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The siderophore-producing bacterium, *Bacillus siamensis* Gxun-6, has an antifungal activity against *Fusarium oxysporum* and promotes the growth of banana

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Abstract

Background: *Fusarium* wilt of banana is a soil-borne disease caused by *Fusarium oxysporum f. sp. cubense* with the Tropical Race 4 (FOC TR4), which seriously restricts the development of the banana industry. The utilization of antagonistic microorganisms to inhibit the propagation of pathogens has become a hot research topic in the field of biological prevention and control because of its green and efficient advantages.

Results: In this study, 60 siderophore strains from banana rhizosphere soil were screened. Three strains showing antifungal activity were screened out using FOC TR4 as the antagonistic pathogen. Among them, the strain Gxun-6 showed the highest antifungal activity, of up to 68.8%. It also showed significant inhibitory effect on the other 8 plant pathogens tested, thereby demonstrating broad-spectrum antifungal activity. Combined with colony morphology, physiological and biochemical analysis, and 16S rRNA evolutionary tree analysis, Gxun-6 was identified as *Bacillus siamensis*. Pot experiments showed that this strain had remarkable *Fusarium* wilt prevention and growth-promoting effect on banana. The control effect can reach 88.26%. The fresh weight increased by 25.36%.

Conclusions: The strain had strong *Fusarium* wilt control and growth promoting effects on banana and can be used as a strain resource for developing banana.

Keywords: Siderophores, *Fusarium* wilt of banana, Biocontrol, *Bacillus siamensis*, Plant growth promotion

Background

Banana (*Musa* spp.) is the most popular marketable fruit crop grown all over the world, and a dominant staple food in many developing countries (Panigrahi et al. 2021). *Fusarium* wilt of banana, also known as Panama disease, is among the most serious fungal soil-borne diseases caused by *Fusarium oxysporum* f. sp. *cubense* Tropical Race 4 (FOC TR4) (Damodaran et al. 2020). FOC TR4 can infect banana roots, penetrate into the root xylem, and spread into the rhizome and pseudostem xylem

within several days after infection (Xu et al. 2020). It has a wide range, easily leads to an epidemic and is difficult to control (Lin et al. 2009). The existing control methods include chemical control, using breeding disease-resistant varieties and biological control (Yellareddygarri et al. 2014). Although chemical control has a preventive effect in a short period of time, it has caused serious environmental and health problems due to the long-term abuse of pesticides in recent years (Minuto et al. 2006). Abuse of pesticides may also result in the chemical resistance of the pathogen (Abbas et al. 2019). Biological control, with its advantages of requiring a relatively short research and development cycle and environmental protection, has

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become one of the hot spots in the prevention and control of plant soil-borne diseases (Atalla et al. 2020).

Plant growth-promoting rhizosphere bacteria (PGPR) is the most promising agent for promoting cash crop production. PGPR increases crop yield and reduces disease occurrence (Borriss et al. 2019). Members of the genus *Bacillus* are preferred for PGPR (Sivasakthi et al. 2014). Torres et al. (2020) screened a *Bacillus* XT1 in a saline habitat in Spain. Interestingly, XT1 can also produce siderophore and has nitrogen fixation and phosphorus dissolution characteristics. The experiment verified that XT1 had an inhibitory effect on 5 plant pathogenic bacteria in vitro. *Bacillus amyloliquifaciens* colonises bananas successfully, showed control of banana wilt in the field and promoted biocontrol and production in the banana industry (Wang et al. 2016).

Iron is an essential cofactor for almost all microbial life activities (Yu et al. 2011). Previous studies have shown that siderophore bacteria can bind to iron ions to compete with plant pathogens for iron ions (Crowley 2006), which cannot use iron ions, thus limiting their growth (Dutta et al. 2006). Moreover, the siderophore bacteria can secrete active substances, such as phenazine, surfactants and antibiotics, thereby inhibiting the growth of pathogens (Rungin et al. 2012). Siderophore strains can also promote plant growth (Ahmed and Holmström 2014). For example, Ghazy and El-Nahrawy (2021) screened 2 siderophore strains by using Chrome Azurol Sulphonate (CAS) double-layer plate method and proved that these were effective in inhibiting the hypha growth of *Cephalosporium maydis* in maize plant. Derbyshire et al. (2018) studied 40 PGPR strains, which produced siderophore and significantly inhibited the growth of the pathogenic *F. oxysporum* and *Ralstonia solanacearum*. Therefore, siderophore plays an important role in the competition among microorganisms and can be used as a basis for screening biocontrol bacteria (Laslo et al. 2012).

In this study, the siderophore strain was screened out by CAS plate, and the strain with the highest antibacterial rate was screened out by re-screening the antagonistic effect of FOC TR4. On this basis, the screened strains were classified and identified, and their antibacterial spectra were determined. Then, the control effect of banana wilt flower pot was determined.

Methods

Fungal pathogen

Fusarium oxysporum f.sp.cubense with the Tropical Race 4 (FOC TR4), *Botryosphaeria dothidea*, *Fusarium pseudograminearum*, *Cryphonectria parasitica*, *Fusarium sacchari*, *Colletotrichum musae*, *Alternaria alternata*, *Colletotrichum fructicola* and *Fusarium commune* were obtained from Guangxi Academy of Agricultural

Sciences, Nanning, China. They were all kept on potato dextrose agar (PDA) medium at 4 °C.

Screening of siderophore bacteria

Soil samples (root and adhering soil) collected in the rhizosphere of banana plants in Guangxi Jinsui farm, Nanning, China (23.18° N, 107.68° E) was screened for siderophore producing bacteria according to the universal CAS agar plate assay (Schwyn and Neilands 1987). The soil suspensions were prepared by gentle shaking for 24 h at 30 °C in sterilized water under aseptic conditions and then centrifuged at 1500 rpm for 2 min. Serial dilutions (10^{-2} to 10^{-6}) of the soil suspension samples were spread on Luria–Bertani (LB) agar and Nutrient agar (NA; Difco, USA) plates to separate single colonies. Colonies were selected on the basis of variation in morphology (shape, size and color) purified, maintained on agar slants at 4 °C. Pure isolates were stabbed on CAS agar plates using sterile toothpicks and incubated for 2–4 d at 30 °C in the dark (Dutta et al. 2006). The colonies with orange zones were considered as siderophore-producing strains. The siderophore units (SU) was determined by CAS liquid test. The SU was calculated by the following formula: $SU = [(Ar - As)/Ar] \times 100\%$. Where: Ar represents the absorbance of reference (uninoculated broth), and As is the absorbance of the sample (culture supernatant) at 630 nm (Sheng et al. 2020).

In vitro antibacterial activity

Firstly, fungal pathogens were inoculated into potato dextrose agar (PDA) plate and cultured at 30 °C for 7 days. Then, an 8 mm mycelial plug of FOC TR4 from a fresh growing colony was placed at the centre of PDA plate, and the bacterial solution of strain Gxun-6 was inoculated at a point 2.5 cm away from the center. Four points were symmetrically selected for each culture medium, and PDA plate only inoculated with pathogenic bacteria was used as the control. Each group was set up with 3 replicates, and cultured at a constant temperature of 28 °C for 7 days. To observe the inhibitory effect of antagonistic strains on pathogenic bacteria and calculate the bacteriostatic rate, the percentage inhibition of mycelial radial growth was calculated by the following formula: $\text{inhibition of mycelial radial rate} = \frac{\Sigma(\text{average diameter of target colony in control group} - \text{average diameter of target colony in experimental group})}{\text{average diameter of target colony in control group}} \times 100\%$ (Nimaichand et al. 2015).

Species identification of Gxun-6

Genetic characterization

Further species identification of strain Gxun-6 was conducted according to the method described by Cao et al. (2011). Genomic DNA was extracted from Gxun-6

bacterial solution cultured overnight in LB agar. Universal primers Eubac27f (5'-agagtttgatcctggctcag-3') and Eubac1492r (5'-aaggaggtgatccagcc-3') were used as the primers for the amplification of bacterial 16S rRNA. Sequencing results were compared in NCBI. A phylogenetic tree of Gxun-6 was constructed and analysed with the MEGA X software using the neighbour-joining method (the self-expanding number was 1000) (Kumar et al. 2018).

Morphological, physiological and biochemical characterisations

Strain Gxun-6 was cultured on LB agar plate at 28 °C for 24 h. The colony morphology, colour and transparency were observed and recorded. The bacterial morphology was observed under the optical microscope and the scanning electron microscope. Salt tolerance was tested on LB medium with 0%–7.5% (w/v) NaCl and determined visually. The physiological and biochemical reactions of strain Gxun-6 were determined. The results were analysed with reference to Berger's Manual Systematic Bacteriology (Buchanan and Gibbons 1949).

Pot experiments

Preparation of FOC TR4 suspension

FOC TR4 was added to a flask containing potato-dextrose broth (PDB), which was subjected to shaking at 200 r/min for 5 days at 28 °C. Then, the culture was filtered with 2 layers of gauze to remove the mycelia. The FOC TR4 conidial suspension content was adjusted to 10⁶ CFU/mL by using a biological microscope and stored at 4 °C until use.

Preparation of Gxun-6 strain suspensions

Bacterial suspensions were made by suspending Gxun-6 cultured on LB agar plates in 100 mL/250 mL bottles. These were cultured under shaking condition at 30 °C and 200 r/min for 2 days. They were diluted with sterile water to adjust the concentration to 10⁷ CFU/mL. The bacterial cells were collected by centrifuging at 10,000×g for 20 min and re-suspension in sterile water.

Biocontrol effect on Fusarium wilt and promotes the growth of banana seedlings

The pot experiment was conducted with an average temperature of 28 °C and humidity of 70% in a acclimatized greenhouse of Guangxi University for Nationalities, China from February to April 2020. The banana seedlings used in the pot experiment were Brazilian bananas (*Musa acuminata* AAA genotype cv. Cavendish) with 4–5 true leaves (30–50 cm height), and they had a similar size and health. In addition, soil samples were collected from the banana plantation of Nanning, air dried, and

sifted through a 20-mesh sieve. The soil was light gravel soil with texture of sandy loam (70% sand, 15% silt, and 15% clay) (Baset et al. 2010). One plantlet was sown in each pot (diameter 20 cm; height 18.5 cm) containing 3,500 g of soil and 6 pots were set up for each treatment. The treatments for the pot experiment were designed as follows: (1) control (CK) 1: after root injury, 25 mL conidial suspension of FOC TR4 (1 × 10⁵ cfu ml⁻¹) was added into pot. CK2: 25 mL of sterile LB was added into the pot soil. Treatment 1: 25 mL of Gxun-6 strain solution (1 × 10⁷ cfu ml⁻¹), and 25 mL conidial suspension of FOC TR4 were applied at 7 days after root injury. Treatment 2: 25 mL of Gxun-6 strain suspension. Each group was set up with 6 repetitions. Watering was done once every 3 days, and photoperiod condition was 12 h light/12 h dark. The biocontrol effect was evaluated after 60 days of planting by measuring plant height, leaf area, pseudostem girth, and fresh and dry weights (Yang et al. 2021). The disease severity index (DI) was calculated using the formula described by Huang et al. (2012). The disease grade was determined according to the browning degree of the longitudinal section of the banana seedling corm: Grade 0: No browning occurred in the longitudinal section of the corm; Level 1: browning area in longitudinal section of corm ≤ 25%; Level 3: 25% < browning area in longitudinal section of bulb ≤ 50%; Level 5: 50% < browning area in longitudinal section of bulb ≤ 75%; Level 7: browning area of corm longitudinal section > 75% (Chen et al. 2018). Disease index = \sum (condition level × number of diseased plant of this level) / (the highest level of disease × total number of disease); Control effect (%) = (CK disease index – treatment disease index) / CK disease index × 100% (Qin et al. 2020).

Statistical analysis

All experiments were performed in triplicates, and the results were taken as the mean value ± SD. For optimisation experiments, one-way ANOVA test was performed (using SPSS version 21) to calculate significant differences between means compared with control of each experiment at a 95% confidence level.

Results

Screening of siderophore bacteria

On CAS agar plates, siderophore-producing bacteria formed colonies with an orange halo. This occurred, because iron is removed from the original blue CAS-Fe (III) complex during siderophore production. By observing the formation of the halo and its size, 60 siderophore-producing bacteria were screened from the soil. After culture and purification by streaking thrice, 5 bacterial isolates were obtained. When spotted and streaked on the fresh CAS agar plates, they produced bright orange

halo (Fig. 1). The colour reaction was consistent with the liquid detection, which further confirmed that the 5 bacteria can produce siderophores. The SU ranged from 23.42 to 66.43% with 48 h fermentation, indicating that these bacteria had strong siderophore-producing ability. The bacteria of number 6 also significantly inhibited

the mycelial growth of FOC TR4. Antagonistic effects were tested, and the zone of inhibition was 16.7 mm, thereby indicating that the strain had strong antagonistic activity against FOC TR4 (Fig. 2). Therefore, the strain with the largest size of halo, the maximal production of siderophores (SU=56.43%) and the highest antagonistic

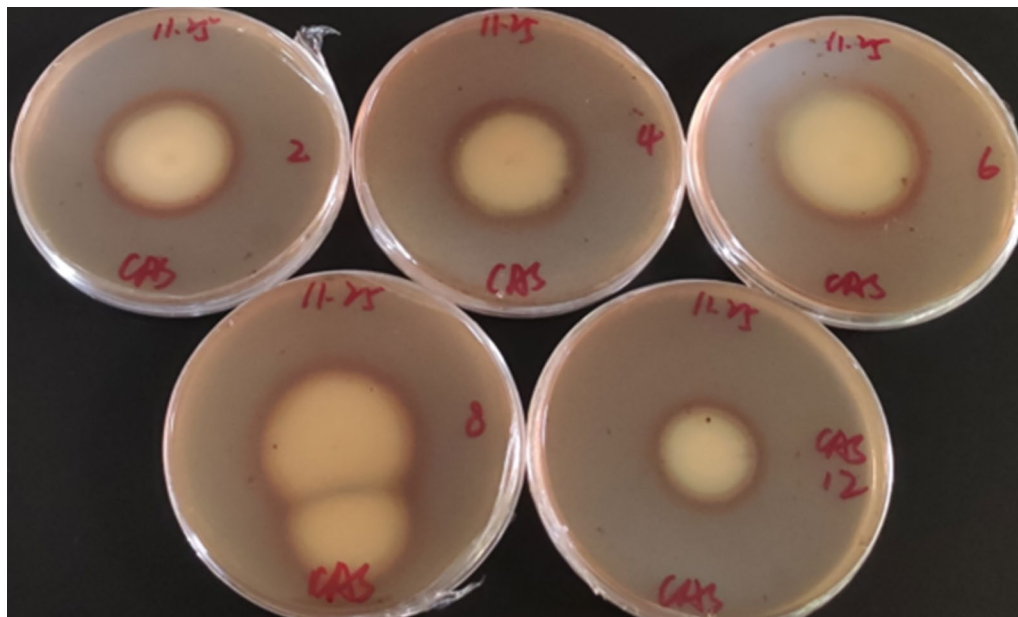


Fig. 1 Primary screening of siderophore strains by CAS plate

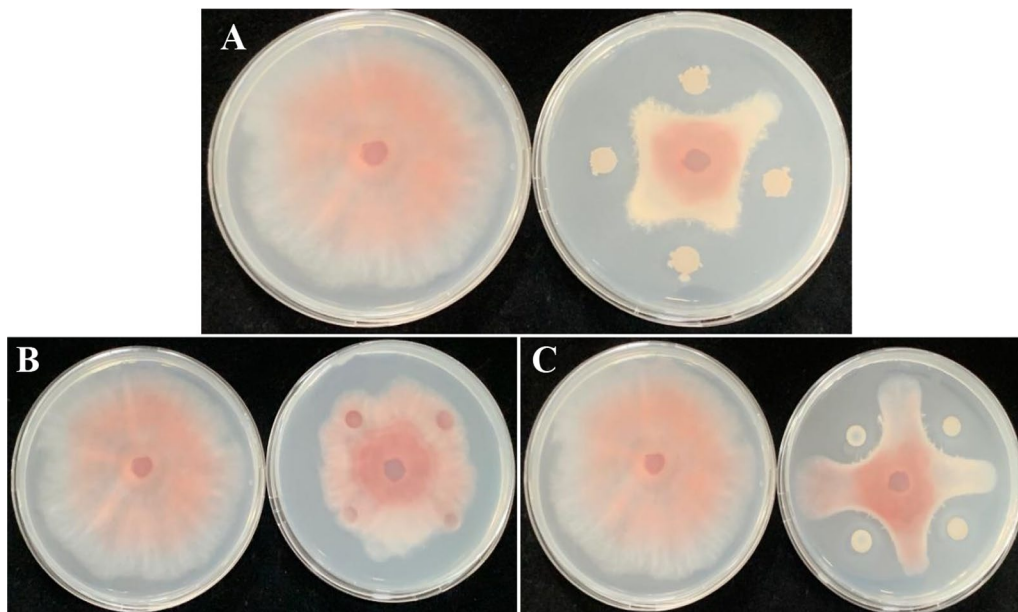


Fig. 2 Antagonistic effects of different strains against *Fusarium oxysporum*. **A** Antagonistic activity of the strain Gxun-6; **B** Antagonistic activity of the strain Gxun-4; **C** Antagonistic activity of the strain Gxun-8

activity, namely, Gxun-6, was selected for the following studies.

Antagonistic activity of strain Gxun-6 against other plant pathogenic fungi

Gxun-6 significantly inhibited the growth of 8 plant pathogens (Fig. 3), and the inhibitory effects on different plant pathogens were shown in Table 1. The antibacterial rates of *B. dothidea*, *F. pseudograminearum*, *C. parasitica* and *F. sacchari* were all above 70%. The antibacterial rate against *C. musae*, *A. alternata*, *C. fructicola* and *F. commune* were in the range 60–70%, which indicated that strain Gxun-6 had a broad-spectrum antifungal activity on other plant pathogenic fungi.

Identification of Gxun-6

Genetic characterization

The 16S rRNA sequence of Gxun-6 was analysed. By PCR amplification and sequencing, the length of the 16S rRNA was confirmed to be 1453 bp. The 16S rRNA nucleotide sequence of Gxun-6 was deposited into the GenBank database under the accession number: OM920894. The 16S rRNA sequence of Gxun-6 was analyzed by EzBio-Cloud server for the identification of subspecies. It shared 99% identity with the 16S rRNA gene sequence of *Bacillus siamense* KCTC13613. A phylogenetic tree was created using the MEGA X software, and the strain Gxun-6 was identified as *B. siamensis* (Fig. 4).

Morphological, physiological and biochemical characterizations

The morphological, physiological and biochemical characteristics of strain Gxun-6 were studied. *B. siamensis* Gxun-6 is a mobile, spore-producing, Gram-positive and salt-tolerant *Bacillus* with a wrinkled surface (Fig. 5). It can grow in the salt concentration range of 0–5.5%. Glucose, fructose and mannose can be used as the only

Table 1 Antifungal activity of strain Gxun-6 against eight plant pathogenic fungi

Target fungal pathogens	Inhibition rate/%
<i>C. musae</i>	61.49 ± 0.05 ^c
<i>B. dothidea</i>	73.81 ± 0.46 ^a
<i>F. pseudograminearum</i>	73.77 ± 1.66 ^a
<i>A. alternata</i>	66.18 ± 1.84 ^{bc}
<i>C. parasitica</i>	78.85 ± 0.27 ^a
<i>C. fructicola</i>	67.59 ± 0.44 ^b
<i>F. sacchari</i>	78.27 ± 17.76 ^a
<i>F. commune</i>	65.91 ± 13.31 ^{bc}

Different lowercase letters in the table show significant differences by Duncan's new complex polarization test ($P < 0.05$)

carbon sources for growth, and no special nutritional requirements are needed. It can grow under aerobic or anaerobic conditions. In addition, strain Gxun-6 could hydrolyse gelatin, lecithin, Tween 80 and casein, but it could not hydrolyse sulphur-containing amino acids and nitrates.

Effects of Gxun-6 strain on the growth and morphology of FOC TR4 hyphae

The hyphal morphology of the pathogen on the Gxun-6 antagonism plate was observed under a light microscope (Fig. 6). The hyphae of the control group were smooth, uniform in thickness and robust in growth. However, the pathogenic hyphae on the antagonistic plate were distorted, grew thicker, had more branches, grew disorderly, became dark and got bent and knotted. Many hyphae showed hyphal rupture. Possibly, the metabolic substances produced by strain Gxun-6 damaged the cell wall of the pathogen and caused the distortion of hyphae (Gong et al. 2015).

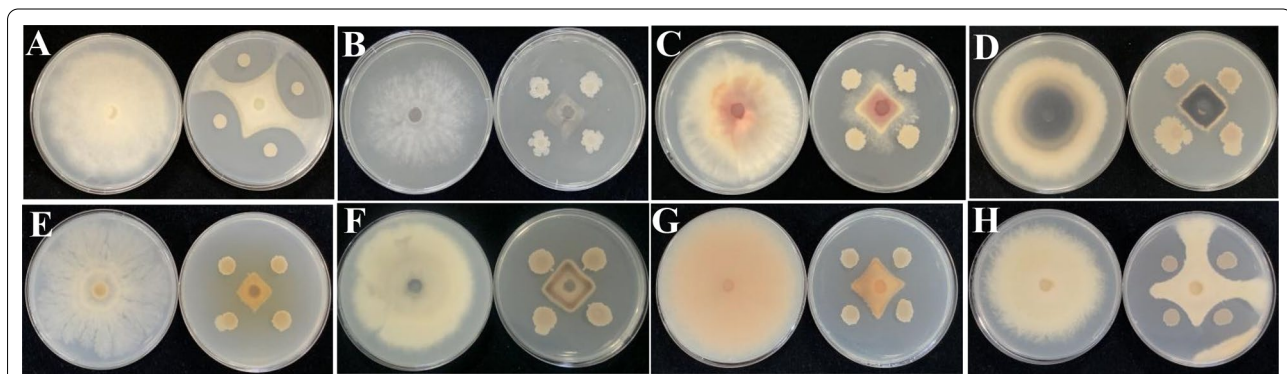
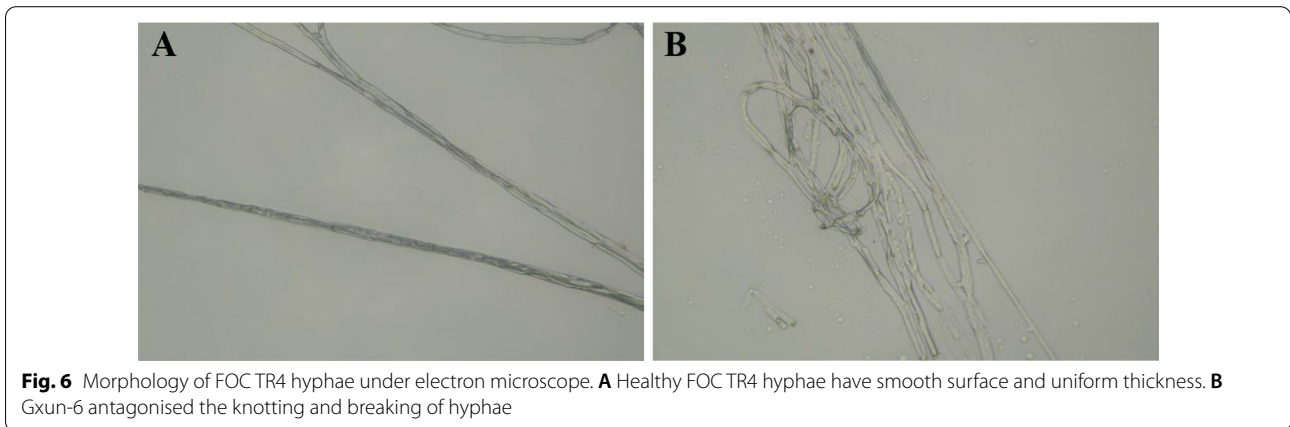
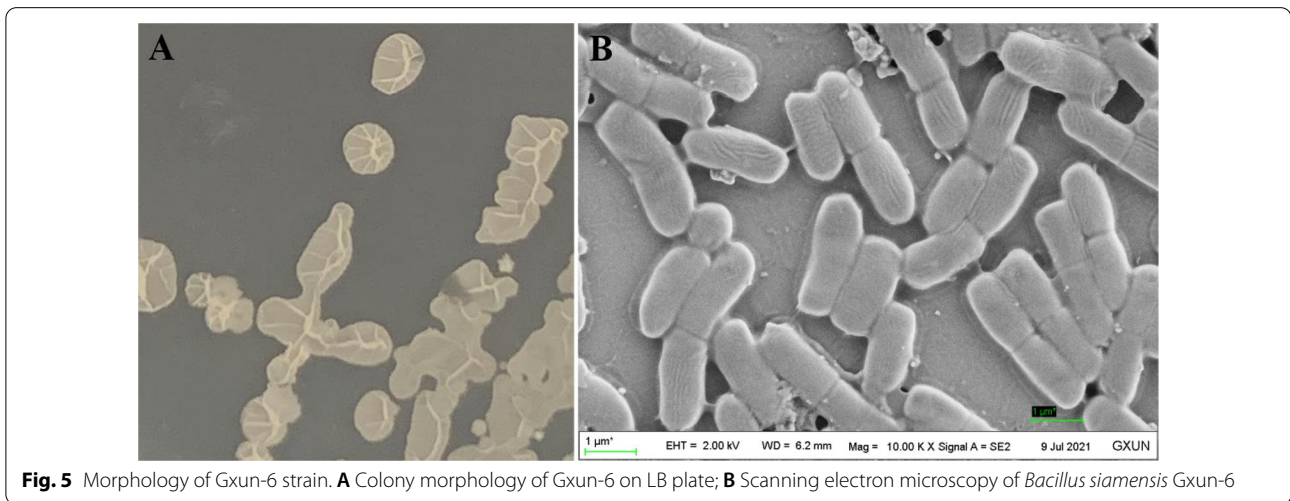
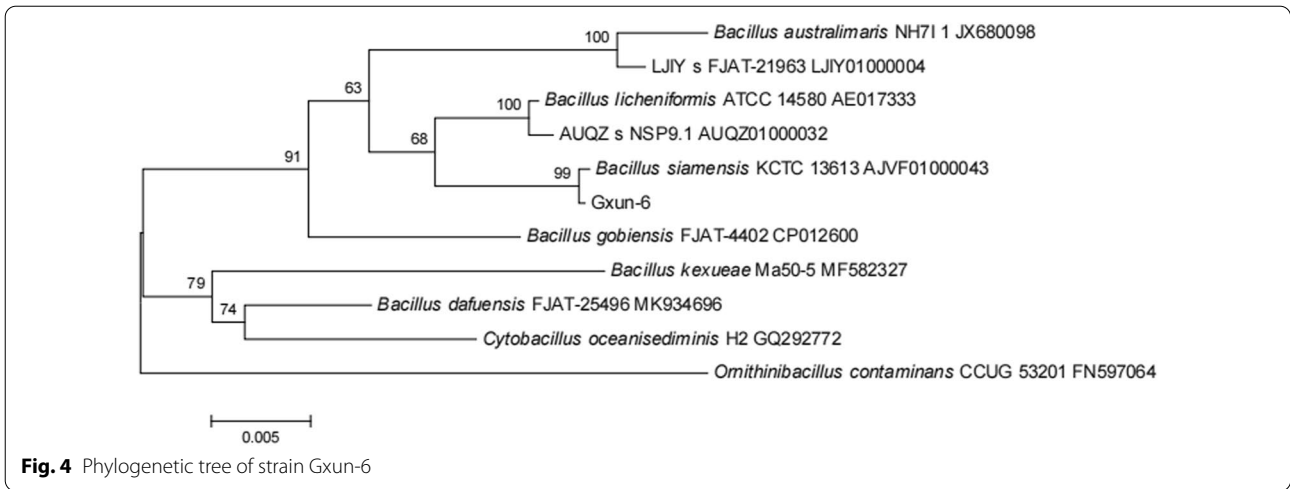


Fig. 3 Antimicrobial effects of Gxun-6 on other plant pathogenic fungi (A–H are the antagonist effects of strain Gxun-6 on *C. musae*, *B. dothidea*, *F. pseudograminearum*, *A. alternata*, *C. parasitica*, *C. fructicola*, *F. sacchari* and *F. commune*)



Growth promotion of banana seedlings in pots

The plant height of banana seedlings treated with Gxun-6 strain for 60 days was remarkably higher than that of the control group ($P < 0.05$). The average plant height and the average fresh weight of the control group were 129.25 cm and 52.12 g, whereas those of the Gxun-6 treatment group were 160.3 cm and 65.34 g, respectively. These results showed a height increase of about 24.02% and a total fresh weight increase of 25.36% ($P < 0.05$) (Fig. 7).

Pot control effect of strain Gxun-6 on banana wilt

Compared with the control (only adding FOC TR4 conidial suspension), the treatment group significantly reduced the incidence of wilt on banana seedling. The side section of banana seedling corm in the control group obviously showed browning (Fig. 8). When *B. siamensis* Gxun-6 was added in front of FOC TR4 conidial suspension, the control effect reached 88.26%, indicating that the application of Gxun-6 could inhibit banana wilt (Fig. 8).

Discussion

Banana wilt is a serious fungal soil-borne disease, and there is currently no effective control method for it (Zhang et al. 2011). Biological control using PGPR, which promotes plant growth, has become one of the urgent spots in recent years (Guo et al. 2004), because of its advantages of safety, effectiveness and durability. Many studies have been reported on the prevention and control of banana wilt by using biocontrol microorganisms (Bubici et al. 2019). Two major classes of *Bacillus* spp. and *Pseudomonas* spp. were found (Panpatte et al. 2016). For example, *Bacillus* LBF-01 increased the germination rate of tomato seeds by 20% and the viability index by 854.03% than in the control group. Under in vivo conditions, LBF-01 treatment significantly increased the total chlorophyll and carotenoid content of leaves by 77.78 and 52.5%, respectively, and inhibited tomato wilt (Chowdhury et al. 2020). Rathore et al. (2020) screened a *P. fluorescens* pf-5 that produces chitinase, cellulase and

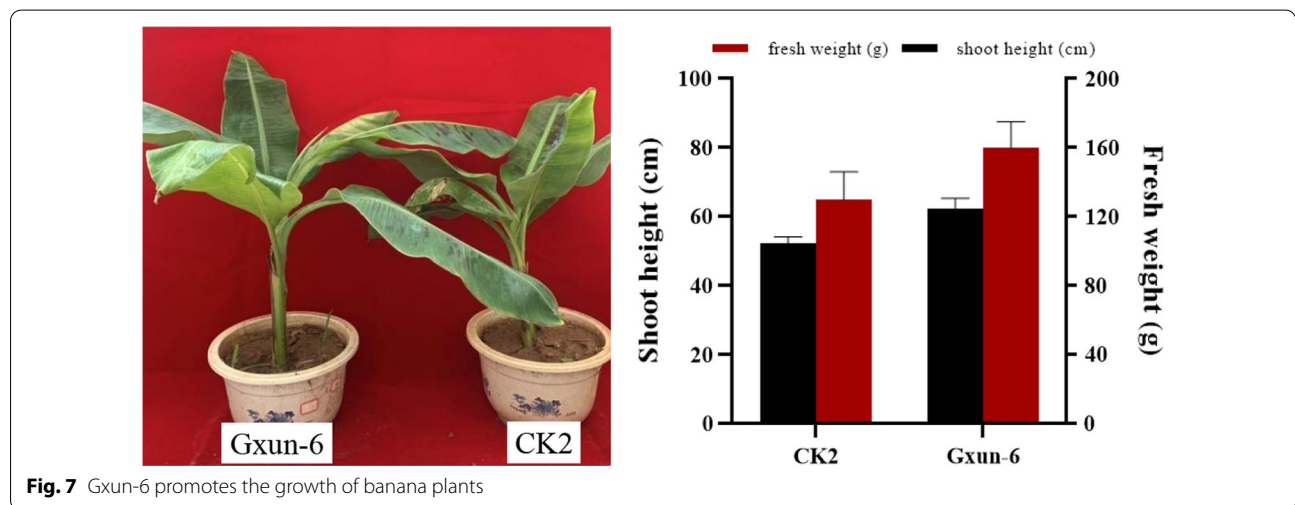


Fig. 7 Gxun-6 promotes the growth of banana plants

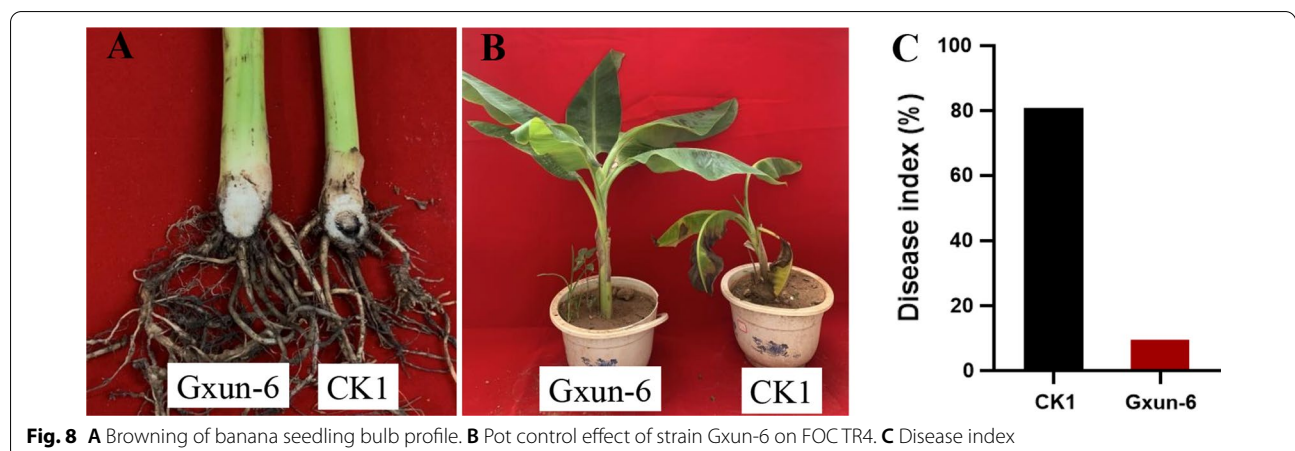


Fig. 8 A Browning of banana seedling bulb profile. B Pot control effect of strain Gxun-6 on FOC TR4. C Disease index

β -1,3-glucanase and conducted an in vitro antagonistic experiment. Results showed that PF-5 could effectively inhibit cumin wilt.

In the present study, 60 siderophore strains were screened out by CAS double-layer plate method, and results confirmed the high efficiency of CAS plate method (Pérez-Miranda, et al. 2007). Siderophore is a small molecular weight (generally < 10 kDa) iron chelate secreted by some microorganisms that have an extremely strong ability to chelate Fe^{3+} under the condition of iron deficiency (Raza and Shen 2010). The siderophore bacteria can compete for the limited iron around the plant rhizosphere through the siderophore (Crowley 2006). Therefore, the pathogenic bacteria cannot absorb enough iron nutrition, and thus, their growth and reproduction are inhibited. This effect reduces the harm to plants and plays a role in biological control (Masalha et al. 2000). At the same time, plants can use the iron chelated by the siderophore produced by microorganisms to improve the iron nutrition of the plants; this has a certain growth-promoting effect on plant growth (Braud et al. 2009). For example, Ghazy and El-Nahrawy (2021) screened 2 strains with high siderophore production by using CAS double-layer plate method. Results proved that hypha growth of corn blight can be effectively inhibited by the strains. In addition, Derbyshire et al. (2018) studied 40 PGPR strains that produced siderophore and significantly inhibited the growth of the pathogenic *F. oxysporum* wilt and tomato bacterial wilt disease.

A siderophore carrier strain Gxun-6, which had the best inhibition effect on FOC TR4 was screened out. Its bacteriostasis rate reached 68.8% in vitro. Therefore, it was used for further research. Based on the morphological characteristics, physiological and biochemical characteristics and phylogenetic tree analysis, Gxun-6 was identified as *B. siamensis*. To study the antagonistic activity of Gxun-6, 8 plant pathogenic fungi were tested for in vitro antagonism. Gxun-6 had strong antagonistic effects on the growth of the 8 plant fungal pathogens, which provided the basis for the control effect in pot experiments. The incidence of banana seedling wilt, banana plant height (cm) and fresh weight (g) were recorded in the pot experiment. The disease incidence of the treated plants was much lower than that of the control. The control effect was 88.26%, which was consistent with the antagonistic result and also consistent with other studies (Torres et al. 2020), indicating that Gxun-6 induced the resistance of banana plants to FOC TR4. In addition, the treatment group showed a significant growth promoting effect. Compared with the control group, the fresh weight and plant height of banana seedlings treated with Gxun-6 significantly increased. This result was consistent with the study of (Wang et al. 2016).

Based on these results, *B. siamensis* Gxun-6 has a great potential for biological control.

Conclusions

The siderophore-producing carrier strain *B. siamensis* Gxun-6 showed a strong ability to promote plant growth, which was verified in the banana plant pot experiment. In addition, Gxun-6 showed spectral antifungal activity in vivo and in vitro. The above result indicated that strain Gxun-6 had a great agricultural production potential.

Abbreviations

FOC TR4: *Fusarium oxysporum* f. sp. *ubense* with the tropical race 4; PGPR: Plant growth-promoting rhizosphere bacteria; CAS: Chrome azurol sulpho-nate; PDA: Potato dextrose agar; PDB: Potato dextrose broth.

Acknowledgements

The authors are thankful to Dr. Gang Fu (Department of Plant Pathology, University of Sargodha) for providing the standard microorganisms

Author contributions

NKS and SYL conceived the idea and designed the study. SYL and YL performed experimentation. YYH and XZH analyzed the data and prepared results. SYL and HYZ wrote the first draft of manuscript. MGJ technically proof-read the manuscript. HYZ and MGJ provided technical and financial assistance for the study. All authors read and approved the final manuscript.

Funding

This research was supported by the Science and Technology Major Project of Guangxi (AA18242026, AB21196019, AB221220020), National Natural Science Foundation of Guangxi Province (2018GXNSFAA28113, 2019GXNSFAA185003), National Natural Science Foundation of China (31660022, 32060020), Guangxi Graduate Education Innovation Plan Project (YCSW2021156), Innovation and Entrepreneurship Training Program for College Students (202010608012, 202110608014), The Scientific Research Project for Introducing High-level Talents of Guangxi University for Nationalities (2018KJQD17) and the Innovation Project of Guangxi Graduate Education (gxun-chxps202078). These funding bodies did not play a role in the design of the study and collection, analysis, and interpretation of data and in writing the manuscript.

Availability of data and materials

All data generated or analyzed in this work are available in the published manuscript.

Declarations

Ethical approval and consent to participate

The ethical approval or individual consent was not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Received: 7 January 2022 Accepted: 3 April 2022

Published online: 12 April 2022

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