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ORIGINAL ARTICLE

Comparative genome analysis of *Bacillus velezensis* reveals a potential for degrading lignocellulosic biomass

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Abstract

Genomes of 24 sequenced *Bacillus velezensis* strains were characterized to identity shared and unique genes of lignocellulolytic enzymes and predict potential to degrade lignocellulose. All 24 strains had genes that encoded lignocellulolytic enzymes, with potential to degrade cellulose and hemicelluloses. Several lignocellulosic genes related to cellulose degradation were universally present, including one GH5 (endo-1,4-β-glucanase), one GH30 (glucan endo-1,6-β-glucosidase), two GH4 (6-phospho-β-glucosidase, 6-phospho-α-glucosidase), one GH1 (6-phospho-β-galactosidase), one GH16 (β-glucanase) and three GH32 (two sucrose-6-phosphate hydrolase and levanase). However, in the absence of gene(s) for cellobiohydrolase, it was predicted that none of the 24 strains would be able to directly hydrolyse cellulose. Regarding genes for hemicellulose degradation, four GH43 (1,4-β-xylosidase; except strain 9912D), one GH11 (endo-1,4-β-xylanase), three GH43 (two arabinan endo-1,5-α-L-arabinosidase and one arabinoxylan arabinofuranohydrolase), two GH51 (α-N-arabinofuranosidase), one GH30 (glucuronoxylanase), one GH26 (β-mannosidase) and one GH53 (arabinogalactan endo-1,4-β-galactosidase) were present. In addition, two PL1 (pectate lyase) and one PL9 (pectate lyase) with potential for pectin degradation were conserved among all 24 strains. In addition, all 24 *Bacillus velezensis* had limited representation of the auxiliary activities super-family, consistent with a limited ability to degrade lignin. Therefore, it was predicted that for these bacteria to degrade lignin, pretreatment of lignocellulosic substrates may be required. Finally, based on in silico studies, we inferred that *Bacillus velezensis* strains may degrade a range of polysaccharides in lignocellulosic biomasses.

Keywords *Bacillus velezensis* · Lignocellulosic enzymes · Lignocellulose degradation · Comparative genomics analysis · Lignocellulosic biomasses

Introduction

Lignocellulosic biomass degradation using microbial is considered as "green biorefinery" and economically viable alternatives to physical and chemical methods (Capolupo and Faraco 2016). Some *Bacillus* bacteria can degrade various kinds of lignocellulose products, including lignin (Bandounas

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et al. 2011; Huang et al. 2013; Zhu et al. 2014) cellulose and hemicellulose (Khelil et al. 2016; Gong et al. 2017b). Detailed knowledge of their genome would provide more insights into lignocellulose degradation; however, *Bacillus* capable of degrading lignocellulose have not been well characterized (Gong et al. 2017a). Recently, *Bacillus amyloliquefaciens* subsp. *plantarum, Bacillus methylotrophicus* and *Bacillus oryzicola* were re-classified into a single species (*Bacillus velezensis*) (Dunlap et al. 2016). Several complete genome sequencing of *B. velezensis* strains have been reported to encoding enzymes related to the degradation of lignocelluloses (Niazi et al. 2014; Chen et al. 2009; He et al. 2012; Kim et al. 2017b; Liu et al. 2017). However, it has yet to attract enough attention of potential use in conversion of lignocellulose into useful chemicals and fuels. There are many reports regarding the use of *B. velezensis* as a biocontrol agent, as it is capable of enhancing plant growth and generating secondary metabolites that suppress proliferation of pathogenic microbes (Jin et al. 2017; Chen 2017; Kim et al. 2017a; Pan et al. 2017; Molinatto et al. 2016; Belbahri et al. 2017). Potential for new applications utilizing *B. velezensis* strains with wide metabolic capabilities may be ignored. Therefore, a thorough analysis of the genome and comprehensive comparative genomics studies are needed to elucidate the potential for degradation of lignocellulose components by strains of *B. velezensis* and for evidence-based predictions regarding their use in biomass transformation. Previously, we reported the complete genome of *B. velezensis* 157 and noted it encoded lignocellulolytic enzymes with potential to degrade cellulose, xylan, lignin, starch, mannan, galactoside and arabinan (Chen et al. 2018). In addition, ANI analysis was used to generate genome comparisons, alignments and phylogenetic reconstructions of *B. velezensis* (Suppl. Figure S1). It was possible to culture *B. velezensis* 157 on pretreated maize straw, with extent of breakdown confirmed by scanning electron microscopy and determination of lignocellulosic concentration (Suppl. Figure S2 and Suppl. Table S1).

In this study, complete genomes of 24 *B. velezensis* strains retrieved from NCBI database have been mined for genes contributing to carbohydrate-active enzymes, and we conducted a comparative genomics analysis of *B. velezensis* to show the important commonality and specificity involving lignocellulolytic enzyme genes in genomics of one species. This is the first report to show that *B. velezensis* was neglectful and unexploited resource for degrading lignocelluloses based on comparative genomics analysis.

Materials and methods

Homology-based gene mining of contributing to ligocellulose degradation

Genomes of *B. velezensis* used in the study were accessed from the GenBank DNA database; they had been submitted without scaffolds as of November, 2017 and listed as *B. velezensis* (Suppl Table S2). Nucleotide data, amino acid sequences and deduced coding sequences were all retrieved. Both dbCAN (http://csbl.bmb.uga.edu/dbCAN/annotate.php) and dbCAN HMMs, version 4.0 (Yin et al. 2012) were used to analyze sequences. Then, a CAZy database (Lombard et al. 2014) was used to assess CAZyme proteins, with OrthMCL software and manual annotations used for analysis of homologous families.

Results and discussion

Genes capable of lignocelluloses degradation were detected in 24 *B. velezensis* strains, indicating commonality and specificity of lignocellulolytic these bacteria (Table 1 and Suppl. Table S3). The use of various *Bacillus* sp. including *Bacillus licheniformis, Bacillus pumilus, Bacillus amyloliquefaciens* DL-3, *Bacillus halodurans* and *Bacillus subtilis* YJ1 as cellulolytic enzymes has been reported. Endoglucanases (EC 3.2.1.4) from *Bacillus* are usually related to GH5 families (Pandey et al. 2014). There were common celluloytic enzyme genes in 24 *B. velezensis* strains, including one GH5 (endo-1,4-β-glucanase) and one GH30 (glucan endo-1,6-β-glucosidase). In addition, other strains (e.g., *B. velezensis* 157) had the GH1 as a potential β-glucosidase to utilize cellobiose. However, due to a lack of cellobiohydrolase, none of the strains were able to directly hydrolyze cellulose (Hahnke et al. 2015). Two GH4 (6-phospho-β-glucosidase, 6-phospho-α-glucosidase), one GH1 (6-phospho-β-galactosidase) and one GH16 (β-glucanase) were also able to degrade cellulose.

Common genes with the ability to degrade hemicelluloses were detected in the 24 strains. One GH11 (endo-1,4-β-xylanase), endo-1, 4-β-xylanase (EC 3.2.1.8), a key enzyme-degrading xylan, catalyzes hydrolysis of β-1,4-xylosidic linkages of xylan into short xylooligosaccharides. Xylanases, are mainly classified into GH10 and GH11. Compared with GH10, xylanases from GH11 that were smaller (~ 20 kDa) and lacked cellulase activity easily penetrated a cellulose fiber network without damaging fiber, making them appropriate for pulp bleaching (Bai et al. 2015). Three GH43 (two arabinan

Table 1 Annotated common genes encoding lignocellulose-degrading enzymes of 24 *B. velezensis* strains mainly on cellulose and hemicelluloses

	Predicted function
Cellulose-related	GH5 (endo-1,4-β-glucanase EC 3.2.1.4)
	GH30 (glucan endo-1,6-β-glucosidase EC 3.2.1.-)
	GH4 (6-phospho-β-glucosidase EC 3.2.1.86) GH4 (6-phospho-α-glucosidase EC 3.2.1-)
	GH1 (6-phospho-β-galactosidase EC 3.2.1.85)
	GH16 (β-glucanase EC 3.2.1.-)
	GH32 (sucrose-6-phosphate hydrolase EC 2.4.1.-) GH32 (sucrose-6-phosphate hydrolase EC 2.4.1.-) GH32 (levanase EC 3.2.1.65) GH13 (α-glucosidase EC 3.2.1.20)
	PL1 (pectate lyase EC 4.2.2.-) PL1 (pectate lyase EC 4.2.2.-)
	PL9 (pectate lyase EC 4.2.2.2)
Hemicellulose-related	GH11 (endo-1,4-β-xylanase EC 3.2.1.8)
	GH26 (β-mannosidase EC3.2.1.78)
	GH43 (arabinan endo-1,5-α-L-arabinosidase EC 3.2.1.-) GH43 (arabinan endo-1,5-α-L-arabinosidase EC 3.2.1.-) GH43 (arabinoxylan arabinofuranohydrolase EC 3.2.1.-) GH43 (1,4-β-xylosidase EC 3.2.1.37)(except strain 9912D)
	GH51 (α-N-arabinofuranosidase EC 3.2.1.55) GH51 (α-N-arabinofuranosidase EC 3.2.1.55)
	GH30 (glucuronoxylanase EC 3.2.1.-)
	CE 7 (acetylxylan esterase EC 3.1.1.72)
	CE 3 (acetylxylan esterase EC 3.1.1.72)
	GH53 (arabinogalactan endo-1,4-β-galactosidase EC 3.2.1.89)

endo-1,5-α-L-arabinosidase, one arabinoxylan arabinofuranohydrolase), two GH51 (α-N-arabinofuranosidase), and one GH30 (glucuronoxylanase) were the other important members, which are responsible for the degradation of xylan. We concluded that enzymes in *B. velezensis* capable of degrading hemicellulose had potential for use in various industries (food, feed, paper production, biofuel and xylooligosacharide production). In addition, there were common carbohydrate esterases (CE), with potential to de-acetylate xylans and xylooligosaccharides. One CE3, a potential acetyl xylan esterase, enhanced solubilization of xylan (Zhang et al. 2011). In addition, one CE 7 (acetylxylan esterase) was expected to be able to degrade xylan (Mamo et al. 2006). The existence of these genes in *B. velezensis* 157 and other *B. velezensis* strains may be important in enzymatic degradation of cellulose and hemicellulose (Suppl Table S1).

There were common lignocellulose-degrading enzymes including three GH32 (two sucrose-6-phosphate hydrolase and levanase) able to hydrolyze sucrose (Bezzate et al. 1994), one GH53 (arabinogalactan endo-1,4-β-galactosidase), an enzyme that hydrolyses (1→4)-β-D-galactosidic linkages in type I arabinogalactans (Vanholme et al. 2009) in plant cell walls, and one GH26 (β-mannosidase) that hydrolyses the terminal mannose of mannan polysaccharides (Onilude et al. 2013). Furthermore, all 24 strains contained two PL1 (pectate lyase) and one PL9 (pectate lyase) capable of degrading pectin. Pectate lyase (EC 4.2.2.2) typically causes eliminative cleavage of (1→4)-α-D-galacturonan, yielding oligosaccharides with 4-deoxy-α-D-galact-4-enuronosyl groups at their non-reducing ends (See-Too et al. 2017). In addition, six CE4 (polysaccharide deacetylase) involved in degradation of plant polysaccharides were also identified. Although these CE4 are highly specific acetylxylan esterases, they are unable to degrade acetyl galactoglucomannan or acetylated manno-compounds. Furthermore, this family also has peptidoglycan N-deacetylates that can degrade chitin (Biely 2012). Moreover, there was one CBM3 with a cellulose-binding function and one CBM6 capable of binding amorphous cellulose and β-1,4-xylan; although these were non-catalytic modules, they could bring GHs into contact with complex substrates (Sun et al. 2016).

Regarding specificity, only *B. velezensis* 9912D lacked the 1,4-β-xylosidase gene related to GH43. This gene is important for degrading xylan, although xylanases are not capable of complete hydrolysis of xylans (Romero et al. 2012). Strain 9912D, with the greatest spore yield and most antagonistic activity against phytopathogenic fungi, had been derived from wild-type 9912 by chemical and physical mutagenesis, which may have resulted in loss of some genes (Pan et al. 2017). *B. velezensis* 157 revealed a significantly higher number of six GH13 (one α-amylase, three

α-glucosidase, α-glycosidase and α-α-phosphotrehalase) and CBM34 than that found in genomes of related *B. velezensis*, which are responsible for hydrolyzing starch (Graebin et al. 2016). Meanwhile, *B. velezensis* 157 with one GH65 (maltose phosphorylase), was expected to be able to degrade trehalose (Inoue et al. 2002). All the *B. velezensis* strains had very limited presence of the auxiliary activities super-family, including AA4, AA6, AA7 and AA10. Family AA4 includes vanillyl-alcohol oxidases (VAO) with the ability to convert various phenolic compounds with side chains located at the para-position of the aromatic ring (Heuvel et al. 2002). In addition, enzymes related to AA7 may be able to biotransform or detoxify lignocellulosic compounds (Levasseur et al. 2013). However, several *Bacillus* strains have been reported to degrade lignin or lignin model compounds. For example, *Bacillus* sp. LD003 was sustained on lignin fractions and it decolorized various dyes, including Azure B, Methylene blue and Toluidine blue O (Luaine et al. 2011). In addition, *Bacillus pumilus* C6 and *Bacillus atrophaeus* B7, chosen due to their substantial laccase activity, degraded kraft lignin and dimer guaiacylglycerol-b-guaiacyl (Huang et al. 2013). Therefore, due to a lack of ligninolytic enzymes among 24 *B. velezensis* strains, lignin processing would require appropriate pretreatments.

Most strains of *B. velezensis* are symbiotic, mainly rhizobacterium with a range of enzymes capable of hydrolyzing various compounds, including polysaccharides and proteins. The enzyme activities of *B. velezensis* enable it to function at the rhizoplane. Based on genomic analysis of 24 *B. velezensis* strains, with its potential to degrade cellulose and hemicellulose, this bacterium should be able to degrade a broad range of polysaccharides and possibly a new application for *B. velezensis* in the conversion of lignocelluloses into useful product.

Conclusion

Various strains of *B. velezensis* are already used in agriculture, as they are able to augment growth of plants and suppress growth of pathogens. Based on the findings herein, we concluded that *B. velezensis* may be able to use lignocelluloses, thereby broadening the industrial use of this bacterium. Genes for common and specific lignocellulolytic enzyme genes were detected in *B. velezensis*. In future studies, effects of strain source and culture conditions on enzyme capabilities should be determined.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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