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SHORT COMMUNICATION

Complete genome sequence of the endophytic bacterium *Cellulosimicrobium* sp. JZ28 isolated from the root endosphere of the perennial desert tussock grass *Panicum turgidum*

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Abstract

Cellulosimicrobium sp. JZ28, a root endophytic bacterium from the desert plant *Panicum turgidum*, was previously identified as a plant growth-promoting bacterium. The genome of JZ28 consists of a 4378,193 bp circular chromosome and contains 3930 CDSs with an average GC content of 74.5%. Whole-genome sequencing analysis revealed that JZ28 was closely related to *C. aquatile* 3 bp. The genome harbors genes responsible for protection against oxidative, osmotic and salinity stresses, such as the production of osmoprotectants. It also contains genes with a role in the production of volatiles, such as hydrogen sulfide, which promote biotic and abiotic stress tolerance in plants. The presence of three copies of chitinase genes indicates a possible role of JZ28 as biocontrol agent against fungal pathogens, while a number of genes for the degradation of plant biopolymers indicates potential application in industrial processes. Genome sequencing and mining of culture-dependent collections of bacterial endophytes from desert plants provide new opportunities for biotechnological applications.

Keywords Genome sequence · Plant growth-promoting bacteria (PGPB) · Endophyte · *Cellulosimicrobium* sp. · Desert microbes · DARWIN21

Introduction

Microbial endophytes, and especially beneficial ones, have received great interest in agriculture for their imperative role in maintaining the health of plants by protecting them against pathogens or promoting their growth under abiotic stresses (Dimkpa et al. 2009; Lata et al. 2018; Lugtenberg et al. 2016). Schumann et al. (2001) proposed the reclassification of the cellulolytic strain *Cellulomonas cellulans* as *Cellulosimicrobium cellulans*. Studies on species within this genus have been shown to possess the potential for application in agriculture as plant growth promoters or biocontrol agents. For example, *C. cellulans* strain 191 produces high quantities of chitinase, a hydrolytic enzyme involved in the degradation of chitin in the cell walls of fungi, suggesting that this bacterial strain might be used for biocontrol against fungal pathogens (Fleuri et al. 2009). *C. cellulans* strain KUCr3 produces the phytohormone auxin/indole acetic acid (IAA), solubilizes phosphate and promotes the growth of green chilli plants and their tolerance to toxic hexavalent chromium (Chatterjee et al. 2009). *C. funkei* strains also possess high resistance against chromium, produce IAA, solubilize phosphate and promote growth of common bean

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(*Phaseolus vulgaris*) and other crops under normal conditions and chromium toxicity (Karthik and Arulselvi 2017; Karthik et al. 2016). *Cellulosimicrobium* sp. strain S16, isolated from salt-affected rhizosphere soil, strongly inhibits growth of the three pathogenic fungi *Fusarium oxysporum*, *Verticillium dahliae* and *Botrytis cinerea*, produces IAA and siderophores (iron chelators), solubilizes phosphate, possesses chitinase and urease activity and promotes the elongation of barley stems (Nabti et al. 2014). This strain was also taxonomically close to *Cellulosimicrobium* sp. CH6 by 16S rRNA phylogenetic analysis.

The application of beneficial microbes, such as plant growth-promoting bacteria (PGPB), for promoting plant growth and alleviating abiotic stresses is well established (Glick 2012; Lugtenberg and Kamilova 2009; Vessey 2003). Although several mechanisms by which PGPB exert their effects on plants are known, the field of plant–microbe interactions remains largely undiscovered and the exact molecular mechanisms by which abiotic stress tolerance is induced remains largely unknown. The integration of omics data will advance our understanding of these mechanisms. In this study, we present the complete genome sequence of the PGPB *Cellulosimicrobium* sp. JZ28, previously isolated from the root endosphere of the perennial desert tussock grass *Panicum turgidum* with salinity stress tolerance-promoting abilities on *Arabidopsis thaliana* (Eida et al. 2018).

Materials and methods

Growth conditions and genomic DNA extraction

Pure cultures of *Cellulosimicrobium* sp. JZ28 were stored in 20% glycerol at − 80 °C. JZ28 was grown on Tryptone Soya broth and agar (g/L: Bacto tryptone-15; Bacto soytone-5; NaCl-5; agar-15) at 28 °C. Fresh bacterial cultures were used for total genomic DNA extraction using Sigma's GenElute bacterial genomic DNA kit (Sigma-Aldrich) following the manufacturer's protocol. DNA quality and quantity were assessed by 0.7% agarose gel electrophoresis (35 V, 12 h), NanoDrop 2000 (Thermo Fisher Scientific) and Qubit dsDNA BR assay kit (Thermo Fisher Scientific).

Genome sequencing and assembly

DNA was size selected to 10 kb using the BluePippin™ Size Selection System (Sage Science), following the "High-Pass™ DNA Size Selection of 20 kb SMRTbell™ Templates" manual. The SMRTbell™ template library was prepared according to the instructions from Pacific Biosciences's "Procedure and Checklist—20 kb Template Preparation using BluePippin™ Size Selection System" guide. The SMRT cells were run at the KAUST Bioscience Core Labs on the PacBio *RSII* (Pacific Biosciences) sequencing platform using P6-C4 chemistry. Raw data from PacBio's platform were assembled using the Hierarchical Genome Assembly Process v4 (HGAP4) (Chin et al. 2013) from PacBio's SMRT Analysis pipeline v2.3.0.140936 patch 5. The assembly workflow can be broken down into three main steps: a preassembly step that mapped single pass reads to seed reads to generate consensus reads that were then quality trimmed. De novo assembly was done using the overlap layout consensus approach. The final step of consensus polishing used Quiver to reduce indels and base substitutions using quality scores embedded in the raw data. To determine whether assembled contigs are circular, dot plots were generated using Gepard (Krumsiek et al. 2007) for detecting overlaps at the peripheries. Overlaps were collapsed and the genome was closed using Minimus2 (Sommer et al. 2007). Finally, additional polishing rounds were performed using Quiver by applying quality scores from raw data to correct for indels and base substitutions where the output from one round was used as input to the next round.

Genome annotation

Genome annotation was carried out using the Automatic Annotation of Microbial Genomes (AAMG) which is an integrated module in the in-house INDIGO-Desert v1.1 pipeline (Alam et al. 2013). Briefly, gene prediction was done using prodigal v2.6.1 (Hyatt et al. 2010). Functional annotation was done using a multitude of tools and databases. InterProScan (Jones et al. 2014) was used to assign domain information, gene ontology (GO) terms and KEGG pathways. Predicted genes were compared using BLAST against UniProt (https://www.uniprot.org/) for generic annotations and cross-references to COGs (Cluster of Orthologous Genes (COGs). For annotation of gene function, genes were compared to KEGG database (Functional Kyoto Encyclopedia of Genes and Genomes) (Kanehisa et al. 2016). RPS-BLAST (Marchler-Bauer et al. 2002) was used to identify conserved domains and COG (Clusters of Orthologous Groups). Predicted genes were also BLAST-ed against NCBI-nr, UniProt and KEGG. Ribosomal RNAs (rRNAs), transfer RNAs (tRNAs) and other non-coding RNAs (ncRNAs) were predicted using RNAmmer 1.2 (Lagesen et al. 2007), tRNAscan-SE 2.0 (Lowe and Eddy 1997), and Infernal software (Nawrocki and Eddy 2013), respectively. Function and pathway analysis was also performed using BlastKOALA web tool of KEGG database (Kanehisa et al. 2016). Identification of gene clusters responsible for the biosynthesis of secondary metabolites was performed using antiSMASH v.4.2.0 (Weber et al. 2015).

Phylogenetic analysis

For distinguishing between *Cellulosimicrobium* strains at species level, digital DNA–DNA hybridization (dDDH) and average nucleotide identity (ANI) calculations were performed. Pairwise BLAST-based average nucleotide identity values (ANIb) were obtained using JSpecies (Richter et al. 2015). The genome sequence data were uploaded to the Type (Strain) Genome Server (TYGS), a free bioinformatics platform available under https://tygs.dsmz.de, for a whole-genome-based taxonomic analysis (Meier-Kolthoff and Göker 2019). All pairwise comparisons among the set of genomes were conducted using GBDP and accurate intergenomic distances inferred under the algorithm 'trimming' and distance formula d5 (Meier-Kolthoff et al. 2013). 100 distance replicates were calculated each. Digital DDH values and confidence intervals were calculated using the recommended settings of the GGDC 2.1 (Meier-Kolthoff et al. 2013).

Sequence accession number

The data for bacterial genome assembly of JZ28 and sequencing were deposited in NCBI/DDBJ/EMBL database under the accession number CP017660, BioProject PRJNA345401, BioSample SAMN05828175. The annotations obtained by the in-house INDIGO pipeline are available through the KAUST library repository (https://doi.org/10.25781/KAUST-6L345).

Results and discussion

PacBio sequencing generated 54,893 reads with a mean insert read length of 12,050 bp and an estimated genome coverage of 151X. Genome assembly generated a single circular chromosome of approximate size of 4.38 Mbp with a high G + C content of 74.69% (Table 1). High G + C content is a characteristic of free-living bacteria as opposed to obligate pathogens and symbionts (Rocha and Danchin 2002), possibly due to environments that are complex and constantly changing and where there is a higher chance of horizontal gene transfer (Mann and Chen 2010). The G + C content of JZ28 (74.69%) falls into the range of that reported for the *Cellulosimicrobium* genus (average G + C content 74.5%). The INDIGO annotation resulted in 4036 open reading frames (ORF) yielding a gene density of approximately 898 genes/Mbp. Approximately 97% (3930) of the ORFs were protein coding sequences (CDS). In addition, there were three 16S-23S-5S rRNA operons, one extra 5S rRNA copy, 46 ncRNAs, and 51 tRNAs in JZ28's chromosome.

Taxonomic analysis of *Cellulosimicrobium* sp. JZ28 using ANIb similarity (Supplementary Table S1), dDDH values (Supplementary Table S2) and whole-genome and 16S rDNA sequences (Fig. 1) revealed high similarity with other reference type strains. Although several strains showed values of ANI and dDDH that exceeded the species cutoff (95% and 70%, respectively), *C. aquatile* 3 bp showed the highest similarity with JZ28 with an ANIb value of 97.79% and dDDH value of 92.4% (formula d_6). Whole-genome-based phylogeny revealed clustering of JZ28 in a clade with several species, namely *C. aquatile* 3 bp *C. funkei* NBRC 104,118 and *C. terreum* JCM 15,619 (Fig. 1a). Based on 16S rDNA sequences (Fig. 1b), the phylogenetic tree showed clustering with *C. aquatile* 3 bp and, thus, JZ28 is not a potentially new species.

Table 1 Summary of JZ28 genome features

Feature	Value
Genome size (bp)	4378,193
G + C content (%)	74.69
ORFs	4036
Gene density (genes/Mbp)	897.63
CDSs	3930
16S-23S-5S rRNA operons	3
ncRNAs	46
tRNAs	51

AntiSMASH analysis identified four secondary metabolite regions, but only one cluster was similar to known clusters. This cluster was 100% similar to alkylresorcinol (BGC0000282) and 75% similar to desferrioxamine (BGC0001478) biosynthesis clusters. Alkylresorcinols are referred to as phenolic lipids that occur in plants, fungi and bacteria and have been associated with a range of biological activities such as antioxidant, cytotoxic, antimicrobial and signaling properties (Baerson et al. 2010; Ortega et al. 2017; Stasiuk and Kozubek 2010). On the other hand, desferrioxamines are hydroxamate-type siderophores (Mawji et al. 2008; Schwabe et al. 2018). JZ28 was previously shown to survive in media under salt (5% NaCl) and osmotic stress (20% PEG 8000) (Eida et al. 2018). To determine what genomic potential JZ28 has in terms of abiotic stress tolerance, a functional analysis (BlastKOALA) of the CDSs was performed and identified 1742 genes (44.3%) with assigned functions.

Genome analysis revealed the presence of genes encoding for potassium-uptake transporters, such as the Kdp-ATPase system (*kdpABCDE*) (Sleator and Hill 2002) and for glutamate transport (*gluABCD*) and biosynthesis (*gltBD*), which along with its potassium counter ions are involved in the primary response to osmotic stress in bacteria (Booth and Higgins 1990; Paul 2013). Genes involved in four of the five pathways for trehalose biosynthesis (*ostAB*, *treYZ*, *treS*, *treP*) (Paul et al. 2008; Strom

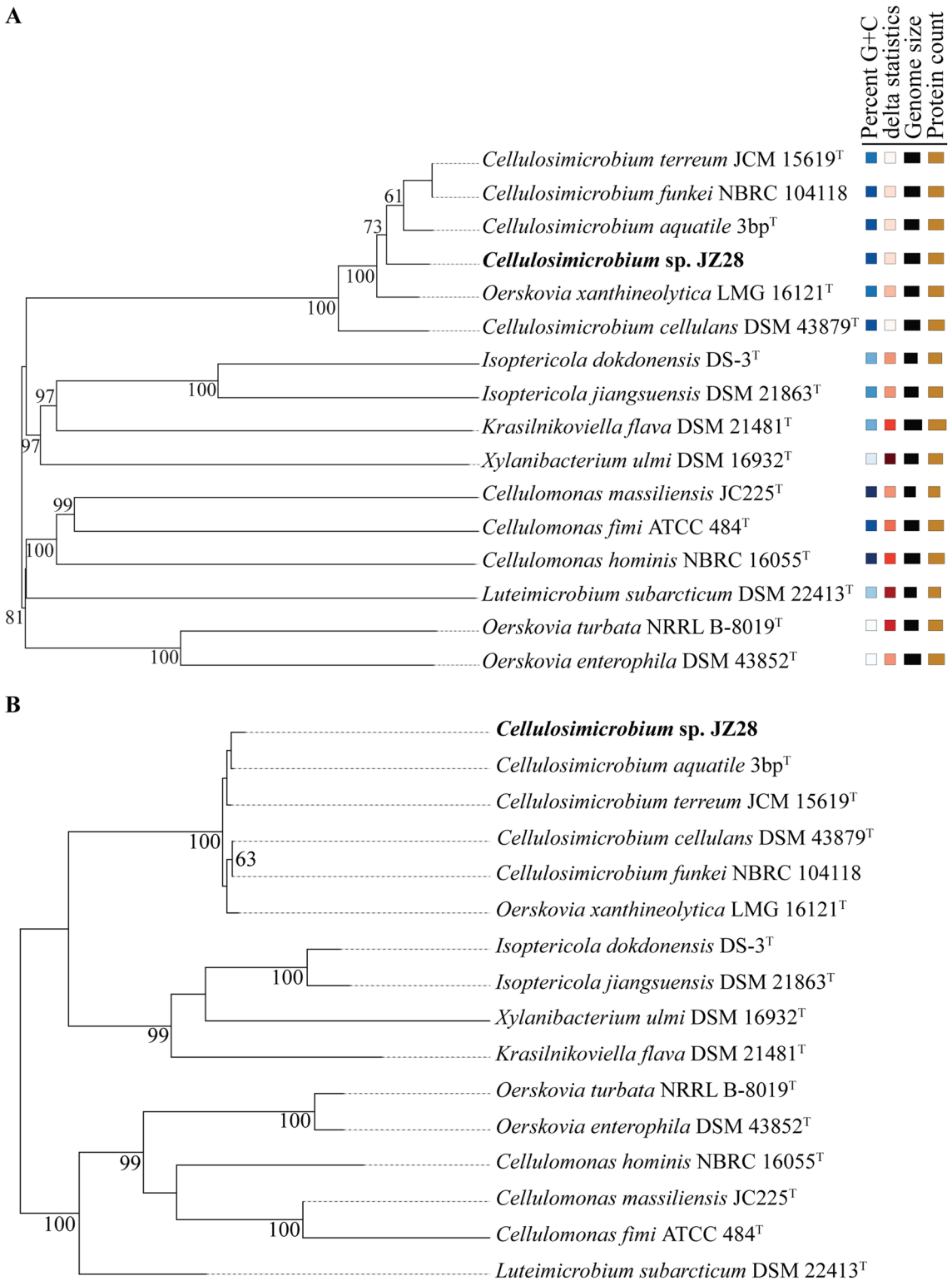

Fig. 1 Genome Blast Distance Phylogeny (GBDP) of *Cellulosimicrobium* sp. JZ28 with reference strains of related species based on whole-genome and 16S rDNA sequences. Tree inferred with FastME 2.1.6.1 from GBDP distances calculated from either genome sequences (Lefort et al. 2015) (**a**) or from 16S rDNA gene sequences (**b**). The branch lengths are scaled in terms of GBDP distance formula d_5. The numbers above branches are GBDP pseudo-bootstrap support values > 60% from 100 replications, with an average branch support of 84.2% (**a**) and 75.5% (**b**). The tree was rooted at the midpoint (Farris 1972). Type strains indicated by ^{T}

and Kaasen 1993) and in proline biosynthesis (*proABC*) (Mandon et al. 2003) and uptake (*proVWX*) (Gul and Poolman 2013; Wood 1988) were also present (Supplementary Table S3). In addition, genes involved in detoxification systems and oxidative stress tolerance, such as glutathione peroxidase (*gpx*), gamma-glutamate-cysteine ligase (*gshA*, two copies), peroxiredoxin (*BCP*), superoxide dismutases (two copies of *SOD2*), hydrogen peroxide catalase (*katE*) and regulator of the superoxide radical response (*soxR*) were present (Fones and Preston 2012; Zhao and Drlica 2014). Other genes are involved in stress tolerance, such as those encoding for antiporters (e.g. *nhaA*), molecular chaperones (e.g. *cspA*, *groEL*, *groES*, *dnaK*) and transcriptional repressors (e.g. *lexA*).

The bacterial production of volatile compounds has been shown to promote plant growth (Ryu et al. 2003). JZ28 harbors genes for acetoin and 2,3-butanediol production (*ilvH*, *ilvB*, *BDH*) (Taghavi et al. 2010). JZ28 also contains genes responsible for uptake of extracellular alkanesulfonate by the ABC transporter *ssuACB*, its conversion to sulfite by the two alkanesulfonate monooxygenases *ssuD* and *ssuE* and subsequently to the volatile compound hydrogen sulfide (H_2S) by the sulfite reductase/ferredoxin *sir*. In addition, the gene encoding cystathionine β synthase (*CBS*) which is also involved in H_2S production is also present in JZ28 (Supplementary Table S3) (Matoba et al. 2017; Rose et al. 2017). The volatile H_2S has been suggested to assist plants in alleviating abiotic stresses, such as oxidative and salinity stress (Eida et al. 2019; Gotor et al. 2019).

JZ28 also possesses two recombinases/integrases (*xerC*, *xerD*), suggesting its ability to colonize the rhizosphere and root surfaces of plants (Martínez-Granero et al. 2005). Three copies of chitinases that break down chitin found in cell walls of fungi are also present, indicating a potential role for JZ28 as a biocontrol agent against pathogens. Finally, JZ28 contains key enzymes involved in the last step of the degradation of cellulose biopolymers called β-glucosidases (six copies of *bglX* and four copies of *bglB*), indicating its potential for industrial applications (Singh et al. 2015). Other enzymes involved in oligosaccharide breakdown were also present (Supplementary Table S3).

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Compliance with ethical standards

Conflict of interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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