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GENOME REPORTS

Paenibacillus polymyxa ND25: candidate genome for lignocellulosic biomass utilization

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Abstract

Genome sequence of *Paenibacillus polymyxa* ND25 isolated from cow rumen is reported for being a potential candidate in hydrolysis of lignocellulosic plant biomass. Draft genome sequence generated 5.73 Mb data containing 4922 putative protein coding genes, of which 140 are annotated for glycoside hydrolases. *P. polymyxa* ND25 strain comprises diverse lignocellulolytic components, especially 12 cellulase along with 23 hemicellulases and 11 esterases, signifying its potential for lignocellulose hydrolysis. Subsequent enzyme assay exhibited the potential of strain to produce 0.49, 0.24 and 0.44 U/ml U/ml of endoglucanase, exoglucanase and β-glucosidase, respectively, utilizing sugarcane bagasse as the sole carbon source. This study signifies the efficient application of *P. polymyxa* ND25 for facilitating plant-biomass utilization.

Keywords *Paenibacillus polymyxa* ND25 · Genome · Glycoside hydrolases · Cellulase · Hemicellulase · Esterase

Introduction

Lignocellulosic biomass is the most abundant complex biopolymer primarily composed of cellulose, hemicelluloses and lignin. The recalcitrant cellulosic constituent of the lignocelluloses is a rich source of fermentable sugar, obtained by the process known as saccharification (Shirkavand et al. 2016). The enzymatic saccharification process of cellulose is therefore gaining much needed attention worldwide, as it offers a potent renewable energy resource by converting glucose into value-added bioproducts (Aggarwal et al. 2017). In nature, lignocellulosic biomass is degraded by the complex set of synergistically acting enzymes (Sukumaran et al. 2009). Majority of these enzymes belongs to one of the families of glycoside hydrolases (GHs), a subgroup of the carbohydrate-active enzymes (CAZymes) (Lombard et al. 2014). The entire cellulolytic system consists of endoglucanases, exoglucanases and β-glucosidases operating in synergy for complete hydrolysis of cellulose to sugars (He et al. 2017; Sadhu et al. 2013). Cellulases are mainly found in GH1, GH3, GH5, GH6, GH7, GH8 GH9, GH12, GH45, and GH48 families. Similarly hemicellulases hydrolyze bonds within hemicelluloses and are further classified into endoxylanases, xyloglucanases, xylosidases, endomannanases, mannosidases, arabinofuranosidases, fucosidases, glucuronidase, arabinosidase, galactosidase, etc. Hemicellulolytic enzymes are mainly found in GH2, GH10, GH11, GH16, GH26, GH30, GH31, GH36, GH43, GH51, GH74 and GH95 families. Along with GHs, other CAZymes such as carbohydrate esterases (CEs), Polysaccharide lyases (PLs) and carbohydrate-binding modules (CBM) that help in binding enzymes to cellulose or hemicellulose also play crucial role in biomass hydrolysis (López-Mondéjar et al 2016). A broad array of microbes, along with bacteria, fungi, and actinomycetes, are reported to produce cellulases (Bomble et al. 2017; Saini et al. 2015). However, current research is shifted towards bacterial cellulase systems as they have unique cellulolytic mechanisms and high enzyme specificity in their arsenal (Woo et al 2014). *P. polymyxa*, a member of

Accession numbers: The 16S rDNA gene sequence of *P. polymyxa* ND25 was deposited in the GenBank database under accession number KX404921. The whole genome shotgun sequence (WGS) of the strain ND25 was deposited in the NCBI-WGS database under accession number LZEL00000000. The accession numbers and locus tag of cellulase, hemicellulase and esterases are listed in Table 2.

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phyla fermicutes has gained considerable attention primarily for their ability to suppress plant disease or promoting crop growth by nitrogen fixation (Padda et al. 2017). However, its potential for lignocellulosic biomass deconstruction remains largely overlooked as the previous studies are mainly focused on the catalytic efficiency of individual enzymes (Gastelum-Arellanez et al 2014; Weselowski et al 2016). Considering the synergy of the enzymes involved in breakdown of lignocellulosic biomass, the hydrolytic potential of *P. polymyxa* needs to be systematically studied. This study provides an in-depth analysis of *P. polymyxa* ND25 genome for cellulolytic and hemicellulolytic potential. The strain was isolated from cow rumen, a naturally adapted and efficient biomass hydrolyzing habitat. Results reveal the presence of a complex multi-component enzymatic system that support the use of *P. polymyxa* ND25 for effective hydrolysis of cellulosic waste for the large-scale production of value added products.

Materials and methods

Strain isolation, identification and enzymatic activity of *P. polymyxa* ND25

Paenibacillus polymyxa ND25 was isolated from the cattle rumen sample by plating the sample on Bergs minimal salt (BMS) agar media (Pawar et al. 2015) amended with CMC and incubated at 37 °C. After 48 h, agar plates were stained with 0.1% congo red for the presence of clear halos around bacterial colonies indicating CMC hydrolysis. Cellulase production efficiency of the bacterial isolates was further tested during growth in BMS minimal medium with CMC, avicel, corn starch, rice straw and sugarcane bagasse as the sole carbon source. Cellulose hydrolyzing efficiency was estimated based on endoglucanacse, exogucanase, β-glucosidase activitiy and soluble COD (sCOD) concentration of supernatant (Nitisinpraserta and Temmes 1991; An et al. 2004).

The bacterial 16S rRNA gene of the strain ND25 was sequenced using the primers 27F and 1492R as described by Dafale et al. (2010). For identification sequencing results were compared using the Basic Local Alignment Search Tool (BLAST) program on NCBI.

DNA extraction, genome sequencing, gene assembly prediction

Genome sequencing approach was used for exploring genes responsible for lignocellulose hydrolysis present in the genome of *P. polymyxa* ND25. Genomic DNA extraction from *P. polymyxa* ND25 was carried out using Fast DNA SPIN Kit for Soil from MP Biomedicals following manufacturer's instruction. Nanodrop 8000 and Qubit® 2.0 Fluorometer were used for determination of A260/280 ratio and concentration, respectively. Illumina TruSeq Nano DNA HT Library Preparation Kit was used for generating paired-end sequencing library which was analyzed using High Sensitivity DNA chip in Bioanalyzer 2100. Cluster generation and sequencing was performed using Illumina Miseq platform. The 5.73 Mb high-quality data was assembled into 105 contigs using Velvet on optimized k-mer. The genome was annotated using the NCBI prokaryotic genomes automatic annotation pipeline (PGAAP). Graphical Comparison of *P. polymyxa* ND25 genome with its closest neighbor, *P. polymyxa* M1 (accession no. NC_017542.1), *P. polymyxa* Sb3-1 (accession no NZ_CP010268.1) and *P. polymyxa SC2* (accession no. NC_014622.2) was performed using CGView server (http://stothard.afns.ualberta.ca/cgview_server/) using default parameters. Analysis of sequenced genome was achieved using dbCAN carbohydrate-active enzymes (CAZy) annotation algorithm from dbCAN pipelines (http://csbl.bmb.uga.edu/dbCAN/index.php) against the Carbohydrate-Active Enzymes database (http://www.cazy.org/) (Yin et al. 2014; Lombard et al. 2014) for identifying genes responsible in lignocellulose deconstruction. Functional characterization of CDSs annotated by dbCAN as GHs was done against NCBI's non-redundant (nr) database and protein data bank (pdb) using the BLASTP algorithm (Gujar et al. 2018). For comparing GHs distribution within *P. polymyxa* strains, genome sequences of 28 available strains were retrieved from NCBI database and were annotated using dbCAN carbohydrate-active enzymes (CAZy) annotation algorithm. Name and accession numbers of the strain retrieved from NCBI database are provided in supplementary table 1.

Results and discussion

Identification and cellulolytic potential of the *P. polymyxa* ND25

Exploration of natural habitat where lignocelluloses represents an important resource is a promising strategy for isolation of bacterial strains helpful in biomass hydrolysis. In this context, cattle rumen was explored for identifying bacterial strains with novel enzymatic machinery well adapted to harsh conditions in biomass conversion occurring in these ecosystems. Bacterial isolate ND25, initially isolated from cattle rumen exhibited the ability to utilize diverse carbon source—CMC, rice straw, corn powder, avicel and sugarcane bagasse (SB) for efficient production of extracellular cellulase (fig. S1). Maximal enzyme production, 0.49 U/ml endoglucanase, 0.24 U/ml exoglucanase and 0.44 U/ml β-glucosidase activity was observed when 2% SB was used as sole carbon source. SB hydrolysis by the strain ND25 was simultaneously depicted by

the significant rise in sCOD from 548 to 1975 mg/l after 48 h with no significant change in sCOD of control variant (fig. S2).The observed rise in sCOD concentration reflects hydrolysis of insoluble organic components of SB into soluble fermentable sugars.

The isolate, referred to ND25, was identified as *P. polymyxa* by analysis of 16S rRNA gene sequence and showed closest match with *P. polymyxa* M1, *P. polymyxa* Sb3-1and *P. polymyxa SC2*. A circular map comparing *P. polymyxa* ND25 with the whole genome of above three closest matches can be viewed in Fig. 1. Graphical representation of genome by CGView server shows nearly 90% similarities with the other three strains. The figure also reveals the presence of protein coding genes which are unique to *P. polymyxa* ND25.

Genomic features of *P. polymyxa* ND25

Genome assembly generated 105 scaffolds containing 5.73 Mb of DNA. Gene prediction revealed 4922 protein-coding genes, 100 tRNA genes and 14 rRNA genes (Table 1). dbCAN carbohydrate-active enzymes (CAZy) annotation algorithm identified 328 (6.66%) genes among the predicted protein belong to CAZy family, comprising 140 glycoside hydrolases (GHs), 52 carbohydrate esterases (CEs), 13 polysaccharide lyases (PLs), 72 Glycosyl transferases (GTs) and 5 proteins with auxiliary activities (AAs). Cazymes often

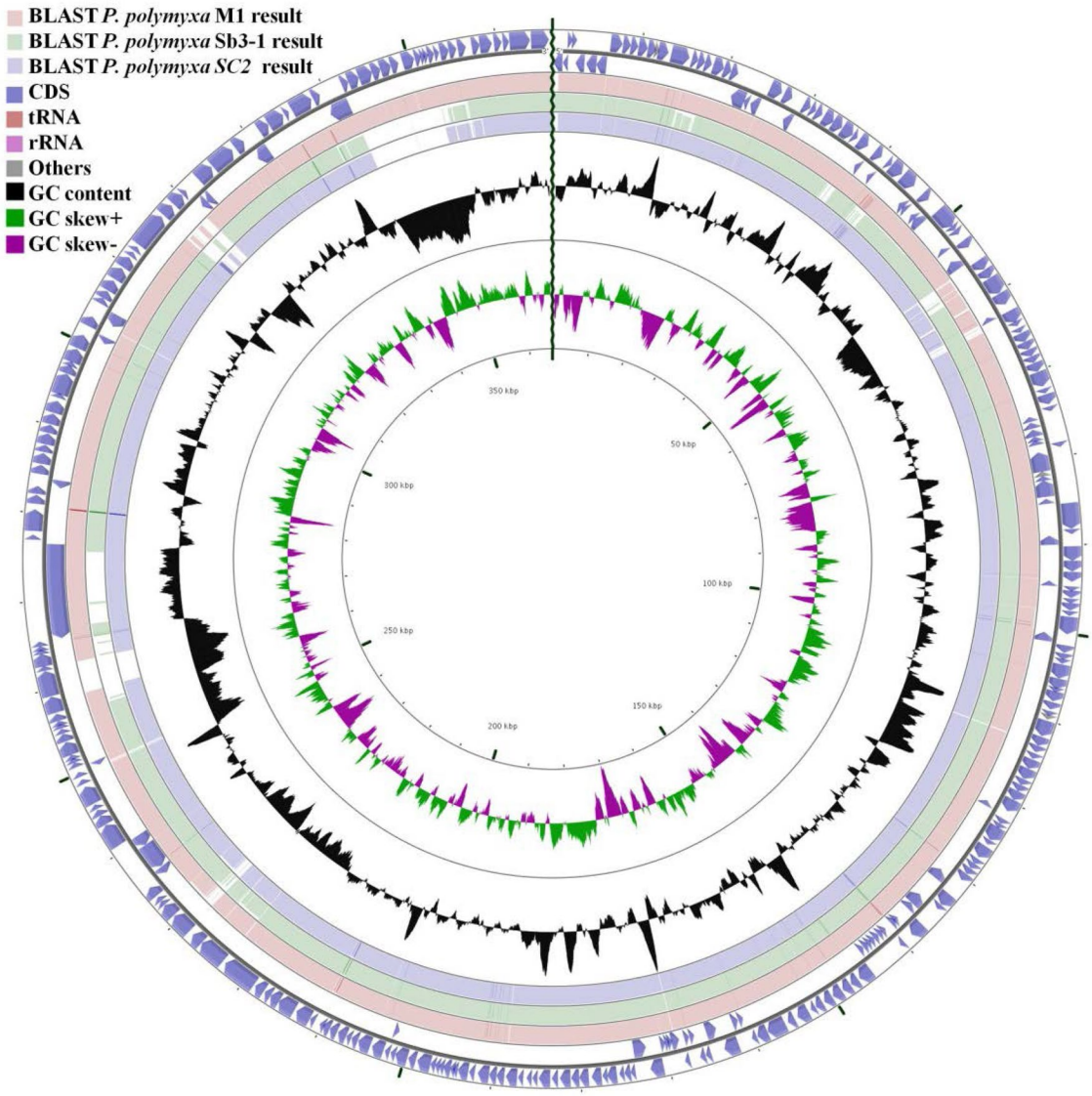

Fig. 1 Graphical comparision of *P. polymyxa* ND25 genome with *P. polymyxa* M1 (accession no. NC_017542.1), *P. polymyxa* Sb3-1(accession no NZ_CP010268.1) and *P. polymyxa* SC2 (accession no. NC_014622.2) genome retrireved from NCBI database using CGView server using default parameters

Table 1 Genome feature of *P. polymyxa* ND25

Features	*P. polymyxa* ND25
NCBI accession no.	LZEL00000000
Genome size (Mb)	5.73
G + C content (%)	45.2
Number of contigs	105
Total number of genes	5265
Protein coding genes	4922
tRNA genes	100
rRNA	14
Pseudo gene	225

display associated modular structure which helps in adhesion to the carbohydrates, additionally covering 66 carbohydrate binding modules (CBMs) and 38 surface layer homology domains (SLH). The predicted GHs belonged to 46 different families and several genes were assigned to GH families engaged in cellulolytic and hemicellulolytic deconstruction. Genes belonging to GH6, GH48 (cellulolytic) and GH11, GH16, GH31, GH95 (hemicelulolytic) families were found in single copy number in the genome. Genes from families GH1 (10), GH2 (3), GH3(4), GH5 (6), GH510 (2), GH26 (6), GH30 (2) GH36 (4), GH43 (9) and GH51 (3) encoding putative β-glucosidases, β-xylanases and α-glucuronidase, α-*N*-arabinofuranosidase, α-arabinosidase, α-galactosidase, β-mannanase, β-mannosidase β-xylosidase, 1,3-β-glucanase, xyloglucanase, and other hemicellulases were more abundant. The number of genes belonging to these families in *P. polymyxa* ND25 were higher (55) in comparison with other *P. polymyxa* strains such as E681, ATCC 842, YUPP-8, CCI-25, YC0136, J and ND25, but were similar in strains SC2, M1, SQR 21, Sb3-1, A18,

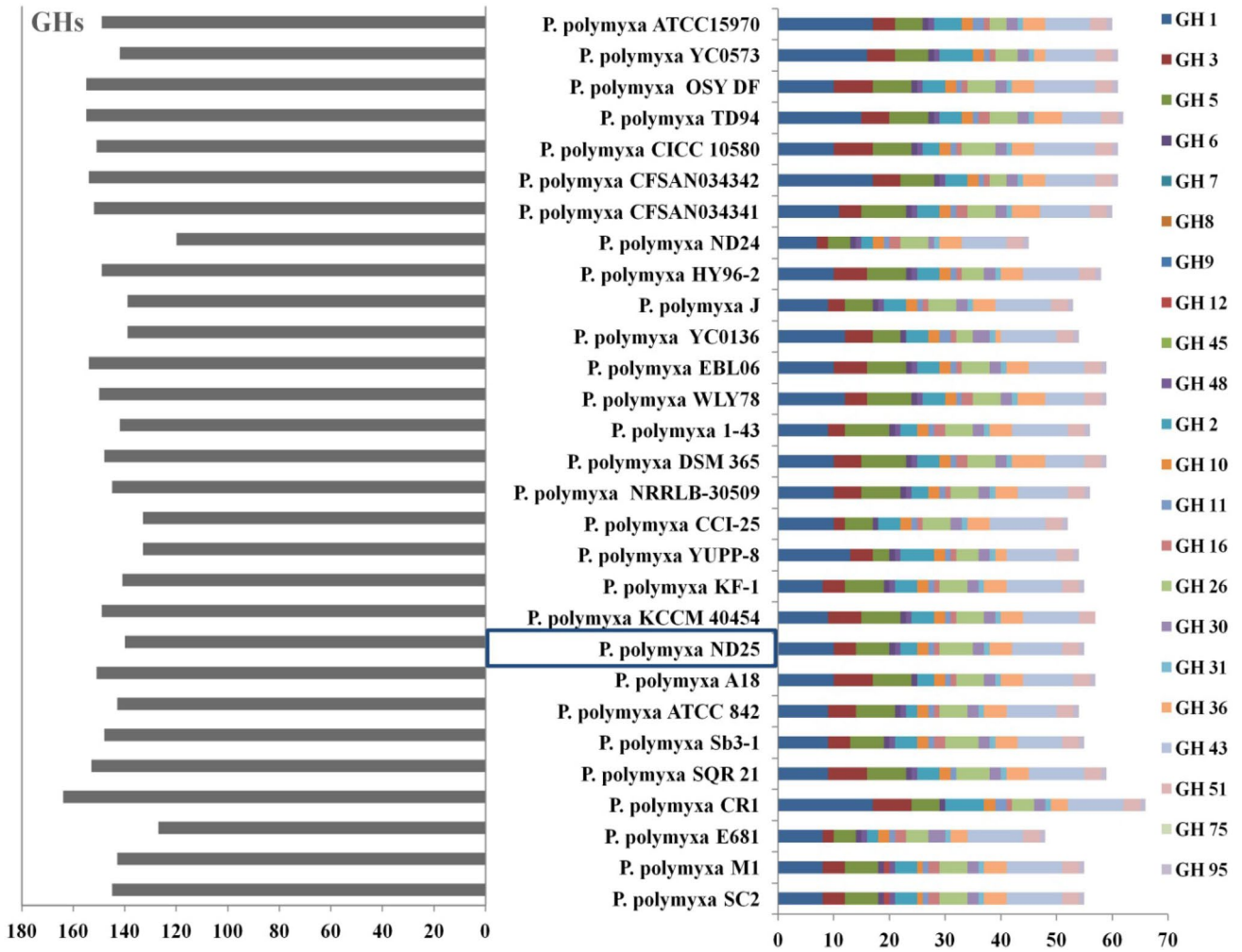

Fig. 2 Predicted numbers of glycosyl hydrolases (GH) in the genome of *P. polymyxa* ND25 and other strains of *P. polymyxa*. On the *left* total number of GHs annotated in the genome; on the *right* gene content in GH families containing enzymes involved in the hydrolysis of cellulose and hemicelluloses

Table 2 Predicted CAZymes and other potential lignocellulolytic enzymes in the *P. polymyxa* ND25 genome

Enzymes	Specific activity	Accession number	Locus tag	protein product
Cellulose hydrolyzing enzyme	1,4-β-glucanase	NZ_LZEL01000017.1	A9Z39_RS03585	WP_064961946.1
		NZ_LZEL01000059.1	A9Z39_RS15650	WP_013370478.1
		NZ_LZEL01000092.1	A9Z39_RS21070	WP_064963809.1
		NZ_LZEL01000105.1	A9Z39_RS25850	WP_064964340.1
		NZ_LZEL01000103.1	A9Z39_RS23700	WP_013371259.1
	Cellobiohydrolase	NZ_LZEL01000038.1	A9Z39_RS08400	WP_064962464.1
	Cellulose 1,4-β-cellobiosidase	NZ_LZEL01000090.1	A9Z39_RS20820	WP_064963763.1
	β-glucosidase	NZ_LZEL01000001.1	A9Z39_RS00395	WP_064961610.1
		NZ_LZEL01000009.1	A9Z39_RS02380	WP_081275875.1
		NZ_LZEL01000038.1	A9Z39_RS08065	WP_064962420.1
		NZ_LZEL01000069.1	A9Z39_RS17230	WP_064963359.1
		NZ_LZEL01000082.1	A9Z39_RS19335	WP_058831074.1
Hemicellulose hydrolyzing enzyme	1,4-β-Xylanase	NZ_LZEL01000051.1	A9Z39_RS10975	WP_064962744.1
		NZ_LZEL01000051.1	A9Z39_RS11750	WP_013373834.1
		NZ_LZEL01000082.1	A9Z39_RS19790	WP_013373220.1
	α-Glucuronidase	NZ_LZEL01000051.1	A9Z39_RS11100	WP_064962760.1
	β-Xylosidase	NZ_LZEL01000051.1	A9Z39_RS11095	WP_064962759.1
		NZ_LZEL01000051.1	A9Z39_RS11205	WP_064962774.1
		NZ_LZEL01000095.1	A9Z39_RS21905	WP_064963876.1
	α-*N*-arabinofuranosidase	NZ_LZEL01000009.1	A9Z39_RS02435	WP_013368995.1
		NZ_LZEL01000052.1	A9Z39_RS12365	WP_064962897.1
		NZ_LZEL01000059.1	A9Z39_RS15295	WP_013370551.1
	α-Arabinosidase	NZ_LZEL01000038.1	A9Z39_RS09345	WP_013369503.1
		NZ_LZEL01000059.1	A9Z39_RS15300	WP_064963160.1
	α-Galactosidase	NZ_LZEL01000002.1	A9Z39_RS01995	WP_064961784.1
		NZ_LZEL01000010.1	A9Z39_RS02585	WP_064961848.1
		NZ_LZEL01000038.1	A9Z39_RS08405	WP_013369680.1
		NZ_LZEL01000038.1	A9Z39_RS08545	WP_064962603.1
		NZ_LZEL01000103.1	A9Z39_RS23940	WP_064964112.1
		NZ_LZEL01000105.1	A9Z39_RS25470	WP_013369213.1
	β-Mannanase	NZ_LZEL01000105.1	A9Z39_RS25500	WP_064964301.1
	β-Mannosidase	NZ_LZEL01000001.1	A9Z39_RS01360	WP_064961733.1
		NZ_LZEL01000017.1	A9Z39_RS05635	WP_016324529.1
	1,3-β-Glucanase	NZ_LZEL01000011.1	A9Z39_RS02725	WP_040103108.1
	Xyloglucanase	NZ_LZEL01000103.1	A9Z39_RS24390	WP_064964170.1
	Acetyl esterase	NZ_LZEL01000001.1	A9Z39_RS00060	WP_064961572.1
		NZ_LZEL01000011.1	A9Z39_RS02710	WP_040103109.1
	Acyl-CoA thioesterase	NZ_LZEL01000095.1	A9Z39_RS21460	WP_064963835.1
		NZ_LZEL01000095.1	A9Z39_RS21910	WP_014599583.1
	Carboxylesterase	NZ_LZEL01000038.1	A9Z39_RS07380	WP_064962350.1
		NZ_LZEL01000038.1	A9Z39_RS09375	WP_064962583.1
	Esterase	NZ_LZEL01000001.1	A9Z39_RS01310	WP_064961709.1
		NZ_LZEL01000017.1	A9Z39_RS05525	WP_064962144.1
		NZ_LZEL01000028.1	A9Z39_RS06675	WP_064962311.1
		NZ_LZEL01000090.1	A9Z39_RS20290	WP_064963675.1
		NZ_LZEL01000095.1	A9Z39_RS21910	WP_014599583.1

KCCM 40454, KF-1, NRRLB-30509, DSM 365, 1–43, WLY78, EBL06 and HY96-2. Although the strains SC2, M1, SQR 21, CR1 and A18 have comparatively higher number of GHs, the total count of genes responsible for cellulolytic and hemicellulolytic activity remains same in SC2, M1, SQR 21 whereas the CR1 lacks hydrolytic enzyme from GH48 family, responsible for exoglucanase activity (Fig. 2). Further analysis of *P. polymyxa* ND25 genome revealed the presence of 12 cellulase genes comprising five endoglucanases gene, two exoglucanases and five β-glucosidase genes. Additionally 42 GH's responsible for hydrolysis of hemicelluloses, four 1,4-β-xylanase, one α-glucuronidase, three β-xylosidase, three α-*N*-arabinofuranosidase, three α-*N*-arabinofuranosidase, two α-arabinosidase, six α-galactosidase, one β-mannanase, two β-mannosidase, one 1,3-β-glucanase, one xyloglucanase were also annotated. Moreover, 11 esterase genes, including two acetyl esterase, two acyl-CoA thioesterase, two carboxylesterase and five esterases responsible for complex carbohydrate degradation have also been annotated in *P. polymyxa* ND25 genome (Table 2). The presence of both types of plant cell wall-degrading enzyme is crucial for hydrolyzing lignocellulosic biomass. The presence of wide ranges of cellulase and hemicellulase in the genome depicts the great potential of *P. polymyxa* ND25 for hydrolysis of various types of hemicellulosic biomass. Therefore, the enzyme system of *P. polymyxa* ND25 exhibits itself as potentially more efficient in degrading lignocellulosic biomass.

Conclusion

Genomic approach for analyzing the hydrolytic arsenal for new cellulolytic isolates reveals a promising strategy for ultimately enhancing the biomass conversion process. Preliminary genomic analysis of *P. polymyxa* ND 25 revealed diverse lignocellulolytic enzyme system covering five endoglucanases (GH5), two exoglucanases (GH6 and GH48) and five β-glucosidase genes (GH1, GH3). Additionally 42 GHs responsible for hydrolysis of hemicelluloses along with 11 esterase genes were observed which support in effective utilization of plant biomass. Genome information will be useful for exploring the potential of *P. polymyxa* ND 25 and substantiate its application for the production of biogas and/or other value-added products.

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Compliance with ethical standards

Conflict of interest The authors declare no financial or commercial conflict of interest.

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