantly increased the HNC in rhizosphere soil samples of blueberry cutting-seedlings by 37.1%, 50.1%, 63.6%, 86.8% and 59.8%, respectively (Fig 2B). All the strain isolates except B4 and B5 increased the TPHC in the rhizosphere soil, while strain B3 treatment had the

182 highest level of APHC in rhizosphere soil samples with 34.9% more than the control (Fig
183 2C). The TPOC in rhizosphere soil samples which were collected from the cutting-
184 seedlings inoculated with the strains, except B4, B5 and B6 were greater than that in the
185 control (Fig 2D). Except B7, all other strain treatments significantly increased APOC in
186 the rhizosphere soils (Fig 2D).

187 **3.2. Effects of PGPR strains on microbial community structure of blueberry**
188 **rhizosphere soil**

189 There were 1145 species of bacterial genera in the rhizosphere soil samples
190 gathered from the cutting-seedlings. Among them, 18 genera with relative abundance
191 greater than 1% were identified as *Granulicella*, *Occallatibacter*, *Solibacter*,
192 *Acidothermus*, *Bryobacter*, *Mucilaginibacter*, *Bauldia*, *Bradyrhizobium*, *Paraburkholderia*,
193 *Buttiauxella*, *Devosia*, *Dongia*, *Haliangium*, *Pseudolabrys*, *Pseudomonas*,
194 *Sphingomonas*, *Lacunisphaera* and *Opitutus* (Fig. 3A). These genera belonged to
195 Acidobacteriota, Actinomycetota, Bacteroidota, Pseudomonadota and Verrucomicrobiota
196 phyla (Fig. 3A).

197 There were significant differences in bacterial diversity between the rhizosphere
198 samples collected from blueberry cutting-seedlings with different treatments. All the strain
199 isolates had higher percentage of *Occallatibacter* and *Pseudomonas* than the control (Fig.
200 3A). The *Occallatibacter* in control soil samples was 5.27%, while the highest percentage
201 of *Occallatibacter* in the strain B6 inoculated cutting-seedlings rhizosphere samples
202 reached 12.53% (Fig. 3A). The highest percentage of *Pseudomonas* could reach 23.96%

in the cutting-seedlings rhizosphere samples inoculated with the strains, while the control soil sample was only 4.43% (Fig. 3A). Compared with the percentage of *Devosia* (1.09%) and *Haliangium* (1.57%) in the control soil samples, the percentage of *Devosia* and *Haliangium* were lower than 1% in all the rhizosphere samples treated with the strains (Fig. 3A). Also, different strains treatment had different effects on bacterial diversity in the cutting-seedlings rhizosphere soil. The percentage of *Buttiauxella* in cutting-seedlings rhizosphere soil samples inoculated with the strains belonged *Buttiauxella* were significant higher than other treatments (Fig. 3A).

For fungal communities, most of the OTUs were classified as Ascomycota, Basidiomycota and Mucoromycota at phylum level (Figure 3B), whereas at genus level, the communities were dominated by *Ascitendus*, *Pezoloma*, *Rhexodenticula*, *Sarocladium*, *Thysanorea*, *Clitopilus*, *Gymnopilus*, *Rhizoctonia*, *Sebacina*, *Sistotrema*, *Sistotremella* and *Mortierella* in blueberry cutting-seedlings rhizosphere (Figure 3B). The significant differences in fungal diversity between the rhizosphere samples collected from blueberry cutting-seedlings with different treatments were found as well. The percentage of *Ascitendus* and *Thysanorea* in cutting-seedlings rhizosphere soil samples inoculated with the strain were significantly higher than the control soil samples (Fig. 3B). Compared with the percentage of *Rhexodenticula* (2.29%), *Clitopilus* (15.36%) and *Sebacina* (49.50%) in the control soil samples, the percentage of *Rhexodenticula*, *Clitopilus* and *Sebacina* were significantly lower in all the rhizosphere soil samples in the treatment groups (Fig. 3B). Different effects on the fungal diversity in rhizosphere samples of

cutting-seedlings inoculated with different strains were found as well. The *Gymnopilus*, *Rhizoctonia*, *Sistotrema*, *Sistotremella* and *Mortierella* in rhizosphere soil were significant enriched by inoculation with *Pseudomonas* isolates (Fig 3B).

A total of 36 distinct bacterial biomarkers were identified by using the LDA threshold score of ≥2.0. The inoculation with *Pseudomonas* isolates enriched phylotypes belonged to the Actinobacteriota (Actinobacteria), Proteobacteria, Myxococcota and Acidobacteriota (Vicinamibacteria) (Fig 4A). And the total number of bacterial biomarkers in the soil samples collected from cutting-seedlings inoculated with *Pseudomonas* isolates was higher than that in the soil samples collected from cutting-seedlings with other treatments (Fig 4A). The bacteria in cutting-seedlings inoculated with *Buttiauxella* isolates rhizosphere soil were abundant by Actinobacteria (Acidimicrobiia) and Firmicutes (Clostridia) (Fig 4A). The specific phylotypes in control were taxonomically diverse and included members of Myxococcota (Haliangiales) , Proteobacteria (Alphaproteobacteria) and Verrucomicrobiota (Opitutaceae) (Fig 4A).

The analysis of fungal communities revealed 39 distinct biomarkers that unevenly distributed among the microorganisms in rhizospheres of the blueberry cutting-seedlings (Fig 4B). The rhizosphere fungi of cutting-seedlings inoculated with Pseudomonas isolates was rich in diverse Ascomycota and Basidiomycota (Agaricomycetes) (Fig 4B). In contrast, the specific fungi in inoculation treatment with Buttiauxella isolates were rich in Ascomycota, Basidiomycota and Mucoromycota (Fig 4B). There were only seven distinct biomarkers which differentially distributed in the rhizosphere samples from

245 cutting-seedlings inoculated with Pseudomonas compared with the rhizospheres of other
246 treatments (Fig 4B).

247 **3.3. Correlations between the strains with rhizosphere microenvironmental factors**
248 **and physiological indexes of blueberry plants**

249 The dominant phyla except Actinomycetota in the soil samples had the greatest
250 correlation with phosphorus solubilizing, and auxin production of PGPR strains (Tab 1).
251 The APOC was the environmental factors that had the correlation with phosphorus-
252 solubilizing and auxin production of the strains, while the impacts of phosphorus-
253 solubilizing and auxin production of the strains on other measured environmental factors
254 were not significant (Tab 1). There was a strong correlation between microbial community
255 and plant branch number (Tab 1). The similar results are shown in Appendix Table 2 and
256 Appendix Table 4 by Kendall's tau correlation coefficient and Spearman's rank correlation
257 coefficient analysis methods.

258 For further understanding the relationship between rhizosphere microbial diversity,
259 rhizosphere soil element contents and plant growth indicators of blueberry seedlings, the
260 Pearson's correlation coefficient were calculated as well. The results showed that the
261 dominant Bacteroidota and Basidiomycota phyla had the greatest correlation with branch
262 number of cutting-seedlings, while the Verrucomicrobiota phyla had the greatest
263 correlation with leaf number, Chl and primary root length of cutting-seedlings (Tab 2). The
264 Actinomycetota was the dominant phyla that had the correlation with TPOC, phosphorus-
265 solubilizing and auxin production of the strains. Pseudomonadota in the soil samples had

the greatest correlation with TPOC and APOC, while Verrucomicrobiota showed a strong correlation with TPHC (Tab 2). There were great correlations between rhizosphere soil element contents and plant growth indicators of blueberry seedlings. The rhizosphere soil element contents except APOC had a significant correlation with each plant growth indexes of blueberry seedlings (Tab 2). Most environmental elements including OCC, TNC, HNC, TPHC, APHC and TPOC in this study were significantly correlated with the plant growth indexes of blueberry seedlings (Appendix Table 3 and Appendix Table 5).

Discussion

4.1. Stimulation of plant growth

The PGPR not only is crucial to provide nutritional elements in soil for plant growth, but also restricts or inhibits the growth of potential pathogens and protects the plant by producing antibiotics, antifungal chemicals and insecticides as well (García-Salamanca et al., 2012). *Bacillus*, *Pseudomonas*, *Enterobacter*, *Acinetobacter*, *Burkholderia*, and *Arthrobacter* are the most common microorganisms present in rhizosphere and referred as the PGPR to improve soil nutritional quality for better plant growth (Dennis et al., 2010; Zhang et al., 2020).

In this study, nine PGPR strains belonged Buttiauxella, and Pseudomonas genus were used for root irrigation experiment. *Pseudomonas* was the most promising groups of rhizobacteria in terms of plant growth promotion, as they are usually manifest a wide range of plant growth-promoting traits, such as antibiotic production, phosphate

287 solubilization, nitrogen fixation, ACCD activity, production of plant-beneficial compounds
288 (plant hormones, siderophores, EPS, IAA, HCN, and ammonia), and stress alleviation
289 (Bhattacharyya et al., 2012, Saber et al., 2015). These PGPR belonged *Pseudomonas*
290 genus showed different growth-promoting effects on blueberry cutting-seedlings. The
291 number of branches and plant height of cutting-seedlings were significantly increased by
292 *Pseudomonas* strains (Fig 1). Other physiological indexes of the blueberry plants were
293 enhanced as well (Fig 1).

294 Genus *Buttiauxella,* a member of the Enterobacteriaceae family isolated from
295 mollusks (slugs and snails), annelids (earthworms), soil and drinking water, were reported
296 as PGPR in 1996 (Müller et al., 1996). More strains belonged *Buttiauxella* genus had the
297 effects on root extension, seed germination, and so on (de Araújo et al., 2021; Wu et al.,
298 2018). Physiological indexes of the blueberry plants were significantly enhanced in the
299 treatments by *Buttiauxella* strains (Fig 1).

300 **4.2. Environmental element contents and microbial diversity in blueberry cutting-**
301 **seedling rhizosphere soils**

302 Nutritional elements present in plant rhizosphere soil and transformed by
303 microorganism are eventually utilized and absorbed during the plant for growth and
304 development (Liu et al., 2021). In modern crop production systems, in which natural
305 plant–microbe-soil interactions have largely been replaced by artificial fertilizer input. The
306 consequence is that the crop varieties may have lost the ability to maintain a diverse
307 microbiome with declining of the sustainability of the soil system (Perez-Jaramillo et al.,

2016). Thus, the PGPR is crucial to provide nutritional elements in soil for plant growth (Shabaan et al., 2022). In this study, the improvement on the content of elements in rhizosphere soil was found by the treatments of the selected PGPR (Fig 2). The Inoculation with the PGPR significantly increased OCC in rhizosphere soil compared with the control. And Most of the PGPR isolates increased the TNC, APHC, and APOC in rhizosphere soil. The PGPR had great potential and could act as a commercial biofertilizer by solubilizing minerals (Rahimi et al., 2020). The PGPR also could improve microbial community structure for better soil quality and sustainable cultivation use of soil (Bhattacharyya andJha, 2012). In the study, there were significant differences in the microbial diversity between rhizosphere soil samples collected from blueberry cutting-seedlings with different treatments. All the PGPR isolates increased the percentage of *Occallatibacter* and *Pseudomonas* compared with the control (Fig. 3A). The percentage of *Ascitendus* and *Thysanorea* in cutting-seedlings rhizosphere soil samples inoculated with the PGPR were significant higher than those in the control soil samples (Fig. 3B). These changes in the blueberry cutting-seedlings rhizosphere soil treated with PGPR might be direct or indirect way to increase crop yields and promote plant growth(Vejan et al., 2016).

4.3. Correlations between the PGPR strains with rhizosphere microenvironmental factors and physiological indexes of blueberry plants

Plant rhizosphere is a complex environment that can significantly affect plant growth. As an important member of rhizosphere environmental factors, the rhizomicrobiome is a

great nutrition driver and plays key roles in promoting plant growth. Research has demonstrated that inoculating plants with PGPR could be an effective strategy to stimulate crop growth. The PGPR evaluated in this study could promote the growth of blueberry cutting-seedlings, increase the photosynthetic rate, and accelerate the growth of above ground parts and roots (Fig 1). Compared with the element contents and physiological indexes in the control and treatment groups, the dominant phyla in the soil samples had the greatest correlation with phosphorus solubilizing, and auxin production of PGPR strains (Tab 1, Appendix Tab 2 and Appendix Tab 4). The treated rhizosphere microbial community structure increased the content of soil elements and changed of the soil element content to promote the growth of plants (Tab 2, Appendix Tab 3 and Appendix Tab 5). At the same time, the growth promoting bacteria themselves and the rhizosphere microbial community would also significantly affected the plant growth. A large diversity of microbial metabolites and physical signals that trigger cell-cell communication and appropriate responses were carried between PGPR and microbial populations inside rhizosphere soil (Besset-Manzoni et al., 2018). The microbial diversity was the biggest influence factor on nutrient elements in soil (Song et al., 2021), while the soil nutrient limitations was major environmental condition that reduce plant growth, productivity and quality (Gong et al., 2020). Therefore, using the PGPRs with different growth promoting effects to improve blueberry plant soil nutrients not only can promote plant growth, but also avoid the negative effects of artificial fertilizer to soil and environment. In general, the isolated strains in our study could be used as a natural

microbial fertilizer instead of traditional chemical fertilizer to promoting blueberry growth and maintain the stability of plant rhizosphere.

Conclusion

In this study, blueberry plant growth could be promoted by irrigation of the rhizosphere with PGPR strains. The rhizospheric microenvironment and soil nutrients had the closely relationship with the PGPR strains. Generally, the rhizosphere soil microbial community structure was changed by the root PGPR irrigation to increase the levels of rhizosphere soil elements that are beneficial to plant growth. The results of this study are very helpful for developing the PGPR fertilizer for promoting blueberry plant growth.

Declaration of Competing 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.

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521 Data Availability Statement

522 The data underlying this article are available in the article and in its online supplementary
523 material.

Table 1(on next page)

Pearson's correlation analysis of phosphorus solubilizing ability and auxin production ability of PGPR strains with rhizosphere soil microbial diversity, soil element content and plant growth status

Phosphorus: Phosphorus-solubilizing capacity of strains used for root irrigation, Auxin: Auxin production capacity of strains used for root irrigation□OCC: organic carbon content, TNC: total nitrogen content, TPHC: total phosphorous content, TPOC: total potassium content, HNC: hydrolysable nitrogen content, APHC: available phosphorous content, and APOC: available potassium content * $p < 0.05$; ** $p < 0.01$

Table 1 Pearson's correlation analysis of phosphorus solubilizing ability and auxin production ability of PGPR strains with rhizosphere soil microbial diversity, soil element content and plant growth status

Capacity of strains	Acidobacteriota	Actinomycetota	Bacteroidota	Pseudomonadota	Verrucomicrobiota	Ascomycota	Basidiomycota	Mucoromycota
Phosphorus	0.967**	0.044	0.923**	-0.579**	-0.698**	0.881**	-0.908**	-0.792**
Auxin	0.761**	0.047	0.818**	-0.499**	-0.618**	0.745**	-0.841**	-0.556**
	OCC	TNC	HNC	TPHC	APHC	TPOC	APOC	-
Phosphorus	0.343	0.308	0.104	0.112	-0.078	-0.144	-0.395*	-
Auxin	0.201	0.152	-0.124	0.228	-0.053	-0.011	-0.390*	-
	Branch Number	Leaf Number	Chl	Primary Root Length	Plant Height	-	-	-
Phosphorus	0.387*	0.457*	0.425*	0.244	0.208	-	-	-
Auxin	0.487**	0.456*	0.123	-0.019	0.239	-	-	-

Phosphorus: Phosphorus-solubilizing capacity of strains used for root irrigation, Auxin: Auxin production capacity of strains used for root irrigation, OCC: organic carbon content, TNC: total nitrogen content, TPHC: total phosphorous content, TPOC: total potassium content, HNC: hydrolysable nitrogen content, APHC: available phosphorous content, and APOC: available potassium content

* $p < 0.05$; ** $p < 0.01$

Table 2(on next page)

Pearson's correlation analysis of rhizosphere soil microbial diversity with plant growth status and soil element contents, Pearson's correlation correlation analysis of soil element contents with plant growth status

OCC: organic carbon content, TNC: total nitrogen content, TPHC: total phosphorous content, TPOC: total potassium content, HNC: hydrolysable nitrogen content, APHC: available phosphorous content, and APOC: available potassium content * $p < 0.05$; ** $p < 0.01$

Table 2 Pearson's correlation analysis of rhizosphere soil microbial diversity with plant growth status and soil element contents, Pearson's correlation correlation analysis of soil element contents with plant growth status

	Branch Number	Leaf Number	Chl	Primary Root Length	Plant Height	OCC	TNC	HNC	TPHC	APHC	TPOC	APOC
Acidobacteriota	0.372*	0.450*	0.446*	0.299	0.314	0.386*	0.331	0.191	0.179	-0.047	-0.096	-0.406*
Actinomycetota	0.368*	0.077	0.041	-0.102	0.117	0.009	0.046	0.225	0.248	-0.233	0.622**	0.177
Bacteroidota	0.464**	0.337	0.298	0.147	0.096	0.238	0.208	0.164	0.195	-0.118	-0.067	-0.324
Pseudomonadota	0.233	-0.167	0.029	0.157	0.341	0.258	0.207	0.316	0.339	-0.136	0.559**	0.716**
Verrucomicrobiota	-0.451*	-0.482**	-0.596**	-0.552**	-0.339	-0.443*	-0.366*	-0.407*	-0.632**	-0.124	-0.133	0.045
Ascomycota	0.381*	0.220	0.322	0.303	0.267	0.318	0.255	0.400*	0.243	-0.122	-0.071	-0.327
Basidiomycota	-0.515**	-0.348	-0.320	-0.252	-0.347	-0.412*	-0.338	-0.264	-0.262	0.151	0.033	0.274
Mucoromycota	-0.087	-0.246	-0.295	-0.215	0.024	0.102	0.087	-0.058	0.038	-0.081	0.242	0.709**
OCC	0.477**	0.574**	0.168	0.123	0.559**	-	-	-	-	-	-	-
TNC	0.389*	0.523**	0.090	0.044	0.431*	-	-	-	-	-	-	-
HNC	-0.011	-0.380*	0.432*	0.635**	0.162	-	-	-	-	-	-	-
TPHC	0.362*	0.233	0.666**	0.694**	0.511**	-	-	-	-	-	-	-
APHC	-0.310	0.032	0.421*	0.398*	-0.066	-	-	-	-	-	-	-
TPOC	0.509**	0.165	0.417*	0.333	0.652**	-	-	-	-	-	-	-
APOC	0.132	-0.010	-0.291	-0.143	0.108	-	-	-	-	-	-	-

OCC: organic carbon content, TNC: total nitrogen content, TPHC: total phosphorous content, TPOC: total potassium content, HNC: hydrolysable nitrogen content, APHC: available phosphorous content, and APOC: available potassium content

* $p < 0.05$; ** $p < 0.01$

Figure 1

Figure 1. Plant physiology in blueberry cutting-seedlings rhizospheres.

Numbers of branches (A) and leaves (B), chl (Chlorophyll) concentration (C), primary root length, and plant height (D) in blueberry cutting-seedlings rhizospheres.*Bars with different letters indicate a significant difference between the data ($p < 0.05$).

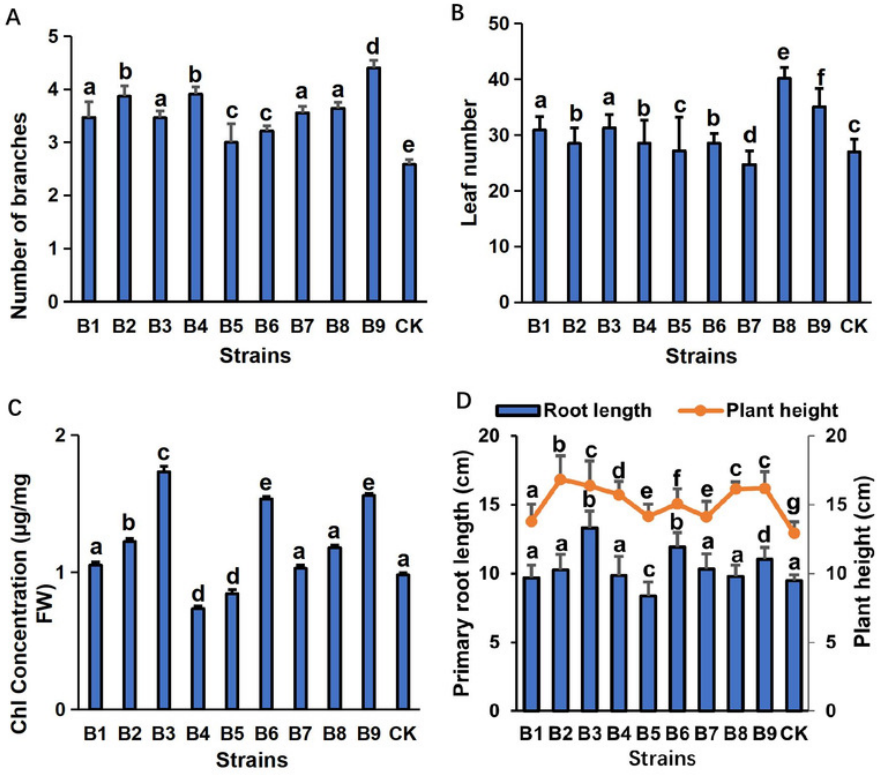

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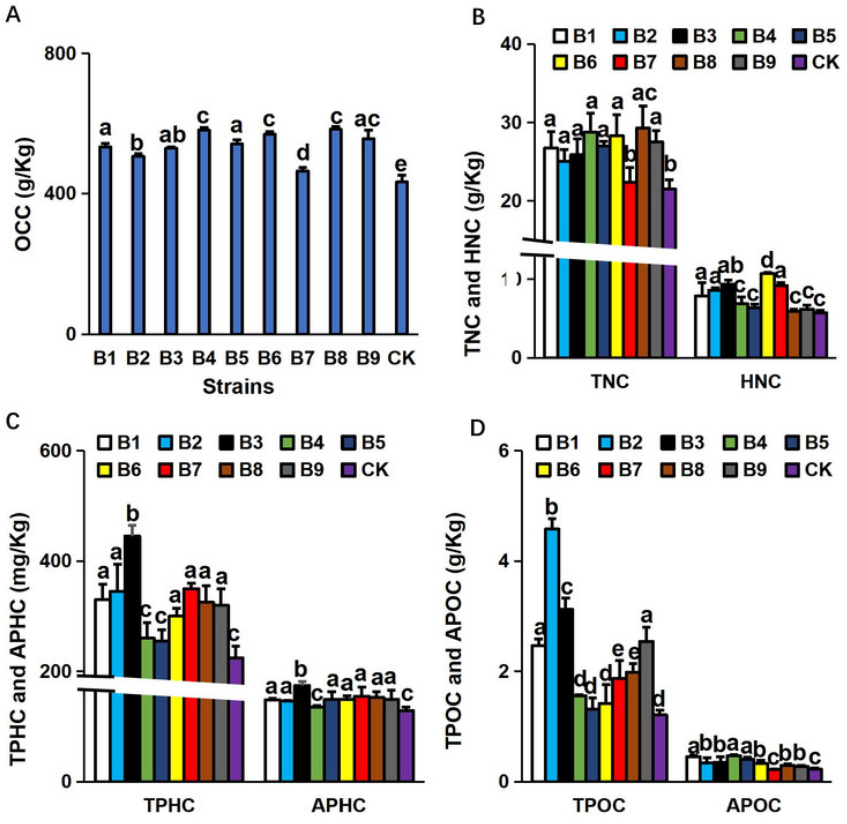
Figure 2

Figure 2. Nutritive element content s in blueberry cutting-seedlings rhizospheres.

Organic carbon content (OCC) (A), total nitrogen content (TNC) (B), hydrolysable nitrogen content (HNC) (B), total phosphorous content (TPHC) (C), available phosphorous content (APHC) (C), total potassium content (TPOC) (D), and available potassium content (APOC) (D) in blueberry cutting-seedlings rhizospheres. *Bars with different letters indicate a significant difference between the data ($p < 0.05$).



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Organic carbon content (OCC) (A), total nitrogen content (TNC) (B), hydrolysable nitrogen content (HNC) (B), total phosphorous content (TPHC) (C), available phosphorous content (APHC) (C), total potassium content (TPOC) (D), and available potassium content (APOC) (D) in blueberry cutting-seedlings rhizospheres.
*Bars with different letters indicate a significant difference between the data ($p < 0.05$).

Figure 3

Figure 3. The distribution of microorganism with relative abundance greater than or equal to 1% in blueberry cutting-seedlings rhizospheres.

(A) and (B) are bacterial genus and fungal genus with relative abundance greater than or equal to 1% in the soil samples.

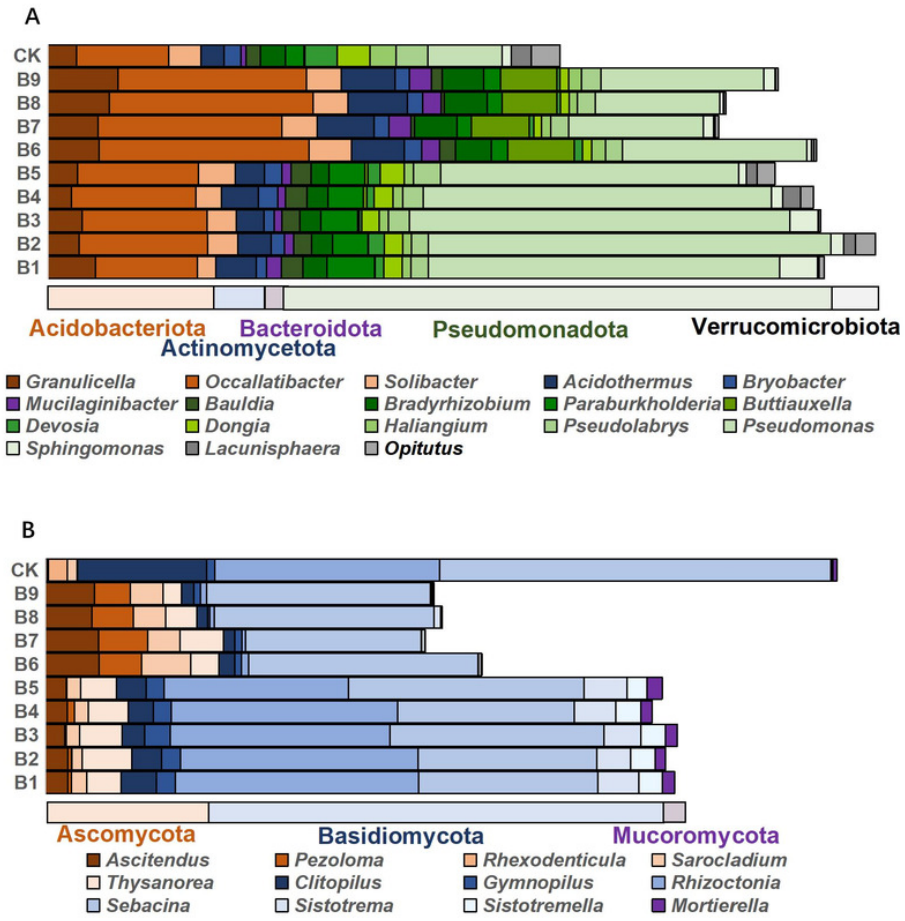

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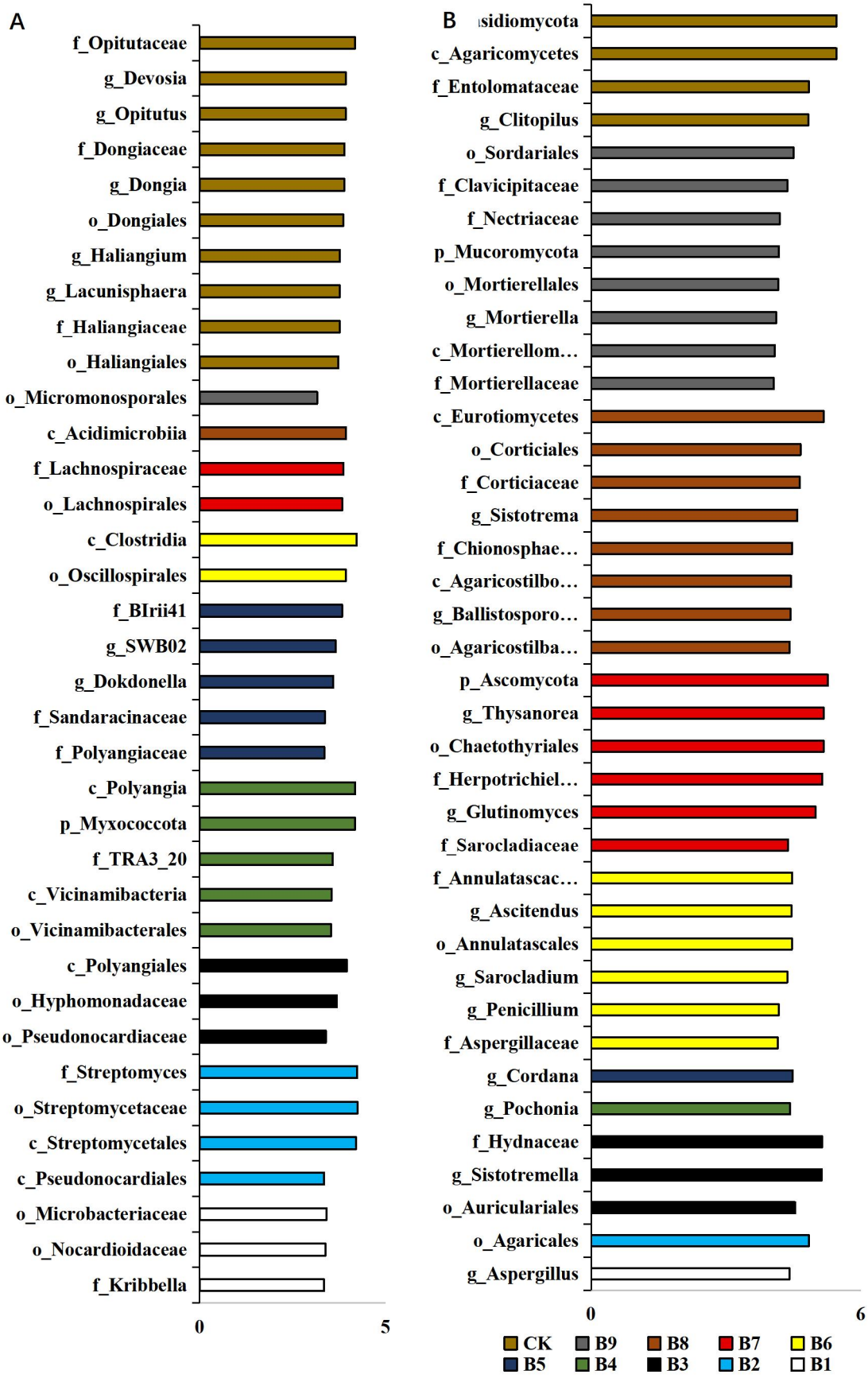
Figure 4(on next page)

Figure 4. LEfSe analysis of differentially abundant classes, orders, families and genera of microorganism in blueberry cutting-seedlings rhizospheres.

(A)The result of bacteria LEfSe analysis of differentially abundant and (B) result of fungi LEfSe analysis of differentially abundant.*The LDA threshold score in the figure was equal or greater than 2.0.

1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f_Opitutaceae
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g_Haliangium
g_Lacunisphaera
f_Haliangiaceae
o_Haliangiales
o_Micromonosporales
c_Acidimicrobiia
f_Lachnospiraceae
o_Lachnospirales
c_Clostridia
o_Oscillospirales
f_BIrii41
g_SWB02
g_Dokdonella
f_Sandaracinaceae
f_Polyangiaceae
c_Polyangia
p_Myxococcota
f_TRA3_20
c_Vicinamibacteria
o_Vicinamibacterales
c_Polyangiales
o_Hyphomonadaceae
o_Pseudonocardiaceae
f_Streptomyces
o_Streptomycetaceae
c_Streptomycetales
c_Pseudonocardiales
o_Microbacteriaceae
o_Nocardioidaceae
f_Kribbella
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f_Entolomataceae
g_Clitopilus
o_Sordariales
f_Clavicipitaceae
f_Nectriaceae
p_Mucoromycota
o_Mortierellales
g_Mortierella
c_Mortierellom…
f_Mortierellaceae
c_Eurotiomycetes
o_Corticiales
f_Corticiaceae
g_Sistotrema
f_Chionosphae…
c_Agaricostilbo…
g_Ballistosporo…
o_Agaricostilba…
p_Ascomycota
g_Thysanorea
o_Chaetothyriales
f_Herpotrichiel…
g_Glutinomyces
f_Sarocladiaceae
f_Annulatascac…
g_Ascitendus
o_Annulatascales
g_Sarocladium
g_Penicillium
f_Aspergillaceae
g_Cordana
g_Pochonia
f_Hydnaceae
g_Sistotremella
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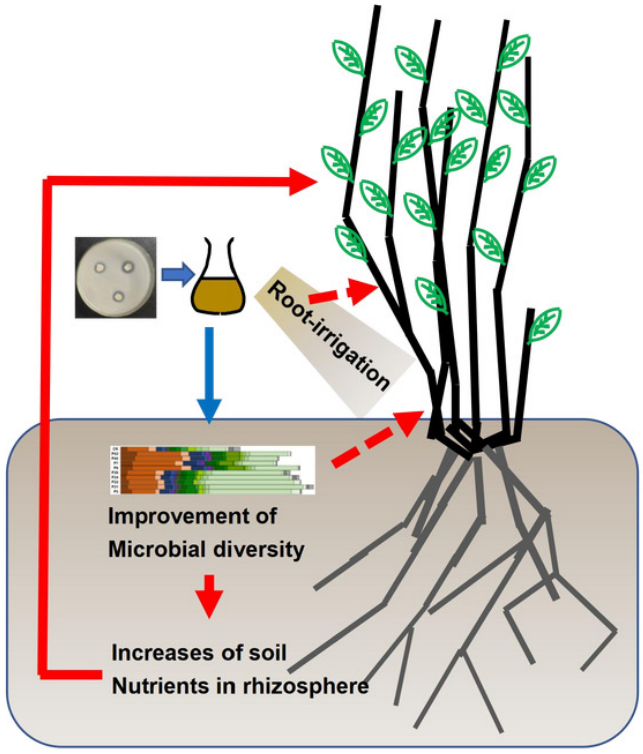
Figure 4. LEfSe analysis of differentially abundant classes, orders, families and genera of microorganism in blueberry cutting-seedlings rhizospheres.
(A)The result of bacteria LEfSe analysis of differentially abundant and (B) result of fungi LEfSe analysis of differentially abundant.
*The LDA threshold score in the figure was equal or greater than 2.0.

Figure 5

Figure 5. The relationship between PGPR strains with rhizosphere microenvironmental factors and blueberry plants

*The solid red line indicates a significant promotion, while the dotted red line indicates a certain promotion



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