A Novel *Streptomyces* sp. Strain PBSH9 for Controlling Potato Common Scab Caused by *Streptomyces galilaeus*

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Abstract

Potato common scab is an important soilborne disease worldwide that can significantly reduce the quality and economic values of potato. The disease is caused by multiple species of *Streptomyces*, which are not well controlled due to lack of effective strategies. *Streptomyces galilaeus* has been recently identified as a dominant species causing potato common scab in Inner Mongolia, China. This study was focused on screening and characterizing antagonists for biological control against pathogenic *S. galilaeus*. Bacterial strain PBSH9 was isolated from a potato tuber. PBSH9 was identified as a *Streptomyces* sp. on the basis of morphological, physiological, and biochemical characteristics, as well as DNA sequence analysis. PBSH9 inhibited *S. galilaeus* with a diameter of inhibitory zone of

19.8 mm on agar plates. The extracellular filtrate of PBSH9 also inhibited *S. galilaeus* growth with a diameter of inhibition zone of 10.0 mm. Furthermore, PBSH9 promoted potato sprouting and emergence. Disease control was up to 81.88% in greenhouse trials, and from 47.64 to 73.97% in 3-year field trials. Among the tested inoculation methods, seed treatment was more effective than soil drenching for PBSH9 application. PBSH9 not only effectively controlled potato common scab but also increased potato growth. Thus, it can be a potential candidate for biocontrol agent.

Keywords: potato, common scab, biological control, *Streptomyces*

Potato common scab is an important soilborne disease which occurs in most potato-growing areas of the world such as Asia (Miyajima et al. 1998; Park et al. 2007; Zhao et al. 2006), North America (Hill and Lazarovits 2005; Liu et al. 1995; Wanner 2007), and Europe (Floresgonzález et al. 2010; Kreuze et al. 1999; Leiminger et al. 2013). This disease mainly affects the surface of the potato tuber, causing cosmetic necrosis around the infection point. It appears as a plain spot (convex or concave lesion) on the potato tuber. Although the disease usually does not reduce yields of potato, it significantly degrades the quality of the tuber and market competitiveness (Hiltunen et al. 2006; King et al. 1991). In rare and severe cases, the infection delays potato emergence and occasionally reduces yield (Hiltunen et al. 2005). Potato common scab has become an urgent problem in China. For example, the incidence has been reported to reach up to 30 to 60% in northern China (Bai et al. 2002), with disease incidence of 50% in commercial potato fields in Yiwu City (Zhang and Du 2010) and averaging 38% in 11 counties of Inner Mongolia (Zhang et al. 2013).

Potato common scab is caused by multiple *Streptomyces* spp. (Xing et al. 2016), among which *Streptomyces scabies*, *S. acidiscabies*, and *S. turgidiscabies* are widely distributed; however, other pathogenic species have also been reported (Hao et al. 2009; Wanner 2007). In China, the pathogens are diverse depending on geographic locations (Yang et al. 2018; Zhang et al. 2009); and new pathogenic species such as *S. bobili* (Zhang et al. 2009) and *S. galilaeus* (Guo et al. 2014) have been added to the list. In Inner Mongolia,

S. galilaeus is the predominant species causing common scab of potato (Zhang et al. 2009; Zhao et al. 2006).

Potato common scab is difficult to control. At present, available methods in potato production include using resistant varieties (Jansky et al. 2018; Haynes et al. 2010), cultural practices (Brown and Morra 1997; Lapwood et al. 1973), chemicals (Hosny et al. 2014; McIntosh 1973), and biological control (Liu et al. 1995; Meng et al. 2013; Sarwar et al. 2019; Singhai et al. 2011). However, these methods still need to be improved for better and consistent control efficacies. The resistance to common scab is not a single-gene-controlled attribute; thus, it is difficult to obtain from current germplasm (Wharton et al. 2012). Cultural practices can only be partially effective depending on the year and location (Lapwood et al. 1973). For controlling the Gram-positive bacteria, few antibiotic products can be applied in the field because of concerns of antibiotic resistance and environmental pollution (Lin et al. 2018). Biocontrol measures have a great potential in the control of common scab. A promising biocontrol product could take the place of chemical agents due to its environmentally friendly characteristics and high efficacy (Chen et al. 2017; Sarwar et al. 2019).

A number of biocontrol agents have been studied and applied for the control of potato common scab. For example, *Trichoderma asperellum* (Koyama et al. 2007), *T. harzianum* (Wang et al. 2019), *Bacillus velezensis* (formerly *B. amyloliquefaciens*) (Lin et al. 2018; Meng et al. 2013), *B. subtilis* (Wang et al. 2019), *Pseudomonas* spp. (Singhai et al. 2011), and *Brevibacillus laterosporus* (Chen et al. 2017) were found to control potato common scab. It is common to use nonpathogenic and antagonistic *Streptomyces* spp. for controlling potato common scab. For example, Neeno-Eckwall et al. (2001) used *S. diastatochromogenes* and nonpathogenic *S. scabies* PonR in the field to control *S. scabies*; Hiltunen et al. (2009) used *Streptomyces* sp. 346 (unknown species) and *S. griseoviridis* K61 to control *S. turgidiscabies*; Agbessi et al. (2003) used *S. melanosporofaciens*; and Liu et al. (2000) used *Streptomyces* spp. for common scab control.

There are some advantages to using *Streptomyces* spp. as biocontrol agents. The bacteria can produce a variety of active substances such as antibiotics and phytohormones, which play an important role in improving the disease resistance and stress resistance of plants, and their metabolites have the potential to work as biological

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pesticides. In addition, both antagonistic and pathogenic *Streptomyces* spp. share similar environmental adaptation; therefore, the application of a biocontrol agent could succeed where the pathogen is prevalent. At present, most of the experiments using *Streptomyces* spp. for common scab control are only carried out in laboratory or greenhouse conditions (Chen et al. 2017; Neeno-Eckwall et al. 2001; Sarwar et al. 2019). For the limited cases of field trials, most of the results are not consistent and stable. In other words, highly effective pathogen inhibition demonstrated in the laboratory does not always transfer to promising field effects (Hiltunen et al. 2009). In this study, we started from isolating novel antagonists, characterized the best-performing strain PBSH9 of *Streptomyces* sp., and demonstrated its effects in both greenhouse and field in controlling potato common scab.

Materials and Methods

Test materials. Soil samples were taken from the field where potato common scab occurred in Hulunbeier, Wulanchabu, and Hohhot of Inner Mongolia, and diseased potato tubers were also collected from Hohhot. Cultures of potato pathogens, including *S. galilaeus* PS1, *Fusarium oxysporum*, *Verticillium dahliae*, *Pectobacterium atrosepticum*, and *Rhizoctonia solani* AG-3, were previously obtained by the Plant Pathology Laboratory of Inner Mongolia Agricultural University. Potato cultivar Atlantic was used throughout the study.

Isolation and screening of antagonistic *Streptomyces* spp. Antagonistic *Streptomyces* spp. were isolated using a dilution plating method (Hiltunen et al. 2005). Briefly, potato tubers with symptoms of common scab were selected, and the tissues with necrotic lesions were peeled off, ground, and shaken in water for 10 min. This ground tissue or suspension was considered to be the original concentration, which was further diluted by adding sterile water to concentrations of 1×10^{-5} , 1×10^{-6} , and 1×10^{-7} . An aliquot of 100 μ l of each dilution was plated onto an oatmeal agar (OMA) plate with two replicates. The plates were incubated at 28°C until bacterial colonies appeared. Single colonies with typical *Streptomyces* spp. based on morphological characteristics were picked and purified on OMA plates. The *Streptomyces* spp. isolates were transferred to the OMA slants and stored at 4°C for later tests.

The pathogenic *S. galilaeus* strain PS1 and other test isolates for potential antagonists were grown for 10 days on OMA plates; then, the culture was scrapped and diluted into 10^7 CFU/ml with sterile water. On an OMA plate, the suspensions of test isolates and *S. galilaeus* PS1 were streaked perpendicularly over the antagonistic bacterium and incubated at 28°C for 10 days. The growth of *S. galilaeus* PS1 was examined. A clear zone where no PS1 grew indicated an inhibitory effect from the test isolate. Those test isolates showing antibiosis were picked as candidate biocontrol agents, transferred to OMA slants, and stored in a refrigerator at 4°C.

Identification of antagonistic strain PBSH9. Strain PBSH9 was confirmed as a strong antagonist against *S. galilaeus* in a pilot trial. PBSH9 was then cultured on a series of identification media for *Streptomyces* designated by the International *Streptomyces* Project as ISP1, ISP2, ISP3, ISP4, ISP5, ISP6, and ISP7 (Shirling and Gottlieb 1966) at 28°C, and its growth was examined on the fifth day of incubation. Morphological characteristics were observed, including colony color, formation of aerial hyphae, and the presence of soluble pigments. Specific morphologies such as spore silk and spores were photographed using an optical microscope and a scanning electron microscope. For characterizing the physiology and biochemistry of PBSH9, methods of Berger's Bacterial Identification Manual (Buchanan and Gibbons 1984) and the *Streptomyces* Identification Manual (Yan 1975) were employed. Utilization of carbon and nitrogen; production of melanin and H_2S ; and cellulose decomposition, starch hydrolysis, and gelatin liquefaction were measured.

Genomic DNA was extracted using the TIANamp Bacteria DNA Kit (Tiangen Biotech Co., Ltd., Beijing, China). PCR was conducted using the extracted DNA as a template. The primer pair required for

PCR was PrimeF: 5'-CATTACGGAGAGTTTGATCC-3' and PrimeR: 5'-AGAAAGGAGGTGATCCAGCC-3' (Hao et al. 2009), which targeted the 16S ribosomal RNA (rRNA) gene. In addition, genes including *atpD*, *rpoB*, and *recA* were amplified in the PCR assay, with primer pairs atpDF: 5'-ACCAAGGGCAAGGTGTTCAA-3', atpDR: 5'-GCCGGGTAGATGCCCTTCTC-3', rpoBF1: 5'-TTCATGGACCAGAACAACC-3', rpoBR1: 5'-CGTAGTTGTGACCTCCC-3', recAF: 5'-ACAGATTGAACGGCAATTCG-3', and recAR: 5'-ACCTTGTTCTTGACCACCTT-3' (Guo et al. 2008). The PCR mixture (total volume 50 μ l) included 34 μ l of double-distilled H_2O , 5 μ l of 10 $\times$ PCR buffer, 4 μ l of dNTPS (2.5 mmol/liter), 2 μ l of PrimeF (10 pmol/ μ l), 2 μ l of PrimeR (10 pmol/ μ l), 1 μ l of DNA template (80 ng/ μ l), and 0.5 μ l of Taq DNA polymerase (5 U/ μ l). The setting of the thermal cycler was predenaturation at 94°C for 5 min, followed by 30 cycles of 94°C for 1 min; annealing temperatures of 56°C (16S rRNA), 57°C (*atpD*), 65°C (*rpoB*), or 48°C (*recA*) for 1 min; and 72°C for 1 min. A final reaction at 72°C was applied for 10 min. PCR products (amplicons) of the target gene segment were detected by electrophoresis on a 1% agarose gel. PCR products were purified using a Gel Extraction Kit (Omega Bio-Tek Co., Ltd., Guangzhou, China). The sequences of the amplicons were obtained by direct Sanger sequencing (Sangon Biotech Co., Ltd., Beijing, China) and deposited into GenBank under the accession numbers MN822703 (16S rRNA), MT035954 (*atpD*), MT035955 (*rpoB*), and MT035956 (*recA*).

DNA sequences of PBSH9 were analyzed against the GenBank nucleic acid database using the BLAST algorithm, which resulted in the selection of 10 strains having the highest homology with PBSH9. Sequences were aligned using the MEGA7.0.21 program (MEGA International, New York, NY, U.S.A.). A new sequence of a pattern strain was assembled by concatenating the sequence segments of the genes 16S rRNA, *atpD*, *rpoB*, and *recA* (Supplementary Table S2) using an online tool (http://www.novopro.cn/tools/combine_fasta.html). The sequence order of concatenation was 16S rRNA, *atpD*, *rpoB*, and *recA*. For each pattern strain, the 16S rRNA gene segment started with GCTTA and ends with GAGC nucleotides of a segment of 1,402 (± 1) bp. Similarly, the starting and ending nucleotide sequences were GGCCT and GCTC of a 496 (± 1)-bp segment for *atpD*, GGCCC and GTAC of a 540 (± 1)-bp segment for *rpoB*, and GACGT and GCTG of a 504 (± 1)-bp segment for *recA*. A phylogenetic tree (an unrooted tree and all branch lengths) was constructed based on the four-gene-concatenated sequence using ClustalW with the neighbor-joining method (Saitou and Nei 1987).

Antagonistic activity of strain PBSH9. The pathogen *S. galilaeus* PS1 was cultured on OMA plates. After incubation at 28°C for 10 days, 10 ml of sterile water was poured into the plate, and bacterial spores were scraped from the culture. The collected spore suspension was diluted to 10^7 CFU/ml with sterile water, which was adjusted based on the measurement of chromatographic data. The suspension was spread onto an OMA plate with an L-shaped glass rod. Meanwhile, a cultural plug (5 mm in diameter) of 10-day-old *Streptomyces* strain PBSH9 was made with a cork borer and placed on the center of an OMA plate loaded with *S. galilaeus*. Each strain had three replicates, and an OMA plug (without bacteria) was used as a control. The plate was incubated at 28°C for 5 days, and the zone of inhibition against *S. galilaeus* PS1 was estimated by averaging two diameters measured perpendicularly.

Antagonistic activity of PBSH9 filtrate. *Streptomyces* sp. strain PBSH9 was cultured in inorganic salt starch at 28°C for 5 days, and the cells were filtered off through a 0.22- μ m filter to obtain a filtrate. An aliquot of 100 μ l of *S. galilaeus* PS1 suspension (10^7 CFU/ml) was spread on an OMA plate. Immediately, an Oxford cup was placed on the center of the PS1-containing plate, and 0.5 ml of PBSH9 filtrate was added into the cup. After 5 days of incubation, the size of inhibition zone surrounding the cut was measured.

Inhibition spectrum of *Streptomyces* sp. strain PBSH9. For testing the response of fungal pathogens to *Streptomyces* sp. strain PBSH9, a 5-mm fungal plug of either *F. oxysporum*, *V. dahliae*, or *R. solani* AG-3 was transferred on the center of a potato dextrose agar plate. Four PBSH9 plugs (5 mm in diameter) were cut from a freshly

growing culture using a cork borer and placed on four corners of the plate with a fungal culture. Colony size was observed daily for the test fungal culture. For testing the response of *P. atrosepticum* to PBSH9, the bacterial culture was diluted into 10^7 CFU/ml, 80 μ l of the bacterial suspension was spread onto a Luria-Bertani agar plate, and a cultural plug (5 mm in diameter) of *Streptomyces* sp. strain PBSH9 was placed at the center of the plate containing *P. atrosepticum*, which were incubated at 28°C. If a zone of inhibition was observed, the diameter was determined and the growth inhibition rate was calculated.

Effect of PBSH9 on the sprouting of potato tubers. Ten-day-old PBSH9 culture was diluted into a 10^7 CFU/ml suspension with sterile water, and 1 ml of the suspension was transferred into a 250-ml flask containing 100 ml of inorganic salt starch. The flask was incubated for 5 days at 28°C on an incubator shaker at 200 rpm. The bacterium was diluted with sterile water to a concentration of 10^7 CFU/ml. Tubers of Atlantic potato were placed in a pot (2,800 cm³) filled with vermiculite, with 15 tubers/pot, and 500 ml of PBSH9 suspension was added. Sterile water (500 ml) was used as a control. Each treatment had three pots as replicates. After 10 days of incubation, the tubers were removed from the pot, and tuber sprouting, bud length, fresh bud weight, and dry weight of shoots were measured.

Effects of PBSH9 in controlling common scab of potato in greenhouse. *Tuber inoculation with PBSH9.* The experiment was carried out in 2017 in a greenhouse at Inner Mongolia Agricultural University. Both *S. galilaeus* PS1 and *Streptomyces* sp. strain PBSH9 were grown on OMA plates for 10 days at 28°C. After incubation, the culture was ground using a blender and diluted with sterile water to a concentration of 10^7 CFU/ml. Pots with an opening 20 cm in diameter and 15 cm in height were filled with sterilized vermiculite and potting soil mixed at a 1:1 ratio, with 50 ml of PS1 inoculum added. Tubers of Atlantic potato of approximately the

same size were immersed in either PBSH9 suspension or streptomycin sulfate at 0.36 mg/ml for 10 min, then sown in the pot. Water (50 ml) was used as a control (CK1). An additional control consisted of no PS1 inoculation and no tuber treatment (CK2). In total, six treatments with seven replications (pots) were established, and each pot had three plants.

Potato tubers were harvested 120 days after planting, and disease was evaluated on tubers. Disease severity was grouped at the following levels: 0 = no symptoms and 1 = lesion accounting for 1 to 5, 2 = 6 to 25, 3 = 26 to 50, 4 = 51 to 75, and 5 = over 75% of total tuber surface. Incidence of potato common scab was calculated as the number of diseased tubers divided by the total evaluated number of tubers $\times$ 100%. Disease index (DI) = $100 \times \sum(N_i)/\text{total number of evaluated tubers} \times 5$, where i is disease level (from 0 to 5) and N is the number of diseased tuber at level i . Control effects (%) = $100 \times [(\text{DI in control plot} - \text{DI in treated plot})/\text{DI in control plot}]$.

Soil drenching with PBSH9. The experiment was carried out in 2017 in the same greenhouse as the tuber inoculation experiment. Both PS1 and PBSH9 were prepared as described above. PS1 inoculum was added into pots as described above, followed by adding 50 ml of either PBSH9 suspension or agricultural streptomycin at 0.36 mg/ml in each pot. Water (50 ml) was used as a control (CK1). An additional control consisted of no PS1 inoculation and no tuber treatment (CK2). In total, six treatments with seven replications (pots) were established, with each pot having three plants. Tuber seed of Atlantic potato was sown into the treated pots. All pots were placed outdoors and watered as necessary. Disease of potato tubers was evaluated at harvest as described above. Potato was harvested 120 days after planting, and disease was evaluated on tubers as described above.

Effects of PBSH9 in controlling common scab of potato in field. Field trials were conducted at three locations in 3 years, including Inner Mongolia Agricultural University in Hohhot in 2015; Chahar Right Wing County, Inner Mongolia in 2016; and Siziwang County, Inner Mongolia in 2017. The accumulated precipitation from April to October in Chahar was 388 mm in 2016, which is higher than Hohhot (around 300 mm in 2015) and Siziwang (around 240 mm in 2015). The average air temperature from April to October was 11.8°C in Chahar in 2016, 16°C in Hohhot in 2015, and 15°C in Siziwang in 2017. Except for rapidly available potassium, the fertility of the three locations was similar, with all possessing alkaline soil (Supplementary Tables S1 and S2).

Bacterial inoculum was prepared as described in the greenhouse trial. Prior to planting, a furrow was opened, and 50 ml of the pathogen PS1 suspension (10^7 CFU/ml) was applied to soil at the point of seeding. The trial was conducted using both tuber and soil treatments. For tuber treatment, potato seed pieces were immersed in either

Table 1. Cultural characteristics of *Streptomyces* sp. strain PBSH9 on different media

ISP medium	Growth ^z	Substrate mycelium color	Aerial mycelium color	Soluble pigment
1	+++	White	White	None
2	+++	White	White	None
3	++	White	White	None
4	+	White	White	None
5	+++	White	White	None
6	+++	White	White	None
7	+++	White	White	None

^z Symbols +++, ++, and + indicate heavy, moderate, and scant growth, respectively.

Fig. 1. Colony morphology of *Streptomyces* sp. strain PBSH9 on **A**, ISP1, ISP2, ISP3, ISP4, ISP5, ISP6, and ISP7 plates; and **B** and **C**, oat agar plates growing for 5 days at 28°C.

PBSH9 suspension (10^7 CFU/ml) or agricultural streptomycin at 0.36 mg/ml. Water was used for a control. After soil infestation, treated tuber pieces were seeded in the furrow, followed by covering the furrow. For soil-drenching treatment, either PBSH9 spore suspension or streptomycin at 0.36 mg/ml was applied at 50 ml per seeding site. Water was used as a control.

The plots were arranged as a randomized complete block design, with four replications per treatment. Twenty seed pieces were used in each plot. Plant spacing was 0.3 m and row spacing was 0.9 m. The experimental field was managed according to local practices. Plant emergence was observed and recorded 50 days after planting. Plant vigor was measured by the numbers from 0 to 5, with 0 indicating no emergence and 5 being the best growth vigor. Potato tubers were harvested after a 120-day period, tubers were examined for disease severity, and yield was measured. Potato weight per plant = total weight of harvested plants/number of harvested plants. Yield increase (%) = [yield of treated plot – yield of control plot]/yield of control plot] $\times$ 100%.

Data analysis. Statistical analysis was performed using SPSS software (IBM SPSS Statistics, version 20; International Business Machines Corporation, New York, NY, U.S.A.). Data were collected in triplicates and subjected to one-way analysis of variance. Means were separated by Tukey's multiple range test at a significance level of $P < 0.05$.

RESULTS

Isolation and screening of antagonistic *Streptomyces*. For bacterial isolation and screening, 44 actinomycetes were isolated from potato tubers. Among them, one actinomycete strain, PBSH9, had

displayed the biggest inhibition zone against potato common scab pathogen *S. galilaeus* PS1; therefore, PBSH9 was selected and used for this study.

Identification of PBSH9. Because strain PBSH9 had the most effective inhibitory effect against *S. galilaeus*, it was further examined for its biological characteristics and identification. The growth of strain PBSH9 on seven ISP plates was examined (Table 1; Fig. 1A). The hyphae and the aerial hyphae were white, and no soluble pigment was observed. Spore heap was white. Spores were cylindrical or nearly circular, and the surface of the spores, which were derived from broken hyphae, was smooth (Fig. 2A). Spore sizes were 0.8 to 1.2 μ m by 0.5 to 0.8 μ m. The spore chain was

Table 2. Physiological and biochemical assays of *Streptomyces* sp. strain PBSH9

Measurement items	Reaction or result ^z
D-galactose	+
D-xylose	–
D-mannitol	+
D-glucose	+
Sucrose	+
D-sorbitol	–
D-fructose	–
Maltose	+
Raffinose	–
L-rhamnose	–
L-arabinose	–
I-inositol	–
Gelatin liquefaction	+
H ₂ S generation	–
Starch hydrolysis	+
Cellulose utilization	+
Melanin production	–
Sodium nitrate	+
Ammonium sulfate	+
Potassium nitrate	+
L-methionine	+
L-hydroxyproline	+
Histidine	+

^z Symbols + and – indicate positive and negative reactions, respectively.

Fig. 2. Mycelial morphology of *Streptomyces* sp. strain PBSH9 observed under a scanning electron microscope at magnification **A**, $\times$ 4,000 and **B**, $\times$ 3,000.

Fig. 3. Phylogenetic tree of *Streptomyces* sp. strain PBSH9 established with select *Streptomyces* spp. based on concatenated sequences of 16S ribosomal RNA, *atpD*, *rpoB*, and *recA* genes (see Materials and Methods for details). Bootstrap values were obtained with 1,000 replications. Confidence values of tree nodes are shown as percentage of same tree generated. The length of the branches reflects sequence divergence (percentage of base changes). The phylogenetic tree was constructed by the neighbor-joining method.

straight-flexible, with individual spirals, and branched (Fig. 2B). Therefore, PBSH9 had typical morphologies of *Streptomyces* spp. (Fig. 1B and 1C).

PBSH9 utilized D-galactose, D-mannose, D-glucose, sucrose, and maltose as the sole carbon source but could not utilize D-xylose, D-sorbitol, D-fructose, raffinose, L-rhamnose, i-inositol, and L-arabinose. The strain might utilize potassium nitrate, ammonium sulfate, sodium nitrate, L-methionine, L-hydroxyproline, and histidine as the sole nitrogen source. The strain could also hydrolyze starch and, by using cellulose to grow, gelatin can be liquefied without producing melanin and H₂S (Buchanan and Gibbons 1984). Thus, PBSH9 belonged to the white spore group of the genus *Streptomyces* (Table 2). In this study, 16S rRNA, *atpD*, *rpoB*, and *recA* genes were amplified, and each gene was compared individually without identifying the specific species of strain PBSH9. However, we spliced the four genes together for phylogenetic analysis again and also without identifying the specific classification status of strain PBSH9 (Fig. 3). Therefore, strain PBSH9 was temporarily identified as a novel *Streptomyces* sp.

Antagonistic activities of PBSH9 culture and filtrate. *Streptomyces* sp. strain PBSH9 was examined for its antagonistic effect against *S. galilaeus* by testing its cells and extracellular compounds. Both culture and filtrate of PBSH9 showed inhibition of the growth of *S. galilaeus*. In a coculture test, the average diameter of the inhibition zone was 19.83 mm (Fig. 4A). In the filtrate test, the average diameter of the transparent circle was 10 mm (Fig. 4B). The antibacterial effect of strain PBSH9 varied against select common diseases of potato (Table 3). PBSH9 did not inhibit *Fusarium*, *Pectobacterium*, and *Rhizoctonia* spp. but it significantly inhibited *V. dahliae* (Fig. 4C).

Effect of strain PBSH9 on potato growth and common scab in pot. After *S. galilaeus*-inoculated seed pieces were treated with PBSH9, potato growth and common scab were examined. Seed tubers had 100% sprouting. The length of seed bud with PBSH9 treatment was significantly higher than the control (Table 4; Fig. 5). Fresh and dry weights of potato shoots were also significantly higher than the control. When seed tubers were treated with PBSH9, the incidence and DI of common scab were the lowest compared with streptomycin treatments. In the soil drenching trial, PBSH9 had a control effect of 81.88%, which was significantly higher than other treatments. There was no significant difference in the control effect of the PBSH9 by application methods between using seed soaking and soil drenching (Table 5).

Effect of strain PBSH9 on potato common scab in field conditions. The three locations used for field trials had similar soil properties. Soil at Hohhot contained organic matter at 18.7 g/kg,

hydrolysis nitrogen at 75 mg/kg, 24.5 mg of available phosphorus, rapidly available potassium at 118 mg/kg, and pH = 8.3. Soil at Chahar contained organic matter at 18.5 g/kg, hydrolysis nitrogen at 74 mg/kg, 23 mg of available phosphorus, rapidly available potassium at 116 mg/kg, and pH = 7.4. Soil at Siziwang contained organic matter at 19.8 g/kg, hydrolysis nitrogen at 82 mg/kg, 20 mg of available phosphorus, rapidly available potassium at 212 mg/kg, and pH = 8.5. There were significant variations of weather conditions at the three locations (Supplementary Table S1). Multiyear and multilocation field trials were conducted to determine the effect of PBSH9 on the control of common scab of potato. Disease severity was consistently reduced throughout all field trials (Tables 6 and 7). Seed tuber treatment with PBSH9 significantly reduced common scab, and the control effect ranged from 59.50 to 73.97%, which was higher than the effect of streptomycin treatment. PBSH9-treated potato had the highest yield of 47,554.35 kg/ha, and the yield increased between 9.70 and 15.93%. PBSH9 applied via soil drenching also significantly reduced common scab, and the control effect ranged from 47.64 to 73.97%, which was higher than the effect of streptomycin treatment in 2 of the 3 years. In addition, PBSH9 promoted plant emergence in 2 of the 3 years (Table 7).

Discussion

We have isolated *Streptomyces* sp. strain PBSH9 and examined its biological and antimicrobial characteristics as a potential biocontrol agent applied in China's potato production. PBSH9 significantly suppressed potato common scab, with its performance better than the commercial product streptomycin. It also promoted emergence and increased yield of potato. In terms of application method, direct tuber treatment was more effective than soil drenching. Therefore, PBSH9 has a great potential for commercialization in the control of potato common scab.

Table 3. Effect of *Streptomyces* sp. strain PBSH9 on the growth of four potato pathogens

Pathogen	Inhibition $\pm$ SD (%) ^z
<i>Fusarium oxysporum</i>	0
<i>Verticillium dahliae</i>	79.07 $\pm$ 1.75
<i>Pectobacterium atrosepticum</i>	0
<i>Rhizoctonia solani</i> AG-3	0

^z Values represent the means $\pm$ standard deviation (SD) of three biological replicates.

Fig. 4. Effects of **A**, culture and **B**, filtrate of *Streptomyces* sp. strain PBSH9 (10^7 CFU/ml) on the growth of *Streptomyces galilaeus* PS1 on the 5th day of incubation; and **C**, culture of PBSH9 (10^7 CFU/ml) on the growth of *Verticillium dahliae* on the 15th day of incubation on potato dextrose agar plates.

There was a pitfall on the results: we only tested the antagonistic activity of *Streptomyces* sp. strain PBSH9 on one pathogen species, which was *S. galilaeus*. It was reasonable to use *S. galilaeus* as a tester, because this pathogen is the predominant species causing common scab of potato in the region where the field trials were conducted (Guo et al. 2014). It would be advantageous if multiple species of pathogen had been examined if we wanted to use strain PBSH9 as a generic biocontrol agent for managing potato common scab in a broader area. However, we anticipate that this strain should work against most of the major *Streptomyces* spp. causing common scab because the pathogens have similar biological characteristics in response to strain PBSH9. This is supported by other researchers (Meng et al. 2012), in which the LCI protein (the active compound responsible for antagonisms) inhibits all five test species of *Streptomyces* causing common scab. Therefore, we are optimistic about the spectrum of inhibition. Because our work is being continued, future results will provide a solid evidence of this issue.

There are many reports on biological control of potato common scab, and different organisms have been used in greenhouse or field conditions (Chen et al. 2017; Koyama et al. 2007; Meng et al. 2013; Wang et al. 2019), including *Streptomyces* spp. (Hiltunen et al. 2017; Liu et al. 2000; Sarwar et al. 2018; Wanner et al. 2013). Our work has added a novel strain to the list. The control effect of PBSH9 was up to 81.88% in potting soil and up to 73.97% in 3-year field trials. In addition, yield increase was up to 15.93%.

In this study, the *16S* rRNA, *atpD*, *rpoB*, and *recA* genes of strain PBSH9 were amplified, and the phylogenetic analysis did not determine the specific classification status of strain PBSH9, which was temporarily defined as a novel *Streptomyces* sp. Due to the complexity of the genome, we were not able to confirm the taxonomic position of PBSH9. The whole-genome sequence is being currently analyzed with the hope to determine the taxonomy of PBSH9.

Using *Streptomyces* spp. as a biocontrol agent may have advantages over other organisms. *Streptomyces* spp. are more adaptive in soil because they are a good soil inhabitant and survive better where pathogenic *Streptomyces* spp. exist. The mechanisms of disease control are mainly contributed by its metabolites such as antibiotics, enzymes, and hormones. Antagonistic *Streptomyces* spp. produce the hormone indole-3-acetic acid for promoting potato growth (Sarwar et al. 2018). *S. anulatus* induces resistance and enhances defense-related enzymatic activities in plants (Couillerot et al. 2013). Metabolites of *S. anulatus* are mainly unsaturated fatty acids, saturated fatty acids, fatty acid esters, alkanes, alkenes, and triterpenes (El-Naggar et al. 2017). In this study, we found that PBSH9 promoted potato seed sprouting and improved the control of common scab as well as the growth vigor of potato plants. The metabolites of PBSH9 also inhibited the common scab pathogen but the active components of its metabolites are yet to be determined. Therefore, further investigation is needed to determine whether PBSH9 produces auxin, gibberellin, and cytokinin, and whether it enhances the internal defense enzyme activity of potato plants.

The efficacy of biological control may be affected by the method of product delivery. For example, vermiculite as a carrier can sustain the liability of antagonistic *Streptomyces* spp. and enhance the efficacy of disease control (Liu et al. 2000). In the field trial of this study, the application of the antagonistic strain PBSH9 with the tuber treatment was superior over the application of soil drenching. In addition to disease control efficacy, tuber treatment also reduced the cost of application. Thus, PBSH9 can be further studied as a biocontrol agent for commercialization.

Development of potato common scab is affected not only by the pathogen species and population but also by physical and other biological factors such as soil properties, plant varieties, cultivation strategies, and weather conditions (Braun et al. 2017; Clarke et al. 2019; Lapwood et al. 1973; Sagova-Mareckova et al. 2015; Sun et al. 2015). Such factors should be considered in developing biocontrol products. In this study, we have demonstrated that, although environmental factors affected the disease development, a consistent result was obtained in 3 years at three locations, showing that PBSH9 was a promising candidate for biocontrol agent. In a broader consideration, PBSH9 could be used for the control of early death of potato caused by *V. dahliae* and other fungal pathogens because PBSH9 and its metabolites showed a strong inhibition against the growth of *V. dahliae*.

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Fig. 5. Effects of *Streptomyces* sp. strain PBSH9 (10^7 CFU/ml) on the sprouting of Atlantic potato seed tubers, which were grown in vermiculite in a plastic pot for 10 days after inoculation at 20°C in the dark.

Table 5. Control effect of *Streptomyces* sp. strain PBSH9 on potato common scab in greenhouse pots^z

Treatment	Incidence (%)	Disease index	Control effect (%)
PBSH9/seed inoculation	36.11 ± 2.41 d	9.17 ± 1.44 c	77.74 ± 3.51 a
Streptomycin/seed inoculation	43.39 ± 0.92 c	18.10 ± 1.65 b	56.06 ± 4.01 b
PBSH9/soil drenching	31.75 ± 2.75 e	7.46 ± 2.25 c	81.88 ± 5.46 a
Streptomycin/soil drenching	53.66 ± 3.57 b	20.35 ± 3.26 b	50.57 ± 7.92 b
CK1: inoculated with <i>Streptomyces galilaeus</i> PS1; nontreated	92.44 ± 0.84 a	41.17 ± 2.35 a	...
CK2: noninoculated; nontreated	0 ± 0 f	0 ± 0 d	...

^z Each treatment had three replications, with each having 15 seeds. Values represent the means ± standard deviation of three biological replicates. Mean values followed by different letters in each column are significantly different ($P < 0.05$).

Table 4. Effect (means ± standard deviation) of *Streptomyces* sp. strain PBSH9 on potato growth in greenhouse pots^z

Treatments	Germination (%)	Bud length (cm)	Fresh bud weight (g)	Dry bud weight (g)
PBSH9	100 ± 0	3.93 ± 0.11 a	0.088 ± 0.009 a	0.009 ± 0.001 a
Nontreated	100 ± 0	2.38 ± 0.27 b	0.057 ± 0.004 b	0.007 ± 0.002 b

^z Each treatment had three replications, with each having 15 seeds. Values represent the means ± standard deviation of three biological replicates. Mean values followed by different letters in each column are significantly different ($P < 0.05$).

Table 6. Control effect of *Streptomyces* sp. strain PBSH9 on potato common scab in field conditions in 2015, 2016, and 2017^y

Year, treatment ^z	Incidence (%)	Disease index	Control effect (%)	Yield (kg/ha)	Yield increase (%)
2015					
PBSH9/seed	26.18 ± 4.33 defg	8.28 ± 1.90 efg	61.73 ± 8.80 abc	47,554.35 ± 7,600.35 a	9.70 ± 17.53 a
Strep/seed	24.84 ± 2.67 efg	9.64 ± 0.23 de	55.45 ± 1.05 bcd	44,582.10 ± 575.85 a	2.85 ± 1.33 cd
PBSH9/drench	21.88 ± 9.22 fghi	9.12 ± 3.41 def	57.87 ± 15.74 bcd	48,606.00 ± 2,370.30 a	12.13 ± 5.47 a
Strep/drench	21.81 ± 1.85 fghi	8.35 ± 0.93 efg	61.43 ± 4.28 abc	43,743.15 ± 431.55 a	0.91 ± 1.00 cd
CK1	54.53 ± 4.17 b	21.65 ± 0.08 b	...	43,182.45 ± 3,432.90 a	...
CK2	11.47 ± 5.25 j	3.03 ± 1.72 hi	...	48,023.40 ± 5,165.55 a	10.78 ± 11.92 a
2016					
PBSH9/seed	14.18 ± 2.69 ij	4.04 ± 0.20 h	59.50 ± 2.04 bc	17,570.70 ± 1,264.05 c	15.93 ± 8.34 a
Strep/seed	17.25 ± 2.90 hij	4.83 ± 0.90 h	51.63 ± 9.02 bcd	16,147.65 ± 1,784.10 c	6.54 ± 11.77 b
PBSH9/drench	18.19 ± 3.50 hij	5.22 ± 0.41 gh	47.64 ± 4.08 ab	16,290.30 ± 1,102.95 c	7.48 ± 7.28 b
Strep/drench	21.28 ± 4.16 ghi	5.60 ± 0.99 fgh	43.90 ± 9.91 d	14,524.95 ± 642.15 c	-4.17 ± 4.24 d
CK1	33.43 ± 4.95 cd	9.98 ± 1.93 de	...	15,156.75 ± 1,024.35 c	...
CK2	27.77 ± 6.37 cdefg	9.04 ± 2.58 def	...	14,202.45 ± 3,881.85 c	-6.30 ± 25.61 d
2017					
PBSH9/seed	29.38 ± 3.02 cdef	8.84 ± 1.32 def	73.97 ± 3.88 a	38,527.20 ± 6,205.50 b	9.77 ± 17.68 a
Strep/seed	35.79 ± 4.09 c	16.74 ± 2.90 c	50.72 ± 8.53 bcd	36,929.10 ± 3,391.50 b	5.22 ± 9.66 b
PBSH9/drench	32.82 ± 3.69 cde	11.97 ± 0.55 d	64.77 ± 1.62 ab	37,757.70 ± 1,882.20 b	7.58 ± 5.36 b
Strep/drench	35.52 ± 5.30 c	15.36 ± 2.77 c	54.79 ± 8.16 bcd	37,749.90 ± 5,642.55 b	7.56 ± 16.08 b
CK1	66.37 ± 2.81 a	33.97 ± 3.87 a	...	35,098.05 ± 4,176.00 b	...
CK2	0 ± 0 k	0 ± 0 i	...	37,041.45 ± 5,949.00 b	5.54 ± 16.95 b

^y Values represent the means ± standard deviation of three biological replicates. Mean values followed by different letters are significantly different ($P < 0.05$).

^z Abbreviations: seed = seed inoculation, Strep = streptomycin, drench = soil drenching, CK1 = inoculated with *Streptomyces galilaeus* PS1 and nontreated, and CK2 = noninoculated and nontreated.

Table 7. Effect of *Streptomyces* sp. strain PBSH9 on the emergence and growth vigor of Atlantic potato under common scab pressure in field conditions^y

Treatment ^z	2015		2016		2017	
	Emergence (%)	Vigor	Emergence (%)	Vigor	Emergence (%)	Vigor
PBSH9/seed	90.00 ± 4.71	4.17 ± 0.28 a	90.00 ± 5.00 ab	4.33 ± 0.29 a	95.00 ± 5.00 a	4.67 ± 0.29 a
Strep/seed	90.00 ± 4.71	4.17 ± 0.28 a	88.33 ± 2.89 bc	4.00 ± 0.50 a	81.67 ± 7.64 b	4.50 ± 0 a
PBSH9/drench	96.67 ± 4.71	4.00 ± 0 a	96.67 ± 5.77 a	4.33 ± 0.29 a	91.67 ± 2.89 ab	4.50 ± 0.50 a
Strep/drench	93.33 ± 4.71	4.00 ± 0 a	93.33 ± 2.89 ab	4.27 ± 0.40 a	85.00 ± 8.66 ab	4.00 ± 0.5 b
CK1	95.00 ± 2.36	3.00 ± 0 b	76.67 ± 2.89 d	2.50 ± 0.00 c	80.00 ± 0 b	4.17 ± 0.29 ab
CK2	90.00 ± 3.33	3.83 ± 0.28 a	81.67 ± 2.89 cd	3.33 ± 0.29 b	81.67 ± 7.64 b	4.17 ± 0.29 ab

^y Growth vigor was measured as 0 to 5, with 5 being the best growth status. Values represent the means ± standard deviation of three biological replicates. Mean values followed by different letters within each column are significantly different ($P < 0.05$).

^z Abbreviations: seed = seed inoculation, Strep = streptomycin, drench = soil drenching, CK1 = inoculated with *Streptomyces galilaeus* PS1 and nontreated, and CK2 = noninoculated and nontreated.

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