Current Microbiology (2021) 78:1135–1141
https://doi.org/10.1007/s00284-021-02429-5

SHORT COMMUNICATION

Complete Genome Sequence of *Cellulomonas* sp. JZ18, a Root Endophytic Bacterium Isolated from the Perennial Desert Tussock-Grass *Panicum turgidum*

Abdul Aziz Eida[1] · Salim Bougouffa[2,3] · Intikhab Alam[2] · Heribert Hirt[1,4] · Maged M. Saad[1]

Received: 8 November 2020 / Accepted: 11 February 2021 / Published online: 8 March 2021

Abstract

Cellulomonas sp. JZ18 is a gram-positive, rod shaped bacterium that was previously isolated from the root endosphere of the perennial desert tussock-grass *Panicum turgidum*. Genome coverage of PacBio sequencing was approximately 199X. Genome assembly generated a single chromosome of 7,421,843 base pairs with a guanine-cytosine (GC) content of 75.60% with 3240 protein coding sequences, 361 pseudo genes, three ribosomal RNA operons, three non-coding RNAs and 45 transfer RNAs. Comparison of JZ18′s genome with type strains from the same genus, using digital DNA–DNA hybridization and average nucleotide identity calculations, revealed that JZ18 might potentially belong to a new species. Functional analysis revealed the presence of genes that may complement previously observed biochemical and plant phenotypes. Furthermore, the presence of a number of enzymes could be of potential use in industrial processes as biocatalysts. Genome sequencing and analysis, coupled with comparative genomics, of endophytic bacteria for their potential plant growth promoting activities under different soil conditions will accelerate the knowledge and applications of biostimulants in sustainable agriculture.

Introduction

Cellulomonas species are Gram-positive, rod-shaped, G + C rich bacteria belonging to the phylum *Actinobacteria*. A major distinguishing characteristic of this genus is their ability to breakdown cellulose and hemicellulose by xylanases, endo- and exoglucanases [1, 2]. Indeed, different species of *Cellulomonas* have been studied and shown to have a potential for biotechnological applications as well as, recently, as biostimulants and biocontrol agents in agriculture. For example, xylan degradation and production of β-xylanase and β-xylosidase activities were studied in *C. uda* [3], *C. fimi* [4] and *C. pachnodae* [5]. *Cellulomonas flavigena* was shown to produce a set of enzymes, cellulases, xylanases and endoglucanases, for the breakdown of plant biomass such as cellulose and hemicellulose [6–9], which indicate their potential for use in biotechnological applications [10].

Cellulomonas species were previously isolated from the roots Mexican husk tomato plants (*Physalis ixocarpa*) [11]. Zinniel et al. [12] isolated *Cellulomonas* sp. SE017 from sorghum (*Sorghum bicolor*) and claimed their ability to colonize wheat (*Triticum aestivum*), potato (*Lycopersicon esculentum*), and tomato (*Solanum tuberosum*). They were also shown to colonize the rhizosphere and phyllosphere of winter wheat (*Triticum aestivum*) and pea (*Pisum sativum*) and to promote the nodulation and shoot and root biomass of pea [13, 14]. Co-inoculation of *C. flavigena* with other bacterial genera was shown to promote growth of rice (*Oryza sativa*) [15]. These studies suggest the ability of *Cellulomonas* to promote plant growth and, thus, to be used as biostimulants in agriculture. In addition, Takegawa et al. [16] previously demonstrated the ability of a polysaccharide lyase (possibly a pectate lyase), isolated from a soil bacterium that was identified as *Cellulomonas* sp., to degrade *Fusarium* and *Gibberella* acidic polysaccharides. The authors speculate a role of

✉ Heribert Hirt
heribert.hirt@kaust.edu.sa

Maged M. Saad
maged.saad@kaust.edu.sa

[1] DARWIN21, Center for Desert Agriculture (CDA), King Abdullah University of Science and Technology (KAUST), Thuwal 23955-6900, Saudi Arabia

[2] Computational Bioscience Research Center (CBRC), King Abdullah University of Science and Technology (KAUST), Thuwal 23955-6900, Saudi Arabia

[3] BioScience Core Lab, King Abdullah University of Science and Technology, Thuwal 23955-6900, Saudi Arabia

[4] Max F. Perutz Laboratories, University of Vienna, Dr. Bohrgasse 9, 1030 Vienna, Austria

these acidic polysaccharides in the two pathogenic fungi in host-parasite interactions and, thus, species of *Cellulomonas* could play a role as biocontrol agents in agriculture.

Here, we report the genome of *Cellulomonas* sp. JZ18, an endophyte isolated from the root endosphere of the perennial desert tussock-grass *Panicum turgidum* in Jizan, Saudi Arabia [17]. It was previously identified using biochemical assays to possess the ability to tolerate growth under salt, osmotic and heat stresses, colonize *Arabidopsis* root surface and produce biofilms and exoproteases [17].

Materials and Methods

Growth Conditions and Genomic DNA Extraction

Isolate JZ18 was grown in/on tryptone soy broth/agar (g/L: Bacto tryptone-15; Bacto soytone-5; NaCl-5; agar-15) at 28 °C. Fresh, pure 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-PassTM DNA Size Selection of ~ 20 kb SMRTbellTM 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. One SMRT cell was run, taking one 360 min movie. Raw data from PacBio's platform was assembled into a draft assembly using the Hierarchical Genome Assembly Process v4 (HGAP4) [18] from PacBio's SMRT Analysis pipeline v2.3.0.140936 patch 5. The assembly workflow can be broken down to three main steps: a pre-assembly 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 is consensus polishing using Quiver to reduce indels and base substitution using quality scores embedded in the raw data. To determine whether assembled contigs are circular, dot plots were generated using Gepard [19] for detecting overlaps at the peripheries. Overlaps were collapsed and the genome was closed using Minimus2 [20]. 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

The annotation of the genome was performed using NCBI's prokaryotic genome annotation pipeline (PGAP) [18, 19]. Function and pathway analysis was also performed using BlastKOALA web tool of KEGG database [20]. The identification of gene clusters for the biosynthesis of secondary metabolites was performed using antiSMASH v.4.2.0 [21].

Phylogenetic Analysis

The 16S rRNA gene sequences of JZ18 were predicted using RNAmmer 1.2 and the most common and identical sequences of the three copies were compared to known sequences listed in NCBI's GenBank using BLASTn [22]. The sequences with the highest similarity in terms of sequence identity and query coverage, along with other *Cellulomonas* strains from similar and distant genera were used for the phylogenetic tree construction. Alignment of 16S rRNA sequences and construction of phylogenetic tree was performed as previously described [23]. For distinguishing between *Cellulomonas* 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 [24]. 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 [25]. 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 [26]. 100 distance replicates were calculated each. Digital DDH values and confidence intervals were calculated using the recommended settings of the GGDC 2.1 [26].

Sequence Accession Number

The data for the bacterial genome assembly of *Cellulomonas* sp. JZ18 and sequencing were deposited in NCBI/DDBJ/EMBL database under the accession number CP045245, BioSample SAMN13011526 (https://www.ncbi.nlm.nih.gov/biosample/13011526).

Results and Discussion

Sequencing of *Cellulomonas* sp. JZ18 using PacBio technology (estimated genome coverage of 199X) resulted in a chromosome of 4,043,325 bp with a GC content of 75.60% (Table 1). Annotation pipeline generated a total of 3658 ORFs of which 3240 are protein coding sequences (CDS), 361 pseudo genes, three rRNA operons, three ncRNAs and 45 tRNAs.

Table 1 Summary of JZ18 genome features

Feature	Chromosome
Genome coverage	199X
Genome size (bp)	4,043,325
GC content (%)	75.60
ORF	3658
Gene density (genes/Mbp)	756.31
CDS	3240
Pseudo genes	361
rRNAs	9
16S-23S-5S operons	3
ncRNAs	3

Phylogenetic analysis based on 16S rRNA sequences of JZ18 and closest relatives (based on top BLAST hits) showed clustering of JZ18 with *Cellulomonas* sp. CPCC 204,705 and *Cellulomonas* sp. Z28 (Fig. 1), which represent the type strains of *C. telluris* and *C. shaoxiangyii* [27, 28]. Whole-genome sequence phylogenetic analysis of JZ18 with other *Cellulomonas* type strains revealed clustering of JZ18 within a clade of *C. telluris* CPCC 204705T and *C. shaoxiangyii* Z28T (Fig. 2). Further analysis revealed displays the highest similarity with *C. iranensis* NBRC 101,100 and *C. flavigena* DSM 20,109 with ANIb values of 80.73% and 80.26%, respectively (ESM_2 Table S1). JZ18 also displayed high similarity with *C. telluris* CPCC 204705T and *C. shaoxiangyii* Z28T with dDDH values of 72.8% and 50.2% (formula d_0), respectively (Table 2; ESM_2 Table S2). However, the ANIb and dDDH values do not exceed the species cut-off of 95% and 70%, respectively. Based on these results, JZ18 may potentially be a new species.

Functional analysis (BlastKOALA) of the chromosome was performed and identified 1,564 genes (43.4%) with assigned functions. Genome mining revealed the presence of genes involved in abiotic stress responses and tolerance (e.g. detoxification systems, trehalose and glutamate biosynthesis), disruption and degradation of plant cell walls

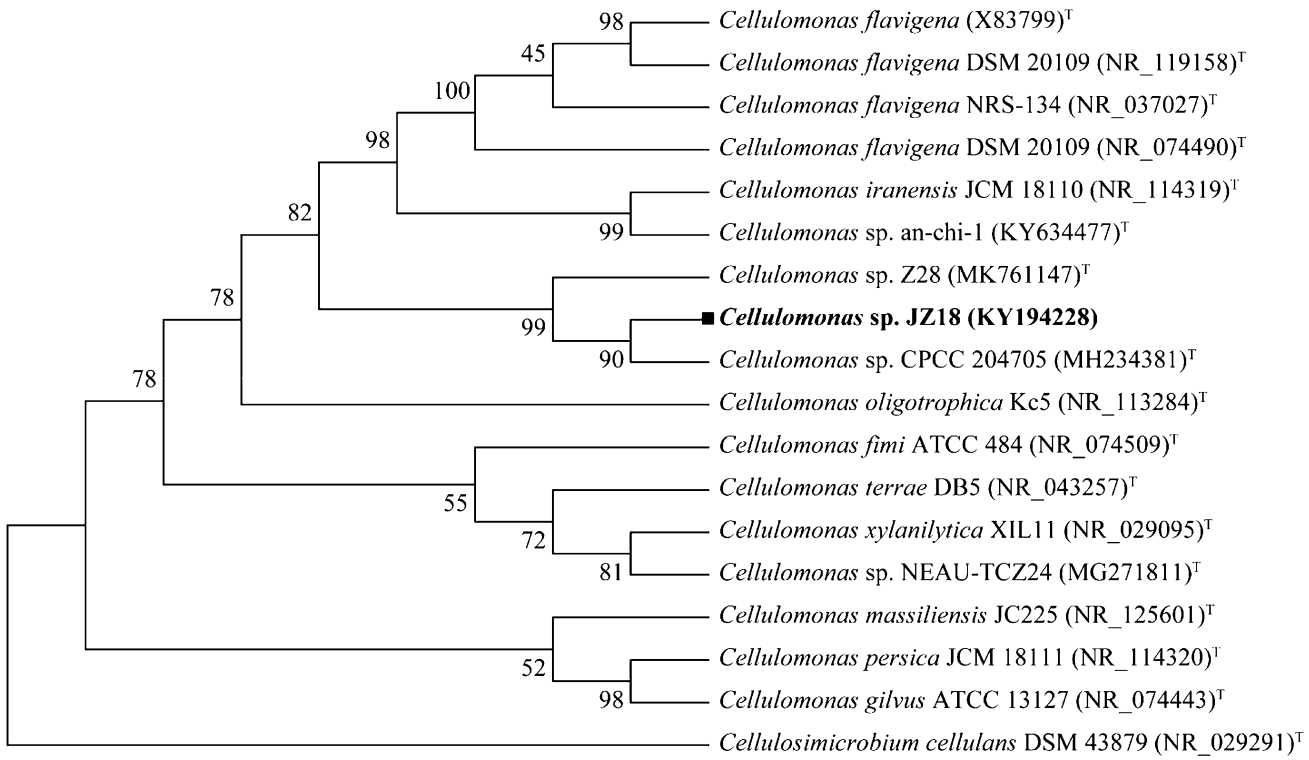

Fig. 1 Phylogenetic analysis of JZ18. Phylogenetic tree generated using 16S rRNA sequence alignment using MUSCLE, evolutionary relationships inferred using the Neighbor-Joining method and the evolutionary distances computed using the Kimura 2-parameter method. GenBank accession numbers of isolates are presented before taxonomic names and type strains are indicated by T. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) are shown next to the branches

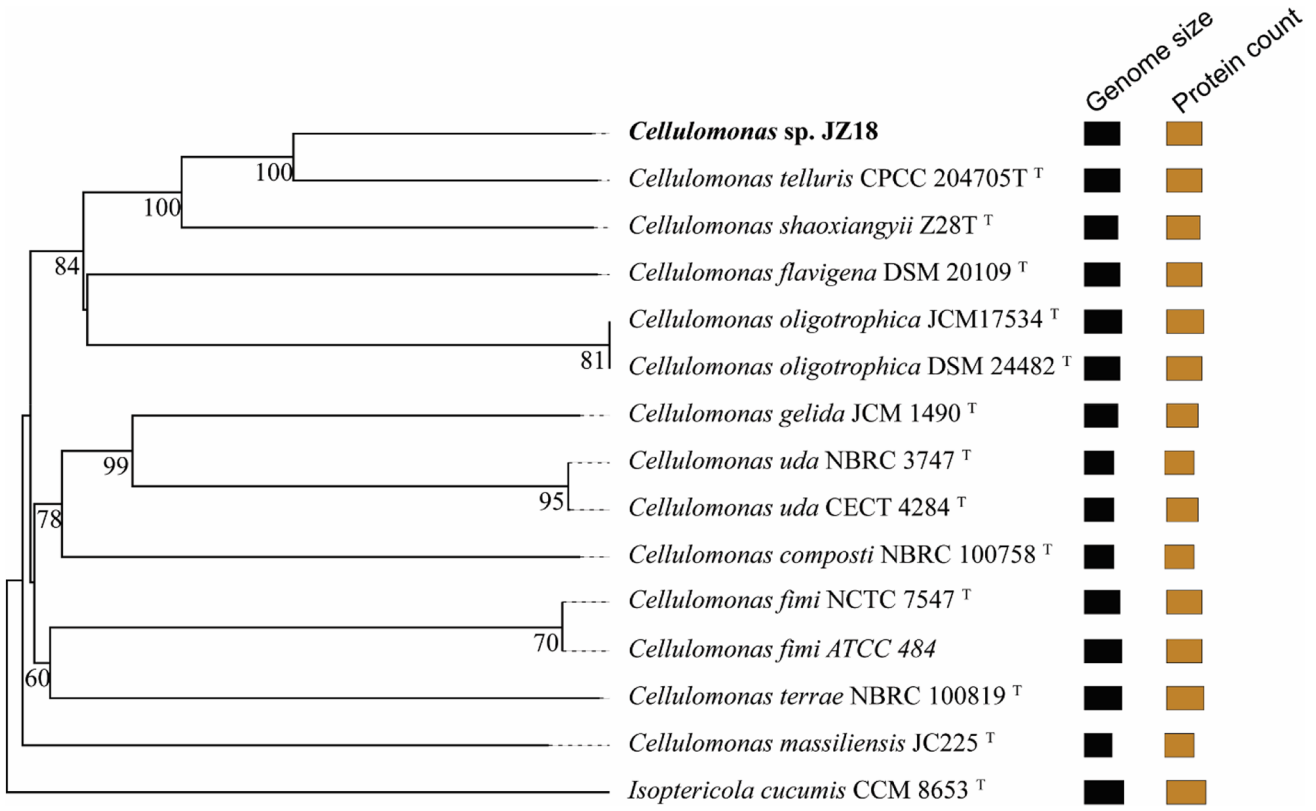

Fig. 2 Genome blast distance phylogeny (GBDP) tree of JZ18 with *Cellulomonas* type strains based on whole-genome sequences. Tree inferred with FastME 2.1.6.1 from GBDP distances calculated from genome sequences [40]. The branch lengths are scaled in terms of GBDP distance formula d_5. The numbers above branches are GBDP pseudo-bootstrap support values > 60% from 100 replications, with an average branch support of 71.7%. The tree was rooted at the midpoint [41]. Type strains are indicated by ^{T}

Table 2 Pairwise comparisons of *Cellulomonas* sp. JZ18 versus type strain genomes

Subject strain	dDDH*			Biosample accession
	(d_0, in %)	(d_4, in %)	(d_6, in %)	
Cellulomonas telluris CPCC 204705T	72.8	35	63.2	SAMN09926135
Cellulomonas shaoxiangyii Z28T	50.2	27.3	43.1	SAMN11356698
Cellulomonas flavigena DSM 20,109	29.8	22.8	27.1	SAMN02598424
Cellulomonas oligotrophica JCM17534	29.4	22.4	26.7	SAMN11869273
Cellulomonas oligotrophica DSM 24,482	31.1	22.4	27.9	SAMN05878280
Cellulomonas fimi ATCC 484	24.9	21.5	23.2	SAMN00713615
Cellulomonas fimi NCTC 7547	24.9	21.5	23.2	SAMEA24553168
Cellulomonas massiliensis JC225	23.1	21.3	21.8	SAMEA2272357
Cellulomonas composti NBRC 1,00,758	20.6	21.2	19.8	SAMD00166262
Cellulomonas uda NBRC 3747	22.6	21.1	21.3	SAMD00093690
Cellulomonas gelida JCM 1490	22	21	20.9	SAMD00245252
Cellulomonas uda CECT 4284	22.7	21	21.5	SAMN12025146
Cellulomonas terrae NBRC 1,00,819	20.4	21	19.6	SAMD00166263
Isoptericola cucumis CCM 8653	15.6	20.4	15.6	SAMD00244873

*The following table contains the pairwise dDDH values between JZ18 genome and the selected type strain genomes. The dDDH values are provided for the three different GBDP formulas: d_0 (a.k.a. GGDC formula 1): length of all HSPs divided by total genome length; d_4 (a.k.a. GGDC formula 2): sum of all identities found in HSPs divided by overall HSP length; d_6 (a.k.a. GGDC formula 3): sum of all identities found in HSPs divided by total genome length

and their constituents (e.g. xylan and cellulose degradation, xylose and cellobiose metabolism), colonization, and motility and chemotaxis (ESM_2 Table S3). These genes may be involved in previously demonstrated salt, osmotic and heat stress in vitro survival phenotypes [23]. However, earlier experiments demonstrated the absence of swimming/swarming motility, which complements the absence of important genes required for flagellar assembly (ESM_1 Fig. S1). A number of xylanses and an endoglucanase were also found and could contribute to potential application for degradation of plant biomass as discussed previously. Interestingly, *C. telluris* CPCC 204705T that was isolated from soil samples in the Badain Jaran desert, and which displayed highest similarity to JZ18 based on the phylogenetic analysis, also produces endoglucanase [27].

AntiSMASH analysis revealed the presence of four clusters for secondary metabolite biosynthesis, three of which were similar to known clusters: Carotenoid (710,466–731,419, BGC0000644, 50% similarity), Desferrioxamine B (2,762,393–2,815,397, BGC0000941, 80%) and Alkylresorcinol (3,770,187–3,782,112, BGC0000282, 100%). Alkylresorcinols are 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 [29–31]. The genome of JZ18 also contains a gene encoding a cutinase (ESM_2 Table S3), a hydrolase that was originally isolated from the fungal plant pathogen *Fusarium solani*, which could play a role in pathogenicity [32, 33].

A gene encoding a pectate lyase is also present and could contribute to plant colonization or virulence [34, 35], but also antifungal potential as discussed in the introduction. Indeed, JZ18 was able to colonize Arabidopsis roots but failed to promote plant growth under salinity stress conditions and had negative growth effects [23]. Despite Arabidopsis not being the native host of JZ18, a previous study found *Cellulomonas* species in the leaves and roots of *Arabidopsis thaliana* [36]. In addition to potentially helping in biocontrol activity, the cutinase and pectate lyase could be of interest as biocatalysts in industrial processes [37–39]. Whether these enzymes, cutinase, endoglucanase, xylanase and pectate lyase, have a superior activity to enzymes currently used in industry has to be tested. Nevertheless, genome sequencing of bacterial endophytes and the biochemical, genomic and phenotypic analyses of these endophytes could pave way for their use in biotechnology and agriculture.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00284-021-02429-5.

Acknowledgements The work presented is part of the DARWIN21 project (http://www.darwin21.org/), with the objective to improve sustainable agriculture on arid lands by exploiting microbes isolated from pioneer desert plants that are able to survive in extreme environmental conditions. The authors would thank all members of Hirt lab, CDA management team and the Bioscience Core Labs in KAUST for the technical assistance and for their help in many aspects of this work.

Author Contributions AE performed the, gDNA extraction and taxonomic analysis. SB performed genome assembly, gene prediction, annotation of genome data, IA integrated all bioinformatics databases and facilitated all genomic annotation platforms. AE, MS, and HH wrote the manuscript. MS, and HH conceived the overall study.

Funding The work was funded by KAUST baseline research project BAS/1/1062-01-01 of H.H.

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.

References

1. Glazer AN, Nikaido H (2007) Microbial biotechnology: fundamentals of applied microbiology, 2nd edn. Cambridge University Press, Cambridge
2. Chaudhary P, Kumar NN, Deobagkar DN (1997) The glucanases of *Cellulomonas*. Biotechnol Adv 15(2):315–331. https://doi.org/10.1016/S0734-9750(97)00010-4
3. Rapp P, Wagner F (1986) Production and properties of xylan-degrading enzymes from *Cellulomonas uda*. Appl Environ Microbiol 51(4):746
4. Clarke JH, Laurie JI, Gilbert HJ, Hazlewood GP (1991) Multiple xylanases of *Cellulomonas fimi* are encoded by distinct genes. FEMS Microbiol Lett 83(3):305–309. https://doi.org/10.1111/j.1574-6968.1991.tb04481.x
5. Cazemier AE, Verdoes JC, van Ooyen AJJ, Op den Camp HJM (1999) Molecular and biochemical characterization of two xylanase-encoding genes from *Cellulomonas pachnodae*. Appl Environ Microbiol 65(9):4099
6. Rajoka MI, Malik KA (1984) Cellulase and hemicellulase production by *Cellulomonas flavigena* NIAB 441. Biotechnol Lett 6(9):597–600. https://doi.org/10.1007/BF00135689
7. Sami AJ, Akhtar MW (1993) Purification and characterization of two low-molecular weight endoglucanases of *Cellulomonas flavigena*. Enzyme Microb Technol 15(7):586–592. https://doi.org/10.1016/0141-0229(93)90021-S
8. Santiago-Hernández A, Vega-Estrada J, del Carmen M-H, Hidalgo-Lara ME (2007) Purification and characterization of two sugarcane bagasse-absorbable thermophilic xylanases from the mesophilic *Cellulomonas flavigena*. J Ind Microbiol Biotechnol 34(4):331–338. https://doi.org/10.1007/s10295-006-0202-4
9. Pérez-Avalos O, Sánchez-Herrera LM, Salgado LM, Ponce-Noyola T (2008) A bifunctional endoglucanase/endoxylanase from *Cellulomonas flavigena* with potential use in industrial processes at different pH. Curr Microbiol 57(1):39–44. https://doi.org/10.1007/s00284-008-9149-1
10. Lisov AV, Belova OV, Lisova ZA, Vinokurova NG, Nagel AS, Andreeva-Kovalevskaya ZI, Budarina ZI, Nagornykh MO, Zakharova MV, Shadrin AM, Solonin AS, Leontievsky AA (2017) Xylanases of *Cellulomonas flavigena*: expression, biochemical characterization, and biotechnological potential. AMB Express 7(1):5. https://doi.org/10.1186/s13568-016-0308-7

11. Marquez-Santacruz HA, Hernandez-Leon R, Orozco-Mosqueda MC, Velazquez-Sepulveda I, Santoyo G (2010) Diversity of bacterial endophytes in roots of Mexican husk tomato plants (*Physalis ixocarpa*) and their detection in the rhizosphere. Genet Mol Res 9(4):2372–2380. https://doi.org/10.4238/vol9-4gmr921
12. Zinniel DK, Lambrecht P, Harris NB, Feng Z, Kuczmarski D, Higley P, Ishimaru CA, Arunakumari A, Barletta RG, Vidaver AK (2002) Isolation and characterization of endophytic colonizing bacteria from agronomic crops and prairie plants. Appl Environ Microbiol 68(5):2198. https://doi.org/10.1128/AEM.68.5.2198-2208.2002
13. Egamberdieva D (2008) Plant growth promoting properties of rhizobacteria isolated from wheat and pea grown in loamy sand soil. Turk J Biol 32(1):9–15
14. Egamberdiyeva D, Höflich G (2002) Root colonization and growth promotion of winter wheat and pea by *Cellulomonas* spp. at different temperatures. Plant Growth Regul 38(3):219–224. https://doi.org/10.1023/A:1021538226573
15. Duy MV, Hoi NT, Ve NB, Thuc LV, Trang NQ (2016) Recent trends in PGPR research for sustainable crop productivity. In: Sayyed RZ, Reddy MS, Al-Turki AI (eds) 4th Asian PGPR conference proceedings, Hanoi, Vietnam, 3-6 May, 2015.
16. Takegawa K, Yamaguchi S, Miki S, Jikibara T, Iwahara S (1991) Purification and characterization of a novel lyase from *Cellulomonas* sp. that degrades *Fusarium* and *Gibberella* acidic polysaccharides. Agric Biol Chem 55(8):1969–1975. https://doi.org/10.1080/00021369.1991.10870925
17. Eida AA, Ziegler M, Lafi FF, Michell CT, Voolstra CR, Hirt H, Saad MM (2018) Desert plant bacteria reveal host influence and beneficial plant growth properties. PLoS ONE 13(12):e0208223. https://doi.org/10.1371/journal.pone.0208223
18. Haft DH, DiCuccio M, Badretdin A, Brover V, Chetvernin V, O'Neill K, Li W, Chitsaz F, Derbyshire MK, Gonzales NR, Gwadz M, Lu F, Marchler GH, Song JS, Thanki N, Yamashita RA, Zheng C, Thibaud-Nissen F, Geer LY, Marchler-Bauer A, Pruitt KD (2017) RefSeq: an update on prokaryotic genome annotation and curation. Nucleic Acids Res 46(D1):D851–D860. https://doi.org/10.1093/nar/gkx1068
19. Tatusova T, DiCuccio M, Badretdin A, Chetvernin V, Nawrocki EP, Zaslavsky L, Lomsadze A, Pruitt KD, Borodovsky M, Ostell J (2016) NCBI prokaryotic genome annotation pipeline. Nucleic Acids Res 44(14):6614–6624. https://doi.org/10.1093/nar/gkw569
20. Kanehisa M, Sato Y, Kawashima M, Furumichi M, Tanabe M (2016) KEGG as a reference resource for gene and protein annotation. Nucleic Acids Res 44(D1):D457–D462. https://doi.org/10.1093/nar/gkv1070
21. Weber T, Blin K, Duddela S, Krug D, Kim HU, Bruccoleri R, Lee SY, Fischbach MA, Müller R, Wohlleben W, Breitling R, Takano E, Medema MH (2015) AntiSMASH 3.0—a comprehensive resource for the genome mining of biosynthetic gene clusters. Nucleic Acids Res 43(W1):W237–W243. https://doi.org/10.1093/nar/gkv437
22. Altschul SF, Madden TL, Schäffer AA, Zhang J, Zhang Z, Miller W, Lipman DJ (1997) Gapped BLAST and PSI-BLAST: a new generation of protein database search programs. Nucleic Acids Res 25(17):3389–3402. https://doi.org/10.1093/nar/25.17.3389
23. Eida AA, Alzubaidy HS, de Zélicourt A, Synek L, Alsharif W, Lafi FF, Hirt H, Saad MM (2019) Phylogenetically diverse endophytic bacteria from desert plants induce transcriptional changes of tissue-specific ion transporters and salinity stress in *Arabidopsis thaliana*. Plant Sci 280:228–240. https://doi.org/10.1016/j.plantsci.2018.12.002
24. Richter M, Rosselló-Móra R, Oliver Glöckner F, Peplies J (2015) JSpeciesWS: a web server for prokaryotic species circumscription based on pairwise genome comparison. Bioinformatics 32(6):929–931. https://doi.org/10.1093/bioinformatics/btv681
25. Meier-Kolthoff JP, Göker M (2019) TYGS is an automated high-throughput platform for state-of-the-art genome-based taxonomy. Nat Commun 10(1):2182. https://doi.org/10.1038/s41467-019-10210-3
26. Meier-Kolthoff JP, Auch AF, Klenk H-P, Göker M (2013) Genome sequence-based species delimitation with confidence intervals and improved distance functions. BMC Bioinform 14(1):60. https://doi.org/10.1186/1471-2105-14-60
27. Shi Y-L, Sun Y, Ruan Z-Y, Su J, Yu L-Y, Zhang Y-Q (2020) *Cellulomonastelluris* sp. nov., an endoglucanase-producing actinobacterium isolated from Badain Jaran desert sand. Int J Syst Evol Microbiol 70(1):631–635. https://doi.org/10.1099/ijsem.0.003806
28. Tian Z, Lu S, Jin D, Yang J, Pu J, Lai X-H, Ren Z-h, Wu X-M, Li J, Wang S, Xu J (2020) *Cellulomonas shaoxiangyii* sp. nov., isolated from faeces of Tibetan antelope (*Pantholops hodgsonii*) on the Qinghai–Tibet Plateau. Int J Syst Evol Microbiol 70(4):2204–2210. https://doi.org/10.1099/ijsem.0.003939
29. Baerson SR, Schröder J, Cook D, Rimando AM, Pan Z, Dayan FE, Noonan BP, Duke SO (2010) Alkylresorcinol biosynthesis in plants. Plant Signal Behav 5(10):1286–1289. https://doi.org/10.4161/psb.5.10.13062
30. Stasiuk M, Kozubek A (2010) Biological activity of phenolic lipids. Cell Mol Life Sci 67(6):841–860. https://doi.org/10.1007/s00018-009-0193-1
31. Ortega MJ, PantojaDelosReyesZubía JJCE (2017) 5-alkylresorcinol derivatives from the Bryozoan *Schizomavella mamillata*: Isolation, synthesis, and antioxidant activity. Mar Drugs 15(11):344. https://doi.org/10.3390/md15110344
32. Lu L, Rong W, Massart S, Zhang Z (2018) Genome-wide identification and expression analysis of cutinase gene family in *Rhizoctonia cerealis* and functional study of an active cutinase RcCUT1 in the fungal–wheat interaction. Front Microbiol. https://doi.org/10.3389/fmicb.2018.01813
33. Schäfer W (1993) The role of cutinase in fungal pathogenicity. Trends Microbiol 1(2):69–71. https://doi.org/10.1016/0966-842X(93)90037-R
34. Yang Y, Zhang Y, Li B, Yang X, Dong Y, Qiu D (2018) A *Verticillium dahliae* pectate lyase induces plant immune responses and contributes to virulence. Front Plant Sci. https://doi.org/10.3389/fpls.2018.01271
35. Kovtunovych G, Lar O, Kamalova S, Kordyum V, Kleiner D, Kozyrovska N (1999) Correlation between pectate lyase activity and ability of diazotrophic *Klebsiella oxytoca* VN 13 to penetrate into plant tissues. Plant Soil 215(1):1–6. https://doi.org/10.1023/A:1004790122353
36. Bai Y, Müller DB, Srinivas G, Garrido-Oter R, Potthoff E, Rott M, Dombrowski N, Münch PC, Spaepen S, Remus-Emsermann M, Hüttel B, McHardy AC, Vorholt JA, Schulze-Lefert P (2015) Functional overlap of the *Arabidopsis* leaf and root microbiota. Nature 528(7582):364–369. https://doi.org/10.1038/nature16192
37. Pio TF, Macedo GA (2009) Cutinases: properties and industrial applications. Adv Appl Microbiol. 66:77–95. https://doi.org/10.1016/S0065-2164(08)00804-6
38. Chen S, Tong X, Woodard RW, Du G, Wu J, Chen J (2008) Identification and characterization of bacterial cutinase. J Biol Chem 283(38):25854–25862. https://doi.org/10.1074/jbc.M800848200
39. Madeira JV, Contesini FJ, Calzado F, Rubio MV, Zubieta MP, Lopes DB, de Melo RR (2017) Chapter 18—Agro-industrial residues and microbial enzymes: an overview on the eco-friendly bioconversion into high value-added products. In: Brahmachari G (ed) Biotechnology of microbial enzymes. Academic Press, Cambridge, pp 475–511. https://doi.org/10.1016/B978-0-12-803725-6.00018-2

40. Lefort V, Desper R, Gascuel O (2015) FastME 2.0: A comprehensive, accurate, and fast distance-based phylogeny inference program. Mol Biol Evol 32(10):2798–2800. https://doi.org/10.1093/molbev/msv150
41. Farris JS (1972) Estimating phylogenetic trees from distance matrices. Am Nat 106(951):645–668