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Whole genome sequence of the multi-resistant plant growth-promoting bacteria *Streptomyces* sp. Z38 with potential application in agroindustry and bio-nanotechnology

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ABSTRACT

The genus *Streptomyces* is widely recognized for its biotechnological potential. Due to a need to improve crops, clean up the environment and produce novel antimicrobial molecules exploiting *Streptomyces* has become a priority. To further explore the biotechnological potential of these organisms we analyzed the genome of the strain *Streptomyces* sp. Z38 isolated from contaminated roots tissues. Our analysis not only confirmed the ability of the strain to produce plant growth promoting traits but also a range of mechanisms to cope with the toxic effect of heavy metals through genes involved in metal homeostasis and oxidative stress response. The production of silver nanoparticles indicated that *Streptomyces* sp. Z38 may find utility in Green, Grey and Red biotechnology.

1. Introduction

The increasing demand for food and technology by an expanding human population has led to increased industrial activity and a demand for raw materials. The negative impacts caused by these activities upon the environment is increasingly evident through environmental pollution such as heavy metal contamination. The increase in human population has the concomitant increased in demand for medicines such as antimicrobial drugs, which, when un-regulated can lead to the emergence of multi-drug resistant pathogens that pose a significant threat to global human health [1]. The current global sustainability challenges recognized by the United Nations (www.un.org) include the improvement of crops, clean water and sanitation, responsible consumption and productions and good health and well-being, which include combatting antimicrobial resistance. These fields are currently thought of as three separate areas of biotechnology - the Green, Grey and Red biotechnology sectors [2]. Thus, accessing the potential of microorganisms that may be applied in these sectors of biotechnology is imperative.

The phylum Actinobacteria is renowned for its members with biotechnological potential [3]. The soil saprophytic genus *Streptomyces* exemplifies this through its ability to produce a wide variety of specialized metabolites, their bioremediation potential and their plant growth promotion ability [4–6]. *Streptomyces* sp. Z38 was isolated from contaminated roots tissues [7] and was shown to remove Cr(VI) and lindane from culture medium containing root exudates as carbon source [7]. In addition, *Streptomyces* sp. Z38 produced metabolites that improved the growth of *Zea mays* plants [7]. These results show that *Streptomyces* sp. Z38 has potential in green and grey biotechnology. Here we present and analyze the whole genome of *Streptomyces* sp. Z38 with a view to investigating the genetic determinants that confer its potential in grey and green biotechnology. Regarding to red biotechnology, biogenic synthesis of nanoparticles has emerged as a powerful strategy for the production of novel antimicrobial compounds [8]. In this sense, we also explored the ability of this strain to produce silver nanoparticles and identified the genes responsible for their synthesis.

2. Material and methods

2.1. Strain, growth condition and DNA extraction

Streptomyces sp. Z38 was previously isolated from contaminated roots tissues [7]. The strain was grown in LB medium at 30 °C, 150 rpm

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for 72 h. After centrifugation, cells were washed twice with phosphate-buffered saline pH 7 (PBS) and DNA was extracted by using QIAamp genomic DNA kit (QIAGEN). DNA quality was verified by agarose (0.8%) gel electrophoresis and the concentration was determined on Nanodrop spectrophotometer.

2.2. Genome sequencing, assembly and annotation

The genome of *Streptomyces* sp. Z38 was sequenced at Strathclyde Institute of Pharmacy and Biomedical Sciences, University of Strathclyde using Illumina technology. Reads obtained from sequencing were filtered and assembled into contigs using the assembler software SPAdes v3.13.0 [9]. Afterwards, contigs were run on the multi-draft based scaffolder MeDuSa [10]. Genome annotation was performed in three different platforms: 1)- RASTtk [11]; 2)- Prokka v1.12 [12]; 3)- NCBI Prokaryotic Genome Annotation Pipeline [13].

2.3. Biosynthesis of silver nanoparticles

Streptomyces sp. Z38 was growth in Tryptic Soy Broth (TSB) medium at 30 °C for 96 h. Cells were harvested by centrifugation and washed twice with PBS buffer pH 7. The cell pellet was then resuspended in triple distilled water and incubated at 30 °C, 180 rpm for 120 h. After centrifugation, the cell free-supernatant containing bioactive components [bioactive water (BW)] was used for the biosynthesis of AgNPs. $AgNO_3$ to a final concentration of 1 mM was added to the BW. The biosynthesis of silver nanoparticles (AgNPs) was evidenced by the formation of an absorption peak at 410 nm (UV–visible) [14].

2.4. Data availability

This Whole Genome Shotgun project has been deposited at DDBJ/ENA/GenBank under the accession WPIR00000000. The version described in this paper is version WPIR01000000. Phylogenomic analysis and Prokka annotation are available in the Kbase website as public narrative named *Streptomyces* sp. Z38 (https://kbase.us/) [15]. Genomic islands search was performed using the software IslandViewer 4 [16].

3. Results and discussion

3.1. General features of Streptomyces sp. Z38 genome

The automated annotation of the genome of *Streptomyces* sp. Z38 by the NCBI, Prokka and RASTtk programs did not reveal any significant differences. Genome size was 7,319,726 bp with a G + C content of 72.4%. The genome consists of 6446 protein coding sequences (CDS; Fig. 1), with 275 Pseudo-genes, 11 rRNAs and 70 tRNAs. The genome of *Streptomyces* sp. Z38 exhibited the general characteristics described for *Streptomyces* genomes [17]. Phylogenomic analysis revealed that *Streptomyces* sp. Z38 is grouped in a cluster with the lignin-degrading strain *Streptomyces viridosporus* (Fig. 2) [18]. Phylogenomic analysis also showed that *Streptomyces* sp. Z38 is related to *Streptomyces parvulus* (Fig. 2) which in turn is able to produce bioactive metabolites and antibiotics [19–21]. As mentioned above, *Streptomyces* sp. Z38 is a rhizospheric strain so that its closeness with a lignin-degrading specie such as *S. viridoporus* is expected. The phylogenetic relationship of *Streptomyces* sp. Z38 with the antibiotic-producing strain *S. parvulus* is also interesting. Genome mining with antiSMASH 5.0 [22] suggests that *Streptomyces* sp. Z38 has also the capability to produce antibiotic such as antimycin, aborycin and alkylresorcinol (data not show). Besides, genes related to the production of siderophores were identified (see section 3.2). Overall, *Streptomyces* sp. Z38 shares traits with its phylogenetic neighbors.

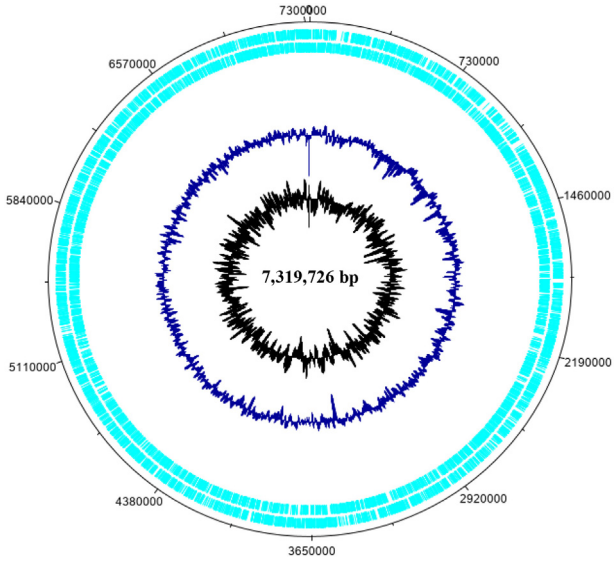

Fig. 1. Circular visualization of *Streptomyces* sp. Z38 genomic maps. The outer circles represent the distribution of the coding regions (CDS). The black and blue circles show GC content (%) and GC skew, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2. Plant growth promotion traits are present in Streptomyces sp. Z38

It is known that *Streptomyces* sp. Z38 is able to produce indole acetic acid (IAA), siderophores and solubilize inorganic phosphate [7]. The genome sequence was interrogated for genes associated with these functions using BLASTp. A gene encoding a putative acid phosphatase (MUT91069.1) was identified in *Streptomyces* sp. Z38. This protein exhibited 78 and 82% of identity with the acid phosphatases, KIZ18601.1 and KUN54552.1, from *Streptomyces natalensis* and *Streptomyces avermitilis,* respectively. In addition, a further six genes encoding alkaline phosphatases (MUT90135.1; 90775.1; 91851.1; 93707.1; 93819.1; 94144.1) were identified.

Phytohormone-like molecules are often produced by rhizosphere bacteria [23,24]. Genome interrogation revealed that *Streptomyces* sp. Z38 has the genetic machinery for the synthesis of IAA through the enzyme indole acetamide hydrolase (MUT89071.1). With reference to siderophore production, the genome of *Streptomyces* sp. Z38 revealed the presence of several genes related to the synthesis of these molecules as well as with the interaction and transport of iron. The analysis with antiSMASH 5.0 [22] showed that all the necessary genes for the synthesis of the tris-hydroxymate siderophores, desferrioxamine B/desferrioxamine E are present in *Streptomyces* sp. Z38. Several works demonstrated that genes encoding for the synthesis of siderophores are under the control of iron boxes (conserved DNA motifs) [25,26]. In *Streptomyces* sp. Z38, we found an iron box located 57 nt from the start codon of *desA* in the desferrioxamine cluster (*desABCD*). The iron box identified consisted of the sequence “TTTGGTTAGGCTAACCTAA” [27]. In addition, the same iron box was identified 45 nt from the start codon of the gen *desE* encoding a siderophore binding protein. The complete putative regulon *desEFABCD* is listed in the Table 1. These data suggest that the genome of *Streptomyces* sp. Z38 has appropriate genes to promote the growth of plants, which is further reinforced by the phenoptypic data of Simón Solá et al. [7].

3.3. Heavy metal resistance and oxidative stress response elements

In addition to the ability of *Streptomyces* sp. Z38 to produce plant growth promotion traits, the strain was able to dissipate the toxic effect of heavy metals such as Cr(VI) and Cd(II) [7]. Heavy metal resistance

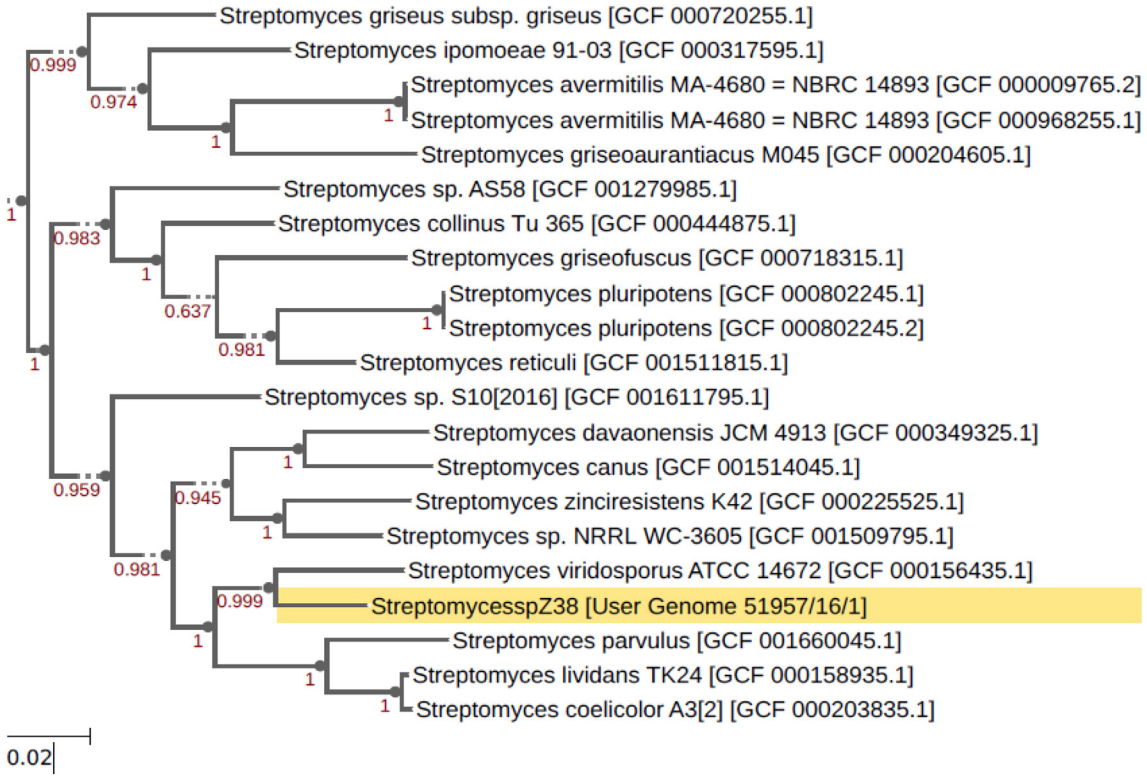

Fig. 2. Phylogenomic analysis of *Streptomyces* sp. Z38. The tree was constructed using a set of 49 core, universal genes defined by COG (Clusters of Orthologous Groups) gene families.

and oxidative stress response are often connected. Metals such as Cr and Cd either direct or indirectly generate reactive oxygen species (ROS) through Fenton reaction.

The genome mining showed that *Streptomyces* sp. Z38 possess a significant number of genes involved in the homeostasis of heavy metals (Table 2). Homeostasis mechanisms often include absorption, adsorption and/or reduction of the metal. In the case of Cr(VI), reduction plays an important role in the homeostasis process (Cr(III) is less toxic than Cr(VI)) [28]. There is not much information about enzymes capable of reducing Cr(VI) in the genus *Streptomyces*. Recently, Sineli et al. [6] identified for the first time a chromate reductase related to Old Yellow Enzymes in the strain *Streptomyces* sp. M7. In the present study, we identified an oxidoreductase from *Streptomyces* sp. Z38 that exhibited 80% identity with the chromate reductase from *Streptomyces* sp. M7 (Fig. 3). The key amino acids for the activity of Old Yellow Enzymes chromate reductases and their position in the primary structure were reported by Opperman et al. [29,30]. These amino acids are also present in the sequence of *Streptomyces* sp. Z38 (Fig. 3) [6,29]. The section 3.2 of this work and a recent study [7], have demonstrated that *Streptomyces* sp. Z38 possess the physiological and genetic potential to produce siderophores. These molecules are natural products that not only promote the plant growth but also may bind to heavy metals with high affinity [31]. The ability of desferrioxamine to form highly stable complexes with Cr(III) was described by Duckworth et al. [32]. This evidence and the genomic mining suggest that *Streptomyces* sp. Z38 could be able to reduce Cr(VI) and subsequently, form a stable complex with the siderophore desferrioxamine.

Regarding to oxidative stress, a complete pool of well-known genes involved in the antioxidant response were identified (Table 2). Our study indicated that the defensive line against ROS in *Streptomyces* sp. Z38 is composed of SODs, Catalases, Mycothiol and Thioredoxins (Table 2). The present study has demonstrated that the heavy metals resistance of *Streptomyces* sp. Z38 is supported by reductases, siderophores and antioxidant mechanisms.

Genes associated with heavy metals homeostasis and oxidative stress response may be located in genomic islands. For instance, the phylogenetic neighbor of *Streptomyces* sp. Z38, *Streptomyces lividans* presents metal-related genomic islands [33]. The analysis of *Streptomyces* sp. Z38 with the software IslandViewer 4 [16] allowed to identify 3 genomic islands (> 25 kb) and 35 genomic islets (< 25 kb) (Supplementary Table). In contrast to *Streptomyces lividans,* genes involved in heavy metal homeostasis in *Streptomyces* sp. Z38 are not located in their genomic islands.

Table 1
Desferrioxamine biosynthetic gene clusters (*desABCD*) and siderophore transporter.

Gene	Annotation	Accession number	Protein size (amino acids)	Identity with *Streptomyces lividans* 1326
desE	ABC transporter substrate-binding protein	MUT90243.1	347	78%
desF	Siderophore-interacting protein	MUT90242.1	289	72%
desA	lysine decarboxylase DesA	MUT90241.1	480	91%
desB	Monooxygenase	MUT90240.1	430	79%
desC	Acetyltransferase	MUT90239.1	180	79%
desD	Siderophore biosynthesis protein	MUT90238.1	590	85%

Table 2
Genes and protein products present in the genome of *Streptomyces* sp. Z38.

Gene	Protein Name	Description
Heavy Metal Resistance		
MUT89049.1; 90977.1	Metal ABC transporter	Heavy metal homeostasis
MUT92864.1	Divalent metal cation transporter	
MUT88401.1	Multicopper oxidase	
MUT92819.1	Copper homeostasis CutC	
MUT90478.1; 91767.1	Arsenate reductase ArsC	
MUT90476.1; 92056.1	Arsenite efflux transporter ACR3	
MUT90578.1	Arsenic transport	
MUT92040.1	Heavy metal translocating P-type ATPase	
MUT92357.1	Heavy metal transporter	
MUT88110.1; 88,796.1	Cadmium-translocating P-type ATPase	
MUT89074.1	Chromate reductase	
Oxidative Stress Response		
MUT92563.1	Alkyl hydroperoxide reductase	Catalyzes the reduction of H_2O_2 and organic hydroperoxides to H_2O
MUT88579.1; 88806.1	Superoxide Dismutase	SOD (Ni)
MUT88537.1;897000.1; 90515.1	Catalase	Decomposition of H_2O_2 to H_2O and O_2.
MUT93042.1	Mycothiol synthase	Synthesis of the antioxidant Mycothiol
MUT92242.1	Mycothiol peroxidase	Control oxidative stress levels by reducing hydroperoxides
MUT89230.1	Thioredoxin-dependent thiol peroxidase	Control oxidative stress levels
MUT89535.1; 90172.1; 91125.1	Thioredoxin	Control oxidative stress levels
MUT90173.1; 90480.1	Thioredoxin reductase	Control oxidative stress levels

3.4. Potential of *Streptomyces* sp. Z38 to synthesize silver nanoparticles (AgNPs)

Silver and gold bio-nanoparticles are probably the most studied with potential applications in targeted drug delivery [34]. Several works have demonstrated the antimicrobial activity of AgNPs produced by *Streptomyces* [35,36]. Using the conditions described in 2.3, *Streptomyces* sp. Z38 was able to produce AgNPs. The biosynthesis of AgNPs was evidenced by the formation of a typical absorption peak at 410 nm [14] which increased according to the incubation time (Fig. 4). Although the specific mechanisms for the biosynthesis of nanoparticles are still subject of study, it is thought their production is mediated by nitrate reductases [8]. The ability of *Streptomyces* sp. Z38 to produce AgNPs was supported by the identification of two nitrate reductases in its genome (MUT90739.1; 91974.1). This trait is directly related to red biotechnology and further studies will be conducted in order to determine the antimicrobial activity of AgNPs.

The ability of *Streptomyces* sp. Z38 to produce AgNPs can be related to the traits described in the sections 3.2 and 3.3. It is known that the synthesis of nanoparticles is mediated by nitrate reductases. However, several studies demonstrated that other reductases may be also involved [8,34]. Based on these antecedents and the low specificity of chromate reductases [37], we may infer that the putative chromate reductase identified in *Streptomyces* sp. Z38 could also participate in the synthesis of AgNPs. Although not yet reported in the genus *Streptomyces*, secondary metabolites such as siderophores can participate in the production of silver and gold nanoparticles [38]. For instance, *Delftia acidovorans* produces a siderophore that may complex, reduce and co-precipitate with soluble Au(III) leading to the formation of nanoparticles [39].

4. Conclusions

Streptomyces sp. Z38 is a promising strain that could be used in different fields of biotechnology, the Green, Grey and Red sectors. Our analysis demonstrated that the strain may act as plant growth promoting through the production of phytohormones. Genes involved in the homeostasis of heavy metals and oxidative stress response also support the hypothesis that *Streptomyces* sp. Z38 may represent an excellent tool for bioremediation. Moreover, the identification of biosynthetic gene clusters for potential production of antimicrobial compound and its ability to produce silver nanoparticles, demonstrates the biotechnological potential of *Streptomyces* sp. Z38 within the red biotechnology. To our knowledge, this is the first genomic analysis of a *Streptomyces* strain that may be used across several biotechnological fields.

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Fig. 3. Alignment of *Streptomyces* sp. M7chromate reductase (NCBI: RDS65860.1) with the putative chromate reductase from *Streptomyces* sp. Z38 (NCBI: MUT89074.1). Asterisks indicate key amino acids for chromate reductase.

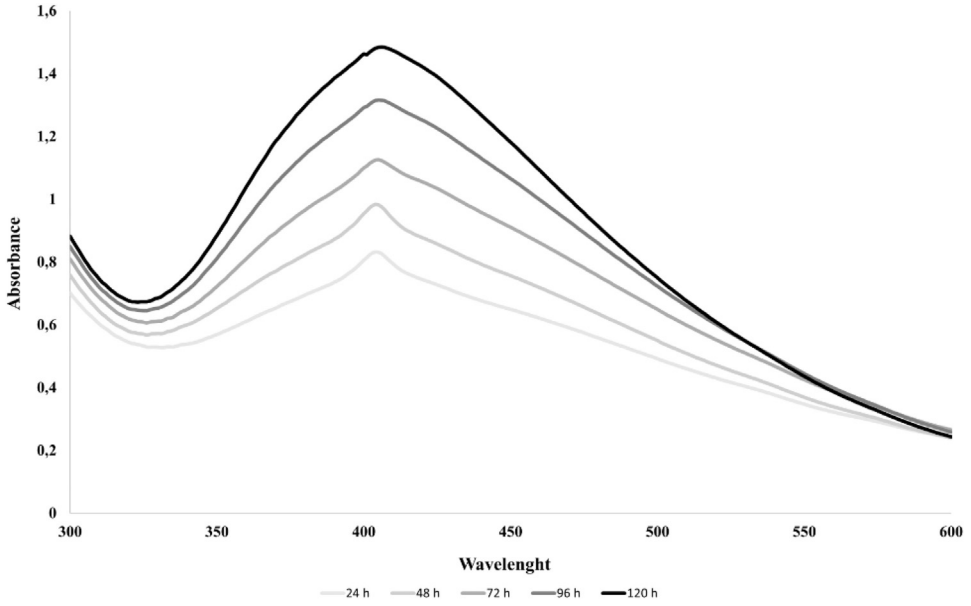

Fig. 4. Plasmon resonance peak (410 nm) of silver nanoparticles. The production of nanoparticles increased according to the incubation time.

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Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ygeno.2020.08.022.

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