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REVIEW ARTICLE

Isolation and Genome Sequence of a Novel Phosphate-Solubilizing Rhizobacterium *Bacillus altitudinis* GQYP101 and Its Effects on Rhizosphere Microbial Community Structure and Functional Traits of Corn Seedling

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Abstract

Bacillus altitudinis is a widely distributed soil bacterium that has various functional activities, including remediation of contaminated soil, degradation of herbicides, and enhancement of plant growth. *B. altitudinis* GQYP101 was isolated from the rhizosphere soil of *Lycium barbarum* L. and demonstrated potential as a plant growth-promoting bacterium. In this work, strain GQYP101 could solubilize phosphorus, and increased the stem diameter, maximum leaf area, and fresh weight of corn in a pot experiment. Nitrogen and phosphorus contents of corn seedlings (aerial part) increased by 100% and 47.9%, respectively, after application of strain GQYP101. Concurrently, nitrogen and phosphorus contents of corn root also increased, by 55.40% and 20.3%, respectively. Furthermore, rhizosphere soil nutrients were altered and the content of available phosphorus increased by 73.2% after application of strain GQYP101. The mechanism by which strain GQYP101 improved plant growth was further investigated by whole genome sequence analysis. Strain GQYP101 comprises a circular chromosome and a linear plasmid. Some key genes of strain GQYP101 were identified that were related to phosphate solubilization, alkaline phosphatase, chemotaxis, and motility. The findings of this study may provide a theoretical basis for strain GQYP101 to enhance crop yield as microbial fertilizer.

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Introduction

Plant growth-promoting rhizobacteria (PGPR) are the beneficial bacteria that exist in the root soil of plants and significantly improve plant growth. PGPR benefit plant growth and enhance plant tolerance for biotic and abiotic stress by solubilizing phosphorus and potassium, secreting growth regulators (e.g., indole-3-acetic acid), producing siderophores, inhibiting plant pathogens, controlling nematodes, fixing nitrogen [1], and so on. The growth-enhancing effect of PGPR has been confirmed on many crops [2], such as wheat [3], rice [4], corn [5], cucumber [6], *Miscanthus giganteus* [7], *Malus hupehensis* Rehd. [8]. Hence PGPR are an environmentally friendly alternative to chemical fertilizers and pesticides in sustainable agriculture [2, 9].

Bacillus altitudinis is a widely distributed, Gram-positive bacterium that was firstly isolated from air and described by Shivaji et al. [10]. At present, there are 82 genome sequences of *B. altitudinis* stored in the GenBank database. *B. altitudinis* has different activities, including remediation of contaminated soil, degradation of herbicides, and enhancement of plant growth. For example, *B. altitudinis* KP-14 can tolerate various abiotic stresses, which can significantly enhance the biomass of *M. giganteus* in metal-contaminated soils [7]. *B. altitudinis* A16 could be used for soil remediation by biodegrading the toxic substance butachlor [11]. *B. altitudinis* WR10 could alleviate Cu stress in wheat by scavenging reactive oxygen species and biosynthesizing phenylpropanoid [12]. Moreover, *B. altitudinis* WR10 alleviated abiotic stress under low-phosphorus and high-salinity conditions in wheat via production of phytases and phosphatases [3], and this could be used as a strategy to increase crop yields in saline-alkali soils. In addition, *B. altitudinis* MS16 could produce biosurfactant and has potential for emulsification and antifungal activity [13].

Phosphorus is an indispensable macronutrient that is instrumental in almost all metabolic processes of plant, such as photosynthesis, respiration, energy storage and transmission, and cell division. Phosphorus exists in the soil predominantly in two forms—inorganic phosphorus and organic phosphorus—but most of the phosphorus is insoluble and cannot be absorbed by plants, thus it becomes a limiting element for plant growth [2]. Many phosphate-solubilizing bacteria in soil can convert insoluble phosphorous to the soluble form by secreting acid, alkaline phosphatase and phytase [14]. Application of phosphate-solubilizing bacteria can increase the absorption of phosphorus by plants, which has important theoretical and practical significance in agricultural production [15] and could relieve the pollution caused by phosphorus fertilizers [2]. However, the organic phosphate-solubilizing activity of *B. altitudinis* has not been studied until now and the growth-promoting mechanism of *B. altitudinis* still needs to be further explored.

In this study, a phosphate-solubilizing bacterium, *B. altitudinis* GQYP101, was screened from the rhizosphere of *Lycium barbarum* L. and verified to enhance corn growth. The in-depth growth-promoting mechanism of strain GQYP101 was further revealed by whole genome sequencing. This study provide a theoretical basis for the application of *B. altitudinis* GQYP101 as a microbial fertilizer strain.

Materials and Methods

Strain Screening and Phenotypic Analysis

Strain GQYP101 was screened from the rhizosphere soil of *L. barbarum* L. through the gradient dilution method. Strain GQYP101 was cultured on Luria–Bertani (LB) medium containing 1% peptone, 1% NaCl, and 0.5% yeast extract, with 1.6% agar added for solid medium. Morphology of the bacterium was determined by Gram stain kit (SL7040, Coolaber, China) following the manufacturer's instructions [16]. Mongina medium was used for screening phosphate-solubilizing bacteria, and was composed of glucose 10.0 g, $CaCO_3$ 5.0 g, $(NH_4)_2SO_4$ 0.5 g, KCl 0.3 g, NaCl 0.3 g, lecithin 0.2 g, $FeSO_4{\cdot}7H_2O$ 0.03 g, $MgSO_4{\cdot}7H_2O$ 0.3 g, $MnSO_4{\cdot}4H_2O$ 0.03 g, deionized water 1 L, agar 1.5%, and pH 7.0–7.5 [17].

Strain GQYP101 was inoculated on Mongina medium and cultured for 4–7 days at 28 °C, then plates were examined for the presence of a phosphate-solubilizing circle. Skimmed milk powder medium (1.5% skim milk powder with 1.5% agar added for solid medium) was used to verify protein-degrading ability. Strain GQYP101 was inoculated in the protein-degrading medium and cultured for 2 days at 37 °C to observe the generation of transparent circle [8]. The presence of siderophores was analyzed using CAS-agar plates. Strain GQYP101 was inoculated on the plate and cultured at 37 °C for 2 days; a yellow circle indicated the presence of siderophores [8]. Motility of strain GQYP101 was detected on semi-solid medium containing 1% peptone, 1% NaCl, and 0.8% agar. A sterile filter paper was placed on the center of the plate and 5 µL bacterial suspension was applied to the paper. The plate was then cultured at 37 °C for 20 h.

Pot Experiment and Measurement

A pot experiment was performed in the greenhouse of Shandong Agricultural University. Approximately 1 kg soil was placed in each pot of 15-cm diameter and 20-cm depth. Two groups were established with 10 replicates for each group. Corn seedlings were cultivated to two cotyledons,

and healthy and consistent seedlings were selected for the experiment. One milliliter (1×10^8 cfu/ml) of the suspension of strain GQYP101 cultured in bean juice was diluted to 800 ml using water and applied to each pot. A control group was treated with the same amount of bean juice without strain GQYP101.

After 30 days of inoculation, the agronomic characteristics of corn, including plant height, stem diameter, and leaf area were measured and recorded. Plant height was the distance from the heart leaf to the soil of the seedlings. Stem diameter was the diameter of the stem at 3 cm above the ground and was determined by a caliper. The maximum leaf area per plant applied the length–width coefficient method, following the formula: $LA = L \times W \times 0.75$ (L, leaf length; W, leaf width). Biomass of the corn was also determined. Plants were collected, washed, and weighed, then heated at 105 °C for 30 min in the oven, followed by heating at 85 °C to a constant weight, after which the dry weight was determined.

The total potassium, phosphorus, and nitrogen contents of the corn were extracted followed by the H_2SO_4-H_2O_2 digestion method [18]. The content of total potassium was detected by the flame photometry method, the total phosphorus was performed by the vanadium-molybdenum yellow colorimetric method, and the total nitrogen was measured by a flow analyzer [8]. The soil available content of the nutrients was also determined. Nitrate nitrogen was extracted by 2 M KCl and then analyzed by calcium chloride-flow injection analyzer. Available potassium was measured by flame spectrophotometer and available phosphorus in the soil was determined by molybdenum antimony colorimetric [19].

At the end of the pot experiment, the rhizosphere soil was collected for extraction of the total soil microbial metagenomic DNA. 16S rRNA gene were amplified by the universal primers B341F (5′-CCTACGGGNGGCWGC AG-3′) and B785R (5′-GACTACHVGGGTATCTAATC C-3′) [8]. Sequencing was performed by Shanghai Paisen Bioengineering Co., Ltd. on an Illumina MiSeq platform. The raw sequencing data were screened by FASTX-Tool kit, mothur, and UCHIME [20, 21] to remove low-quality reads, sequences with N, sequences < 150 bp in length, and chimeras. OTU clustering and annotation were conducted after obtaining high-quality sequences. Based on the OTU results, dilution curve, diversity index analysis, and statistical analysis of community structure and species abundance differences at each classification level were performed [21, 22].

Optimization of Medium

Bean sprout juice acts as an original medium in the process of culture medium optimization. The optimal carbon (glucose, sucrose, maltose, soluble starch, and corn flour), organic nitrogen (peptone, soybean meal, beef extract and yeast powder), inorganic nitrogen (NH_4NO_3, urea, NH_4Cl, and $(NH_4)_2SO_4$), and inorganic salts (KH_2PO_4, K_2HPO_4, $MgSO_4$, and $CaCO_3$) were investigated by single-factor method. The optimal ratio of carbon, nitrogen, and inorganic salts was elucidated by orthogonal experiments. Bacterial numbers were determined by the plate-counting method [23].

Genome Sequencing and Annotation

The whole genome shotgun (WGS) strategy was used to sequence the whole genome of strain GQYP101 and construct a library of different insert fragments. These libraries were separately sequenced by next-generation sequencing and third-generation single-molecule sequencing technology based on the Illumina MiSeq sequencing platform and the PacBio sequencing platform. tRNAs and rRNAs were separately predicted by tRNAscan-SE (version 1.3.1) [24] and Barrnap (0.9-dev) (https://github.com/tseemann/barrnap), while other ncRNAs were mainly obtained by comparison with the Rfam database [25]. Protein-coding genes were predicted by GeneMarkS (version 4.32 April 2015) [26]. Genes of CAZy enzymes and potential signal peptides present in the genome were predicted by hmmscan (3.1b2, February 2015) software [27] and SignalP (version 4.1) software [28], respectively. TMHMM (Server v. 2.0) was used to predict the transmembrane helix structure in protein-coding genes, and the transmembrane, intracellular, and extracellular regions of each transmembrane protein [29]. Cluster of Orthologous Genes (COG) annotations were determined by eggNOG-mapper software [30], a threshold value of 1E-6 was set. Gene Ontology (GO) annotation was performed using InterPro (version 66.0, release 2017.11.23) [31].

Results

Strain Screen, Identification, and Functional Analysis

B. altitudinis GQYP101 was screened from the rhizosphere soil of *L. barbarum* L. and cultured on Luria–Bertani (LB) medium. Cellular morphology, detected by microscopy, revealed that strain GQYP101 was a rod-shaped, spore-forming, Gram-positive bacterium (Fig. 1A). Strain GQYP101 possesses the capacity of producing siderophores, degrading protein, solubilizing organic phosphorus and motility (Fig. 1B–E). These characteristics demonstrated that strain GQYP101 was potentially a member of PGPR.

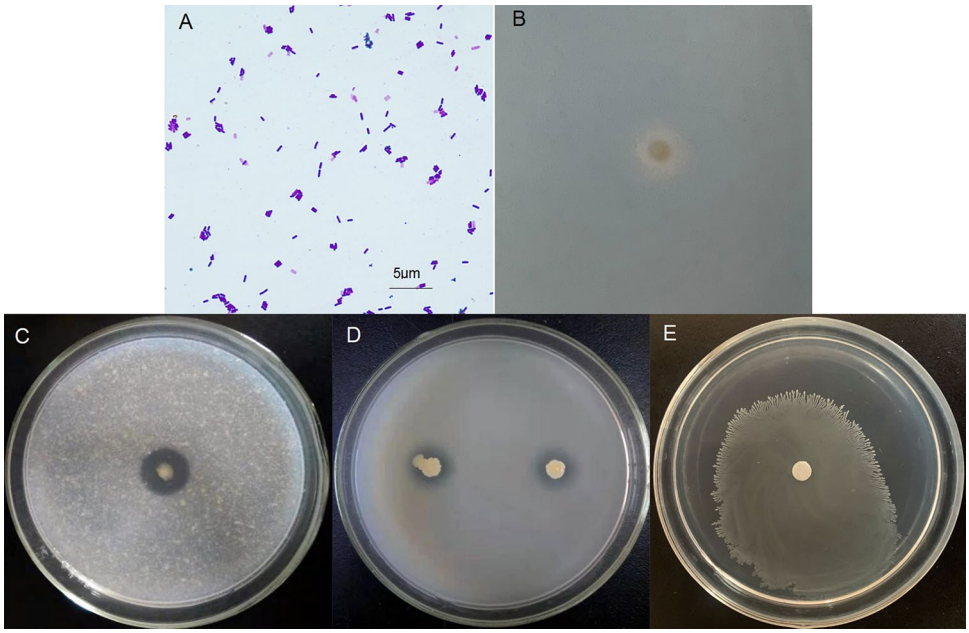

Fig. 1 Strain GQYP101 is a Gram-positive bacterium and can produce siderophores and protease and solubilize organic phosphorus. **A** Strain GQYP101 was stained following the Gram stain method and was observed through an OLYMPUS biological microscope at 1000× magnification. **B** Siderophores production ability test. Strain GQYP101 was cultured on a CAS-agar plate to test the ability of the strain to produce siderophores. **C** Qualitative analysis of protease. Strain GQYP101 was inoculated on a degrading protein plate and cultured for 2 days at 37 °C. **D** Qualitative analysis of organic phosphorus solubilization ability. Strain GQYP101 was cultured on LB plates for 24 h at 37 °C, and then cultivated on Mongina medium plates for qualitative analysis of the ability to solubilize organic phosphorus. **E** Motility of strain GQYP101 was tested on semi-solid medium for 24 h at 37 °C

Strain GQYP101 Promotes Corn Growth

B. altitudinis GQYP101 significantly enhanced the growth of corn. In the pot experiment, corn seedlings were treated for 30 days and then harvested. Images of the corn seedlings at the end of the pot experiment are shown in Fig. 2A. After treatment for 30 days with strain GQYP101, growth of the corn was better than that of the control group (Fig. 2A). The height of corn seedlings inoculated with strain GQYP101 increased significantly, and was 11.9% higher than that of the control group (Fig. 2B). The stem diameter of the seedlings treated with strain GQYP101 was increased by 14.1% compared with the control group, and this was a significant difference ($P < 0.01$) (Fig. 2C). After strain GQYP101 application, the maximum leaf area of the treated group was also significantly different from the control group ($P < 0.01$), increasing by 45.1% (Fig. 2D). After treatment for 30 days, the corn seedlings were harvested and cleaned to measure the fresh weight of the plants. The fresh weight of corn seedlings treated with strain GQYP101 was greater than that of the control group (Fig. 2E). The underground part and total fresh weight reached significant differences ($P < 0.05$), increasing by 57.2% and 16.0%, respectively, after treatment with strain GQYP101. The plants were dried to constant weight and then determined (Fig. 2F). Only the aerial part reached a significant difference ($P < 0.05$) after treatment with strain GQYP101, exhibiting an increase of 28.3% compared with the control group. These findings demonstrated that strain GQYP101 could significantly enhance the biomass of corn.

Effect of Strain GQYP101 on Nutrient Content of Corn and Rhizosphere Soil

Application of strain GQYP101 resulted in significant increases in the nitrogen and phosphorus content of corn seedlings compared with the control group ($P < 0.05$), increasing by 100% and 47.9%, respectively. The total potassium content of corn seedlings with strain GQYP101 was increased by 2.1% compared with the control, but this was not a significant difference. Nutrients in the roots were further determined, and only the phosphorus content in the GQYP101-treated group exhibited a significant difference ($P < 0.05$), increasing by 20.3% compared with the control group. Total nitrogen content in the GQYP101-treated group was increased by 55.40% compared with the control group, but this was not a significant difference (Table 1).

At the end of the pot experiment, the rhizosphere soil of the corn seedlings was collected, and the content of

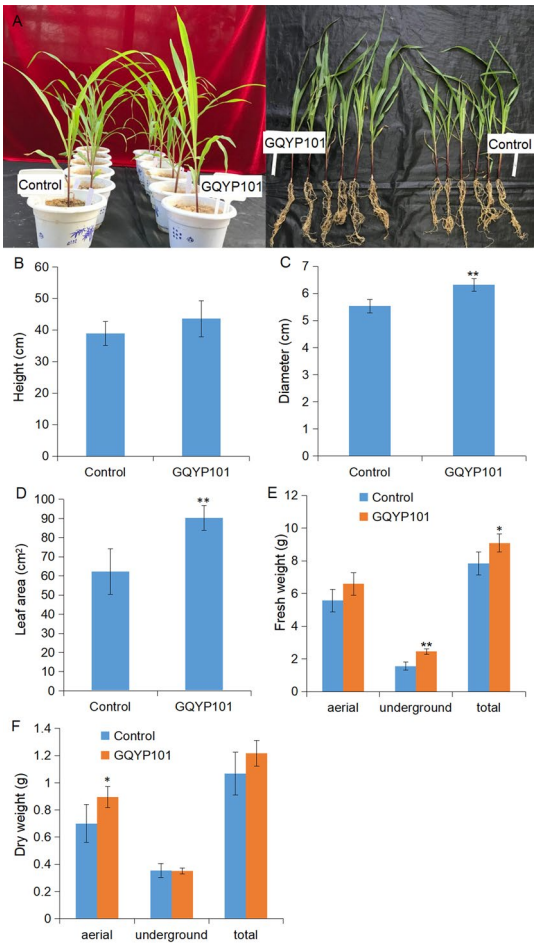

Fig. 2 Agronomic traits of corn seedlings following application of strain GQYP101. One milliliter (1×10^8 CFU/ml) bacterial suspension (bean juice medium) was diluted with water to 800 ml and applied to the corn rhizosphere. A control group was watered with the same amount of medium without strain GQYP101. **A** Corn seedlings after 30 days of application of strain GQYP101 or control medium. The agronomic characteristics of the corn seedlings were measured, including plant height (**B**), stem diameter (**C**), and maximum leaf area (**D**). At the end of the experiment, plants were harvested, washed, and then dried with absorbent paper to measure the fresh weight of corn (**E**). The plants were then dried to a constant weight and the dry weight was determined (**F**). The pot experiment comprised two groups of 10 replicates. Error bars represent the SD of the mean. Asterisks indicate statistical significance (*, $P < 0.05$; **, $P < 0.01$)

nitrate nitrogen, available phosphorus, and available potassium in the soil was determined after drying. The content of available phosphorus in the GQYP101-treated group was significantly increased by 73.2% compared with the control group ($P < 0.05$) (Table 1). Furthermore, although the nitrate nitrogen and available potassium contents were both higher in the GQYP101-treated group than in the control group, the differences were not significant (Table 1).

Strain GQYP101 Influences Microbial Communities of the Rhizosphere Soil of Corn

Microorganisms are sensitive indicators of environmental changes. Variation in soil bacterial community diversity in the rhizosphere of corn was analyzed using Illumina MiSeq sequencing technology. Alpha diversity analysis could embody the diversity and richness of the microbial community. For bacteria, the parameters of Chao1 estimator and ACE estimator were both different between the group treated with strain GQYP101 and the control group. However, Simpson and Shannon indices were similar among the two groups (Table S1). This inferred that soil samples of the group treated with GQYP101 had a higher diversity of microorganisms. A Venn graph was used to count the distribution of unique and common operational taxonomic units (OTUs) in the two different groups. In the bacterial community, 2012 OTUs (accounting for 25.57% of the total) were specific for the control group, 1985 OTUs (containing 25.23% of the total) were unique for the GQYP101-treated group, and 3871 OTUs were common to both groups (Fig. 3A).

The relative richness of the bacterial community at the phylum level is illustrated in Fig. 3B. A total of 41 phyla were classified from the two groups, and Actinobacteria, Proteobacteria, Chloroflexi, Acidobacteria, and Gemmatimonadetes were the dominant phyla. The relative richness of phyla varied after treatment with strain GQYP101. In the treated group, Firmicutes accounted for 2.89% of the total bacteria, while the proportion in the control group was only 1.83%. Moreover, the proportion of Acidobacteria was 11.94% in the treated group, while the relative content was 9.36% in the control group, an increase of 19.41% in the treated group. The relative abundance of Nitrospirae and Planctomycetes was also increased at varying degrees in the treated group. In addition, the dominant phylum Chloroflexi accounted for 14.91% of the total bacteria after application of strain GQYP101; however, the proportion of this phylum was 18.81% in the control group. The relative abundance of other phyla did not change much. The phylum Peregrinibacteria was unique in the treated group. At the genus level, the relative richness of bacterial communities is shown in Fig. 3C. The dominant genera in the group treated with strain GQYP101 were mainly uncultured_f__Gemmatimonadaceae, uncultured_f__Anaerolineaceae, and unidentified_f__Micrococcaceae, while in the control group, uncultured_f__Anaerolineaceae, uncultured_f__Gemmatimonadaceae, and uncultured_p__Acidobacteria were the dominant genera. The genus unidentified_f__Micrococcaceae accounted for 3.00% of the total bacteria in the group treated with strain GQYP101, and only 1.57% in the control group. The content of *Bacillus* was 2.24%

Table 1 The nutrient content of seedlings, and soil after treated with strain GQYP101

		Control	GQYP101
Aerial part	Total nitrogen (g/kg)	9.08 ± 1.76	18.00 ± 1.23**
	Total phosphorus (g/kg)	21.05 ± 0.35	31.9 ± 1.00**
	Total potassium (g/kg)	24.05 ± 2.07	24.67 ± 1.67
Underground part	Total nitrogen (g/kg)	1.39 ± 0.81	2.16 ± 1.25
	Total phosphorus (g/kg)	24.26 ± 0.23	29.18 ± 7.8**
	Total potassium (g/kg)	9.38 ± 0.92	10.02 ± 0.20
Soil	Nitrate nitrogen (mg/kg)	12.78 ± 2.50	13.74 ± 0.92
	Available phosphorus (mg/kg)	16.19 ± 2.68	28.04 ± 3.47**
	Available potassium (mg/kg)	8.75 ± 1.08	10.89 ± 2.63

Values are mean ± SD. "**" represent the differences of two group at the level of $P < 0.01$

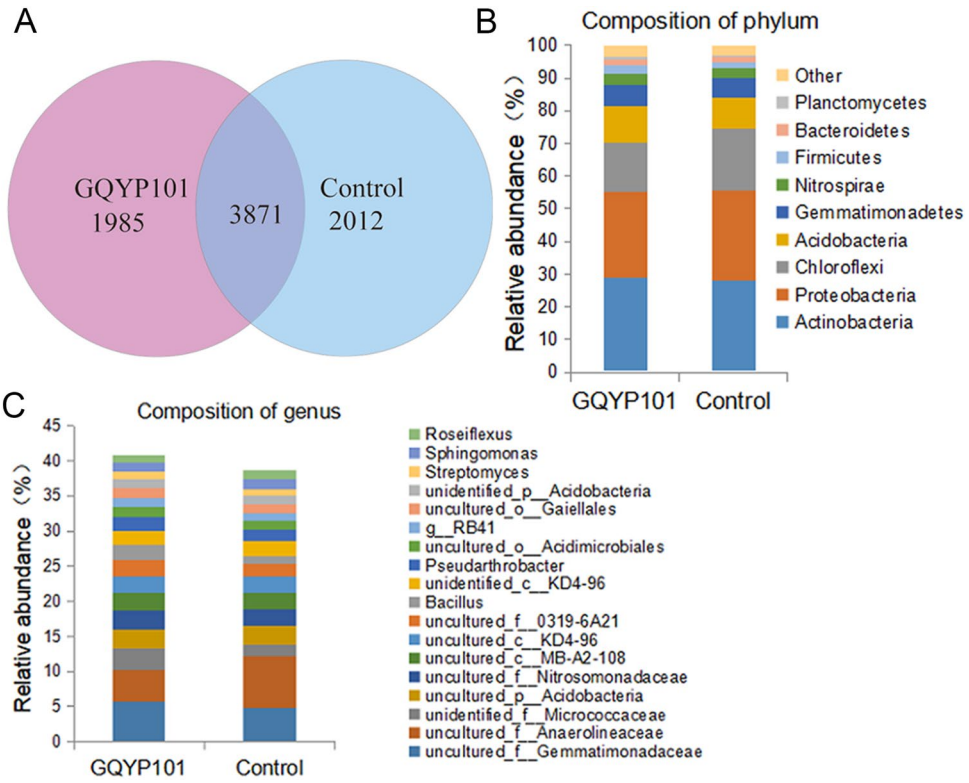

Fig. 3 Relative diversity and abundance of bacterial communities at phylum and genus levels. Venn analysis of the distribution of unique and common OTUs based on 16S rRNA gene (**A**). Relative diversity and abundance of bacterial community at phylum (**B**) and genus (**C**) levels

following application of strain GQYP101, but only 1.14% in the control group.

The increased content of the genus *Bacillus* after application of strain GQYP101 indicated that the strain could be colonized in the rhizosphere of corn. Concurrently, the microbial community increased in diversity and abundance, which was beneficial for plant growth.

Medium Optimization for Strain GQYP101

Strain GQYP101 could enhance corn growth effectively. To utilize strain GQYP101, culture medium optimization for the strain was performed. Single-factor tests indicated the impact of carbon sources was glucose > sucrose > soluble starch > maltose > corn flour, while the influence of organic nitrogen sources were peptone, followed by beef extract, yeast powder and soybean meal. The impact of inorganic nitrogen sources was $NH_4NO_3 > (NH_4)_2SO_4 > NH_4Cl >$ urea, and optimal inorganic salts were $CaCO_3$, followed by K_2HPO_4, KH_2PO_4, and $MgSO_4$. The result of orthogonal tests indicated the optimal medium for strain GQYP101 was 3% glucose, 1.5% peptone, 0.3% NH_4NO_3, and 0.3% $CaCO_3$. Using the optimized medium, bacterial numbers for strain GQYP101 increased to 7.65×10^9 colony forming units (cfu)/ml from 6.54×10^7 cfu/ml.

Genome Features of *B. altitudinis* GQYP101

The genome sequence of *B. altitudinis* GQYP101 was obtained; characteristics and statistics of the genome are presented in Table S2. Strain GQYP101 comprises a 3,880,448-bp circular chromosome (GenBank accession no. CP040514.1) with an average G + C content of 41.3%, and a 10,920-bp linear plasmid (GenBank accession no. CP040513.1) with an average G + C content of 36.99%. Among the 4012 predicted genes, 3842 genes were protein-coding genes in the chromosome, while the plasmid contains nine predicted genes and five protein-coding genes. In the chromosome, there were a total of 24 rRNAs (eight each of 5S rRNAs, 16S rRNAs, and 23S rRNAs), 81 tRNAs, and five noncoding RNAs (ncRNAs) (Fig. 4). There were 272 proteins assigned to signal peptides, 1090 genes coding for transmembrane helices, and 136 genes coding for secretory proteins. Approximately 3421 genes were assigned to COG functional categories, accounting for 85.16% of the total genes (Table S2 and Fig. 4).

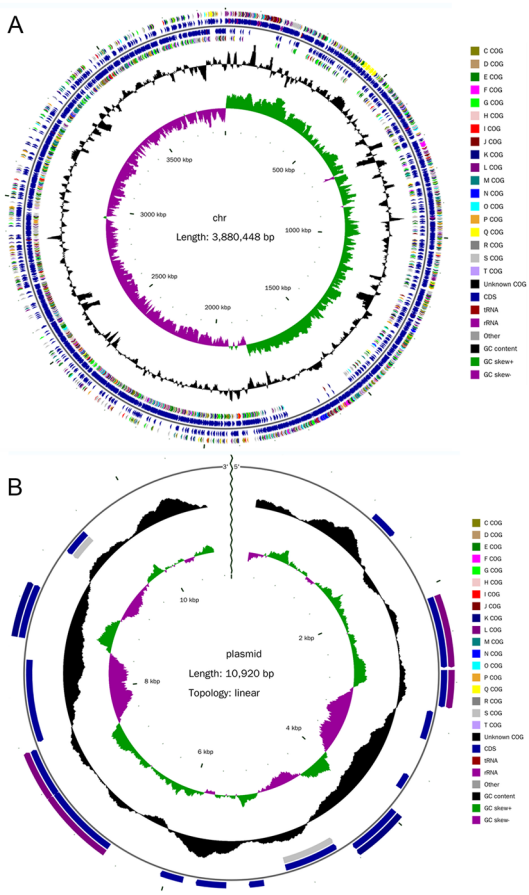

Fig. 4 Genomic circle map of chromosome (**A**) and plasmid (**B**) of strain GQYP101. From inner to outer circle, circle 1: Gene scale; circle 2: GC Skew; circle 3: GC content; circle 4, 7: Each CDS belongs to COG; circle 5, 6: The position of CDS, rRNA, and tRNA on the genome. The whole genome circle map was visualized by CGView software (http://wishart.biology.ualberta.ca/cgview/)

COG Annotation

The COG database was used for functional research of the genome sequence of strain GQYP101, and the assignment of genes in the COG database is presented in Table S3. Among the 4012 coding genes in the GQYP101 chromosomal genome, 3413 genes could be classified in the COG database, and included 19 of the 25 categories within the COG database. Among these categories, the largest group encodes function unknown proteins (S), with 961 genes (23.95%), followed by transcription (K) (305 genes, 7.60%), amino acid transport and metabolism (E) (282 genes, 7.03%), and carbohydrate transport and metabolism (G) (222 genes, 5.53%), all of which are predominantly related to physiological functions and basic metabolism. The high percentages of genes in the categories of cell wall/membrane/envelope biogenesis (M) and inorganic ion transport and metabolism (P) may indicate that strain GQYP101 has the potential to enhance plant growth by solubilizing phosphorus and producing siderophores. Furthermore, there remain 599 genes that are not assigned to the COG database, accounting for approximately 14.93% of the total genes of strain GQYP101.

In the plasmid of strain GQYP101, eight genes were annotated in the COG database; four genes are related to replication, recombination, and repair (L), two genes are related to transcription (K), and two are assigned to function unknown proteins. One plasmid gene was not annotated to any COG database.

Gene Ontology (GO) Annotation

To investigate the attributes of genes and gene products of strain GQYP101, gene ontology was studied. The first level of GO classification can be divided into molecular function (MF), cellular component (CC), and biological process (BP). A total of 16,721 genes were annotated into 81 secondary classifications—44 BP class, 13 CC class, and 24 MF class (Fig. S1). Biological processes belonging to the BP and molecular functions belonging to the MF accounted for the most plentiful classifications, with approximately 5157 genes, which was 30.84% of all annotated genes. Cellular nitrogen compound metabolic process and biosynthetic process, both belonging to the BP, and cell subclass belonging to CC comprised the second largest group, accounting for 5.72%, 5.56%, and 5.37% of all annotated genes, respectively. For cytoskeleton organization and mRNA processing subclass belonging to BP, only one GO term was assigned for each.

Genes Related to Phosphate Solubilization and Metabolism

Functional screening of the phosphate-solubilizing capacity of strain GQYP101 was conducted from the genomic aspect. Generally, bacteria can solubilize insoluble phosphorus into the soluble form by producing organic acids and phosphatase, thus benefiting the uptake of phosphorus by plants [15]. Strain GQYP101 was known to solubilize phosphorus (Fig. 1). Several putative phosphate solubilization genes were screened from the genome of *B. altitudinis* GQYP101 (Table 2). Secretion and production of organic acids facilitates solubilization of inorganic phosphorus [2], such as acetate kinase and citrate synthase. Strain GQYP101 possesses a complete phosphate ABC transporter system (PstS, PstA, PstB, PstC) that can transport extracellular substrates. In addition, strain GQYP101 is able to solubilize organic phosphorus into the soluble form through alkaline phosphatase [32]. Several phosphatases were identified in strain GQYP101, such as pyrophosphatase, alkaline phosphatase, and haloacid dehalogenases (HAD) family phosphatase.

Other Potential Growth-Promoting Genes in Strain GQYP101

Nitrogen is the first macronutrient that essential for plant growth. P(II) proteins are a key factor controlling nitrate metabolism in bacteria and are functionally related to nitrate transporter and nitrate reductase [33]. P(II) family nitrogen regulator and other genes related to nitrogen metabolism were presented (Table S4). The results indicated strain GQYP101 could regulate nitrogen metabolism.

Secondary metabolism gene clusters in strain GQYP101 were predicted by antiSMASH, which revealed that there were 11 secondary metabolism gene clusters present (Table S5), including two types of NRPS gene cluster. Among the 11 gene clusters, three clusters with 85% similarity were sactipeptide, ranthipeptide, lichenysin in NRPS type, and bacilysin, respectively. Bacilysin inhibits bacterial and fungal pathogens by inducing the cell wall to dissolve [34]. Iron is necessary for the growth of microbes. In a low-iron environment, some microbes secrete ferric iron chelators, called siderophores, which are important in iron homeostasis [35]. One siderophore-biosynthesis cluster for absorbing iron was identified in the genome of strain GQYP101 (Table S4, S5). 2,3-Butanediol, a volatile compound that can regulate plant growth [36], might be produced by strain GQYP101 due to the presence of putative genes of acetoin utilization protein *AcuC*, 2,3-butanediol dehydrogenase, acetolactate decarboxylase *budA*, and acetolactate synthase *AlsS* in the genome of strain GQYP101 (Table S4). In addition, strain GQYP101 has the properties of chemotaxis and motility (Table S4). Chemotaxis

Table 2 Genes related to putative phosphate solubilization and metabolism

NCBI accession	Protein id	Gene
BPGQ101_RS14070	WP_008346063.1	Citrate synthase citZ
BPGQ101_RS10110	WP_025207495.1	Citrate synthase mmgD
BPGQ101_RS14060	WP_007501693.1	Malate dehydrogenase
BPGQ101_RS14180	WP_024718669.1	Acetate kinase
BPGQ101_RS12040	WP_007501259.1	Phosphate ABC transporter permease PstA
BPGQ101_RS12030	WP_017367606.1	Phosphate ABC transporter ATP-binding protein PstB
BPGQ101_RS12035	WP_056705269.1	Phosphate ABC transporter ATP-binding protein
BPGQ101_RS12045	WP_017357999.1	Phosphate ABC transporter permease subunit PstC
BPGQ101_RS12050	WP_017367609.1	Phosphate ABC transporter substrate-binding protein PstS
BPGQ101_RS06720	WP_017359158.1	Inorganic phosphate transporter
BPGQ101_RS08185	WP_008344915.1	Inorganic phosphate transporter
BPGQ101_RS15975	WP_024719769.1	Phosphate-starvation-inducible protein PsiE
BPGQ101_RS17015	WP_007500058.1	Pyrophosphatase PpaX
BPGQ101_RS05255	WP_024719962.1	Alkaline phosphatase
BPGQ101_RS06000	WP_008348537.1	Cof-type HAD-IIB family hydrolase
BPGQ101_RS07620	WP_024719544.1	Cof-type HAD-IIB family hydrolase
BPGQ101_RS17590	WP_041091444.1	Cof-type HAD-IIB family hydrolase
BPGQ101_RS02200	WP_047945855.1	HAD-IIB family hydrolase
BPGQ101_RS02745	WP_008347194.1	HAD family phosphatase
BPGQ101_RS15970	WP_138278976.1	HAD family phosphatase
BPGQ101_RS17715	WP_138279089.1	HAD family phosphatase
BPGQ101_RS19425	WP_017359922.1	Alkylphosphonate utilization protein

enables bacteria to move in a direction that is favorable for survival and is conducive to effective colonization [37].

The chromosome of strain GQYP101 contains a number of carbohydrate active enzymes, including 37 carbohydrate esterases (CE), 35 glycosyl transferases (GT), four auxiliary activities (AA), three polysaccharide lyases (PL), 15 carbohydrate-binding modules (CBM), and 45 glycoside hydrolases (GH) (Table S6). The carbohydrate esterases CE1, CE3, CE4, and CE7 may serve as acetyl xylan esterase (EC 3.1.1.72). The genome of *B. altitudinis* GQYP101 might consist of fifteen GT2 that act as cellulose synthases, one GH18 that acts as chitinase and one GH48 that acts as endoglucanase. These carbohydrate enzymes can act as growth-promoting factors as reported [38].

Discussion

B. altitudinis GQYP101 was screened from the rhizosphere soil of *L. barbarum* L. This study confirmed the traits of *B. altitudinis* GQYP101 as a plant growth-promoting bacterium by pot experiment and whole genome sequencing. *B. altitudinis* GQYP101 can effectively solubilize organic phosphorus and enhance the growth of corn. Concurrently, the diversity and abundance of the microbial community of corn rhizosphere soil was significantly altered in the presence of strain GQYP101. The complete genome sequence of strain GQYP101 revealed that this bacterium has a circular chromosome and a linear plasmid. The capacities of phosphate solubilization, nitrogen metabolism regulation, protein degradation, and motility were further indicated by functional analysis of the whole genome of strain GQYP101.

The pot experiment indicated that strain GQYP101 could enhance corn seedlings growth effectively. Strain GQYP101 has the functions of producing protease, producing siderophore, and solubilizing phosphorus, which could degrade proteins and increase soluble iron and phosphorus for plant uptake and growth, respectively. Moreover, strain GQYP101 could alter the nutrients of corn and the rhizosphere soil, especially the phosphorous content. Phosphorus is the second macronutrient that is indispensable for promoting plant growth and development. The content of phosphorus in the soil that can be uptaked and utilized by plants is usually about 1 mg/kg or less [39]. In agricultural production, the strategy of applying phosphorus fertilizers is generally used to resolve phosphorus deficiency issues. However, most phosphorus applied in the form of fertilizer will precipitate out and only a tiny part is able to be absorbed by plants. There are microbes present in the soil that can convert insoluble phosphorus into soluble phosphorus, and these microbes release various organic acids and/or phosphatases into the soil, making phosphorus soluble and available for plants [15, 40]. Strain GQYP101 has the capacity of phosphate solubilization, hence can dissolve insoluble phosphorus in the soil into the soluble form, thereby increasing available phosphorus in the soil and total phosphorus of plants, as shown in Table 1. Analysis of the genome of strain GQYP101 demonstrate the presence of genes associated to phosphate solubilization, such as HAD family phosphatase and alkaline phosphatase. Phosphatase released by microorganisms is a widely distributed enzyme that is instrumental in the dissolution of organic compounds and making the components available for plants [41]. Strain GQYP101 may solubilize organic phosphorus by secreting alkaline phosphatase. Strain GQYP101 also possesses genes related to inorganic phosphorus solubilization, such as pstSCAB and inorganic phosphorus transporter, but it cannot solubilize inorganic phosphorus. It may be that strain GQYP101 lacks the *pqq* operon that is related to the biosynthesis of pyrroloquinoline quinone [2] and the glucose dehydrogenase (*gcd*) gene that is responsible for phosphate solubilization [42].

In addition, the nitrogen content of tissue and rhizosphere soil of corn also increased after inoculation with strain GQYP101 (Table 1). There are two possible reasons: firstly, strain GQYP101 has the function of secreting protease, which could degrade surrounding macromolecular proteins and provide small molecular proteins or free amino acids for plants. Secondly, after application of strain GQYP101, the phyla Acidobacteria and Nitrospirae were increased, which involved in the metabolism of inorganic and organic nitrogen sources [43].

Soil microbes are an intrinsic part of the soil ecosystem and act a pivotal part in biochemical cycles via their various functions [26]. In addition, the diversity of the soil microbial community serves as a sensitive indicator of soil quality [44]. Bacterial diversity and abundance in the corn rhizosphere soil in the presence of strain GQYP101 were explored by high-throughput sequencing. Ace and Chao1 indices act as indicators of microbial abundance, while Shannon–Weaver and Simpson indices are indicators of microbial diversity [8]. Felici et al. [45] reported that the inoculation of *Bacillus subtilis* and *Azospirillum brasilense* on tomato rhizosphere could influence bacterial communities. In the current study, the diversity and abundance of the microbial community in the corn rhizosphere were altered after inoculation with strain GQYP101 compared with the control, congruent with the findings of Felici et al. [45]. Actinobacteria, Proteobacteria, and Chloroflexi were the dominant bacterial phyla in the two groups. Acidobacteria was increased by 19.41% after treatment with strain GQYP101, and members of this phylum play a significant part in the soil ecosystem and material recycling including the nitrogen metabolism [46]. Nitrogen could promote the abundance of Acidobacteria within a certain concentration range [47]. Nitrospirae plays a key role in nitrification by oxidizing nitrite to nitrate [43]. After inoculation with

strain GQYP101, the content of nitrate nitrogen of soil was increased, which could affect the relative abundance of Acidobacteria and Nitrospirae. Chloroflexi is a group of anaerobic bacteria that is negatively correlated with organic matter content [43, 48]. The nutrient of rhizosphere soil was richer after inoculation of strain GQYP101, phylum Chloroflexi was decreased. There was a sharp increase in Firmicutes after application of strain GQYP101. The genus *Bacillus* is a dominant part of the phylum Firmicutes, and the relative richness of this phylum may be associated to the increase of *Bacillus*, which reflects that strain GQYP101 could colonize the rhizosphere of corn.

Cooperation between microbes is common in nature. Arbuscular mycorrhizal fungi (AMF) can release carbon sources to the surrounding environment. Fructose is one such carbon source, which acts as a signal molecule and promotes growth of phosphate-solubilizing bacteria and secretion of phosphatase. Simultaneously, the increase of phosphatase activity promotes the mineralization of organic phosphorus and further benefits the growth of AMF [49, 50]. Beneficial fungi may cooperate with phosphate-solubilizing bacteria such as strain GQYP101 to increase available phosphorus in the rhizosphere soil, thereby enhancing uptake of phosphorus by plants.

Conclusion

B. altitudinis GQYP101 was screened with the functions of producing protease, producing siderophore and solubilizing organic phosphorus, which could increase the nitrogen and phosphorus contents of corn seedling and promote corn seedling growth. The content of available phosphorus in the rhizosphere soil was increased after application of strain GQYP101. The mechanism by which strain GQYP101 improved plant growth was further investigated by whole genome sequence analysis and some key genes related to phosphate solubilization, alkaline phosphatase, chemotaxis, and motility were figured out in strain GQYP101. The results of this study provide a theoretical basis for strain GQYP101 and this species as a microbial fertilizer to improve crop yield in agricultural application.

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Author Contributions DZ and YC performed the work and analyzed the data. DZ and YD wrote the original draft. CW revised the manuscript. YZ, KL, LY, XH, YP, and JG advised the manuscript. CW and BD supported the study.

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Data Availability All data of this study are available within the manuscript and supplementary materials.

Declarations

Conflict of Interest All the authors declare no competing interests.

Ethical Approval The research does not involve human and animal subjects.

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