TROPICAL LIFE SCIENCES RESEARCH

# Invited Review: Biodeviersity of Plant Polysaccharide-Degrading Bacteria in Mangrove Ecosystem

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## Highlights

- Mangrove ecosystems are rich in plant polysaccharide-degrading bacteria and its enzymes.
- Metagenomic analyses revealed that many kinds of anaerobic bacteria may play an important role in degrading plant polysaccharides in mangrove sediments.
- Metagenomic approaches are a powerful tool for exploring novel polysaccharide-degrading enzymes in mangrove ecosystems.

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**INVITED REVIEW**

# Biodiversity of Plant Polysaccharide-Degrading Bacteria in Mangrove Ecosystem

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**Abstract:** The mangrove ecosystem is the most productive environment and represent a rich biological diversity including microorganisms. Plant polysaccharides, such as cellulose, hemicellulose and pectin are significant carbon sources of the ecosystem. Bacteria play an important role in carbon cycle in the ecosystem as a decomposer. Based on culture-dependent methods, many plant polysaccharide-degrading bacteria were isolated from mangrove sediments. However, only four bacterial phyla were found in the isolates. In contrast, functional and taxonomic analysis of metagenomic datasets indicated that 10 to 12 bacterial phyla involve in hemicellulose degradation. A large number of anaerobic bacteria, such as the genera Clostridum, Dictyoglomus Marinitoga, Petrotoga, Thermotoga and Verrucomicrobia, were found among them. In addition, many hemicellulose degradation enzymes were found in the phylum Acidobacteria which are abundant and ubiquitous across soil environments. These results suggest that various kinds of bacteria including anaerobic bacteria contribute Plant polysaccharide degradation.

**Keywords:** Cellulose, Hemicellulose, Pectin, Mangrove, Metagenome

## INTRODUCTION

Mangrove forests are unique interface ecosystems between land and sea covering approximately 60%–70% of the coastal areas of tropical and subtropical regions (Holguin *et al.* 2001; Taketani *et al.* 2010). Mangroves are consisted of about 70 higher plants species, between 36 and 46 of the known mangrove species occur in the Indo-Malay Philippine Archipelago (Polidoro *et al.* 2010). The mangrove forests are known to be highly productive ecosystems that contribute to the maintenance of coastlines, preserving water quality and supporting the wood and fisheries industry (Kathiresan & Bingham 2001). The ecosystems also play an important

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role in cycling of carbon, nitrogen, phosphorus sulfur and the micronutrients. Accordingly, the ecosystems represent a rich biological diversity of plants, animals and microorganisms (Thatoi *et al.* 2013).

Based on metagenomic approach, Mendes and Tsai (2018) reported that taxonomic and functional diversity in mangrove soil is higher than that of Atlantic Forest (seasonal moist and dry broadleaf forest) and restinga (moist broadleaf forest) soils in Brazil. In addition, more than 94% of sequencing reads from mangrove metagenomes from Brazil, India, Malaysia and Saudi Arabia were assigned to the domain Bacteria (Alzubaidy *et al.* 2016; Imchen *et al.* 2017; Priya *et al.* 2018).

Bray and Gorham (1964) suggested that mangrove forests have higher rates of litter production than temperate forest. Aksornkoae (1986) also suggested that the high productivity of mangrove ecosystems is attributed to high leaf production, leaf fall and rapid breakdown of the litters. Bunt and co-researchers have estimated that litterfall is account for 30%–60% of total primary production of mangrove ecosystem (Bunt *et al.* 1979). These observations indicate that plant litter is an important source of organic materials in the mangrove soil. The litters are decomposed by microorganisms, such as fungi and bacteria. The decomposition influences nutrient release for growth of plant and microorganisms and carbon reservoir, indicating that microorganisms play an important role in carbon cycle via litter decomposition.

The plant litter is rich in polysaccharides, such as cellulose, hemicellulose and pectin, which are main components of plant cell wall, and the polysaccharides are main carbon sources of the carbon cycle. Accordingly, the investigation of bacterial polysaccharide decomposers and its polysaccharide-degrading enzymes are essential for understanding the carbon balance in mangrove ecosystems. Up till now, many polysaccharide-degrading bacteria and its enzymes were isolated from mangrove areas based on culture-dependent method. However, it has been reported that more than 99% microbes in the environment are not able to be easily cultivated, indicating that the culture-dependent methods can recover a limited number of microbes from the environment. On the other hands, culture-independent metagenomic approaches are based on the isolation of genetic materials directly from environmental samples. Therefore, the approaches are a powerful tool for studying microbial communities including uncultivable microorganisms. In the last decade, metagenomic approaches have been employed for isolating novel polysaccharide-degrading enzymes including cellulases from mangrove ecosystems (Li *et al.* 2012; Mai *et al*. 2014; Ottni *et al*. 2017; Priya *et al.* 2018; Thomson *et al.* 2013).

The present review focuses on the plant polysaccharides, such as cellulose, hemicellulose and pectin, their degrading mechanisms, and polysaccharide-degrading bacteria and their enzymes isolated by culture dependent methods and detected by current metagenomic approaches based on metagenomic libraries and next generation sequencing (NGS).

## POLYSACCHARIDES OF PLANT CELL WALLS

Higher plant cell walls are consisted of three major polysaccharides, cellulose, hemicellulose and pectin. These polysaccharides account for about 90% of the dry weight of primary cell walls (Pettolino *et al.* 2012). These polysaccharides construct the interlinking network in the cell walls (Fig. 1). Cellulose is the most abundant carbohydrate in the cell walls and consists of a linear chain containing 500–14,000 of β -1,4 linked glucan. The cellulose chains interact with each other through hydrogens bounds to form cellulose microfibrils which are make up the core component of the cell walls (Fig. 1) (Keegstra 2010; Somerville 2006).

The second component is hemicellulose consisted of xylan, the most common hemicellulosic polysaccharides, xyloglucan, mannans, galactomannans, glucomannans and galactoglucomannan (Scheller & Ulvskov 2010). Hemicelluloses cross-link noncellulosic and cellulosic polymer, such as cellulose microfibrils (Fig. 1).

Pectin is a third major plant cell wall component. Pectin mainly consists of linear chains of (1,4)-linked-α-d-galacturonic acid and composed of at least four subclass, homogalacturonan, xylogalacturonan, rhamnogalacturonan I and II (Harholt *et al.* 2010). The pectin structurally supports to the cell wall because of forming gel-like matrix in the presence of divalent cations (Fig. 1) (Siew *et al.* 2005). These polysaccharides are degraded and metabolised by bacteria using polysaccharide-degradation enzymes.

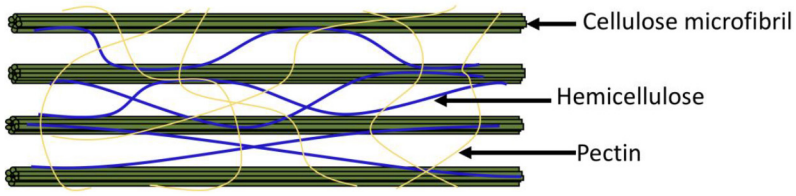


**Figure 1:** Schematic model of plant cell wall. Green, blue and yellow lines indicate cellulose microfibrils, hemicellulose and pectins, respectively.

## DEGRADATION MECHANISMS OF CELLULOSE, HEMICELLULOSE AND PECTIN

Cellulose is hydrolyzed endo-1,4-D-glucanase (Cellulase, EC 3.2.1.4) to reducing or nonreducing cellooligosaccharides. Cellulose 1,4-β-cellobiohydrolase, CBHI (EC 3.2.1.176) and CBHII (EC3.2.1.91) catalyzes hydrolysis of reducing ends and non-reducing ends of cellooligosaccharides, respectively (Sakai *et al.* 2017) and produces cellobiose as a major product. Exoglucanase (EC 3.2.1.74) also catalyzes hydrolysis of non-reducing ends of cellooligosaccharides (Soccol *et al.* 2017). Finally, β-glucosidase (EC 3.2.1.21) hydrolyzes cellobiose to glucose (Behera *et al.* 2017).

The major hemicellulolytic enzymatic components are endoxylanase (EC 3.2.1.8) and β-D-ylosidase (EC 3.2.1.37). Endoxylanas hydrolyzes 1,4-β-d xylosidic linkages in xylan and involves in the production of xylo-oligosaccharides (Collins *et al.* 2005; Biely *et al.* 2016). β-D-xylosidase hydrolyzes xylobiose or xylo-oligosaccharides at the non-reducing end, producing monosaccharide, D-xylose sugar (Biely *et al.* 2016). In addition, α-L-arabinofuranosidase (EC 3.2.1.55), acetylxylan esterase (EC 3.1.1.73), α-galactosidase (EC 3.2.1.22), α-glucuronidase (EC 3.2.1.139), feruloyl esterase (EC 3.1.1.72), β-mannosidase (EC 3.2.1.25) and mannan endo-1,4- β-mannosidase (EC 3.2.1.78) involve in the hydrolysis because of the heterogeneity and complexity of xylan (Shallom & Shoham 2003; Liao *et al.* 2016; Wang *et al.* 2016; Contesini *et al.* 2017). Endo-1,4-β-D-mannanase (EC 3.2.1.78) catalyzes hydrolysis of β-D-1,4-mannopyranosyl linkages consisting of the main chain of mannans, galactomannans, glucomannans and galactoglucomannan (Dekker & Richards 1976). α-galactosidase (EC 3.2.1.22) and β-mannosidase (EC 3.2.1.25) are necessary for the complete conversion of galactomannan into D-galactose and D-mannose. The two enzymes are capable of cleaving the branched α-galactosidic linkage on mannose residues of galactomannan and β-1,4-linked D-mannan backbone, respectively (Ademark *et al.* 1998; Liao *et al.* 2016; Katsimpouras *et al.* 2016).

Pectinases include pectin esterase (EC 3.1.1.11), endo-(EC 3.2.1.15) and exo-polygalacturonase (EC 3.2.1.67), pectin (EC 4.2.2.10) and pectate lyase (EC 4.2.2.2) and oligogalacturonide lyase (EC 4.2.2.6) (Collmer & Bateman 1981; Lang & Dörnenburg 2000; Wang *et al.* 2017). Pectin esterase removes methoxyl groups from carboxyl groups of pectic polymer. Although pectate lyase catalyses the hydrolysis of non-methylated pectin and produces unsaturated oligogalacturonates, pectin lyase catalyses the hydrolysis of highly methylated pectin and produces unsaturated methyl oligogalacturonates (Mayans *et al.* 1997; Dubey *et al.* 2016). The oligogalacturonates are converted to 5-dehydro-4-deoxy-D-glucuronate by oligogalacturonide lyase (EC 4.2.2.6) (Collmer & Bateman 1981). Endo/exopolygalacturonase is capable of cleave α-1,4-glycosidic linkages of non-methylated pectin or polygalacturonic acid (Lang & Dörnenburg 2000) and produces mono- and digalacturonic acid (Nasuno & Starr 1966). These mechanisms were summarised in Table 1.

**Table 1:** Summary of polysaccharide degradation mechanisms.

| Enzymes | EC number | Function |
|---|---|---|
| **Cellulose degradation** | | |
| Cellulase | 3.2.1.4 | Endohydrolysis of (1→4)-β-D-glucosidic linkages in cellulose |
| Cellobiohydrolase I | 3.2.1.176 | Hydrolysis of (1→4)-β-D-glucosidic linkages in cellooligosaccharides, releasing cellobiose from reducing ends |

(*continued on next page*)

**Table 1** (*continued*)

| Enzymes | EC number | Function |
|---|---|---|
| Cellobiohydrolase II | 3.2.1.91 | Hydrolysis of (1→4)-β-D-glucosidic linkages in cellooligosaccharides, releasing cellobiose from non-reducing ends |
| Exoglucanase | 3.2.1.74 | Hydrolysis of (1→4)-β-D- glucosidic linkages in (1→4)-β-D-glucans |
| β-glucosidase | 3.2.1.21 | Hydrolysis of cellobiose to glucose |
| **Hemicellulose degradation** | | |
| Endoxylanase | 3.2.1.8 | Endohydrolysis of 1,4-β-D xylosidic linkages in xylan |
| β-D-xylosidase | 3.2.1.37 | Hydrolysis of xylobiose or xylo-oligosaccharides to the non-reducing end, producing monosaccharide, D-xylose sugar |
| Arabinofuranosidase | 3.2.1.55 | Cleavage of α-(1→2), α-(1→3), or α-(1 → 5) linked l-arabinofuranosyl residues from non-reducing ends in oligo- and polysaccharide |
| Acetylxylan esterase | 3.1.1.72 | Deacetylation of xylans and xylo-oligosaccharides |
| α-galactosidase | 3.2.1.22 | Hydrolysis of the branched α-galactosidic linkage on mannose residues of galactomannan |
| α-glucuronidase | 3.2.1.139 | Hydrolysis of the α-1,2-glycosidic bond of the α-D-glucuroic acid and 4-O-methyl-glucuronic acid side chains attached to the xylan |
| Feruloyl esterase | 3.1.1.73 | Releasing ferulic acid from arabinose residues attached to the xylan |
| β-mannosidase | 3.2.1.25 | Cleavage of β-D-mannoside linkages in β-1,4-D-mannan |
| Mannan endo-1,4-β-mannosidase | 3.2.1.78 | Hydrolysis of β-1,4-linked D-mannan backbone |
| **Pectin degradation** | | |
| Pectin esterase | 3.1.1.11 | Removal of methoxyl groups from carboxyl groups of pectin |
| Endo-polygalacturonase | 3.2.1.15 | Hydrolysis of (1→4)- α-linked glycosidic bonds between two nonesterified galacturonic acid units in a random |
| Exo-polygalacturonase | 3.2.1.67 | Hydrolysis of (1→4)- α-linked glycosidic bonds between two nonesterified galacturonic acid units in a terminal fashion |
| Pectate lyase | 4.2.2.2 | Eliminative cleavage of (1→4)-alpha-D-galacturonan to give unsaturated oligogalacturonates |
| Pectin lyase | 4.2.2.10 | Eliminative cleavage of (1→4)-alpha-D-galacturonan methyl ester to give unsaturated methyloligogalacturonates |
| Oligogalacturonide lyase | 4.2.2.6 | Catelysis of conversion of oligogalacturonates to 5-dehydro-4-deoxy-D-glucuronate |

## CELLULOSE-DEGRADING BACTERIA AND ITS ENZYMES

Cellulose degrading bacteria have attracted much attention because of not only the decomposer of lignocellulosic biomass but also the producer of celluloses that are useful for various industrial processes, such as biofuels. Accordingly, numerous cellulose-degrading bacteria were isolated from mangrove areas. Several investigators focused on Indian mangroves. *Pseudomonas* spp. *Bacillus polymyxa*, *B. mycoides* and *B. brevis* were isolated as cellulose-degrading bacteria from mangrove soil of Bhitarkanika, Odisha, India (Thatoi *et al.* 2012). The authors reported that the cell density of these four species was 2.5-7.0 × $10^5$/g of soil (Thatoi *et al.* 2012). Pandey and colleagues isolated four cellulose-degrading bacteria from 300 isolates. *Bacillus* sp. and *Paenibacillus* sp. were isolated from Sunderban, and *B. cereus* and *Lysinibacillus* sp. were isolated from Bhitarkanika (Pandey *et al.* 2013). Two cellulose-degrading bacteria belonging to *Klebsiella ozeanae* and *Pseudomonas aeruginosa* were isolated from decayed mangrove twigs in Uppanar estuary, India (Kalaiselvi *et al.* 2013). Haldar and Nazareth (2018) isolated six cellulose degrading bacteria belonging to *Bacillus cereus*, *B. toyonensis* and *Lysinibacillus macrolides* from Mandovi estuary and 17 strains belonging to *B.cereus*, *B. toyonensis*, *L. macrolides*, *Paenibacillus illinoisensis*, *P. Spabull, P. xylanilyticus* and *Staphylococcus hominis* from Zuari estuary, Goa, India. Furthermore, 15 cellulose-degrading bacteria belonging to *Bacillus* spp., *Brucella* spp., *Micrococcus* spp., *Pseudomonas* spp. and *Xanthomonas* spp. were isolated from mangrove soil of Mahanadi river delta, Odisha, India (Behera *et al.* 2014). These results showed that bacteria belonging to the family *Bacillaceae* overrepresent cellulose-degrading bacteria isolated from Indian mangroves. Cellulose-degrading bacteria isolated from Philippines mangrove also belong to the genus *Bacillus*, such as *B. cereus*, *B. licheniformis*, *B. pumilus* and *Bacillus* sp. (Tabao & Monsalud 2010). In two mangrove systems in Bertioga and Cananéia, Brazil, 25 isolates showed endo-1,4-D-glucanase activity, and 12 out of the isolates belong to the genus *Bacillus* (Castro *et al.* 2014).

On the other hand, Bibi and co-researchers reported that several bacterial strains belonging to genera, *Aidingimonas*, *Altermonas*, *Bacillus*, *Chromohalobacter*, *Erwinia*, *Halomonas*, *Marinobacter*, *Microbulbifer* and *Vibrio* were isolated as cellulose-degrading bacteria from six different plant specimens collected from coastal area of Thuwal, Jeddah, Saudi Arabia (Bibi *et al.* 2017). A novel *Vibrio* species, *Vibrio xiamenensis*, was isolated from mangrove soil in Xiamen, Fujian, China and was identified as a cellulase producing bacterium (Gao *et al.* 2012). Based on 16S rRNA sequence analysis, Soares Júnior and colleagues identified twelve isolates, which exhibit endo- and exo-1,4-D-glucanase activity, from soil of mangrove located at the Ilha do Cardoso, Brazil (Soares Júnior *et al.* 2013). The isolates were classified as the phyla *Actinobacteria*, *Bacteroidetes, Firmicutes* and *Proteobacteria* including the classes *Alphaproteobacteria* and *Gammaproteobacteria*. Cellulose-degrading bacteria were also isolated in Malaysia. Naresh and co-researchers isolated seven cellulose-degrading bacteria, five *Anoxybacillus* sp., one *Bacillus* sp. and one *Paenibacillus* sp. from four

mangrove areas in northern part of Malaysia (Perak, Pulau Pinang, Kedah and Perlis) (Naresh *et al.* 2019). In addition, a novel actinobacterium, *Streptomyces monashensis*, which can produce antioxidants, exhibited cellulose degradation (Law *et al.* 2019).

As mentioned above, many cellulose-degrading bacteria were isolated by culture-dependent techniques. However, <1% of the microorganisms are readily cultured with traditional culture-based methods (Amann *et al.* 1995). Accordingly, culture-independent metagenomic approaches, such as functional screening of metagenomic library and metagenomic analysis using NGS, are useful for exploring new enzymes and for diversity and functionality analysis. Li and colleagues were constructed a metagenomic library from soil samples of Shenzhen Magrove Reserve of Shenzhen city, Guangdong, China (Li *et al.* 2012). After functional-based screening using LB medium with carboxymethylcellulose (CMC), a β-glucosidase gene, *Bgl1269*, was isolated. The deduced amino acid sequence showed 99.29% identity of glycoside hydrolase family 1 protein (GH1) of *Bacillus korlensis*, indicating that *Bgl1269* may derived from *Bacillus korlensis.* A novel endo-1,4-D-glucanase gene, *mgcel44*, was isolated from a metagenomic library of mangrove soil of Mangrove Reserve of Sanya city, Hainan, China (Mai *et al.* 2014). The deduced amino acid sequence demonstrated identity of 48% with endo-1,4-D-glucanases from *Micromonospora lupini* strain Lupac 08, *Streptomyces bingchenggensis* BCW-1 and *S. himastatinicus*. This result suggested that *mgce144* may derive from bacteria belonging to the order of *Actinomycetales.*

Ottoni and colleagues conducted taxonomic analysis of the hydrolase sequences including cellulase in fosmid library constructed from mangrove sediment in São Paulo state, Bertioga, Brazil (Ottoni *et al.* 2017). As a result of the analysis, cellulase related to the families *Pseudomonadaceae* and *Thermoanaerobacteraceae* were the most abundant. Functional metagenomic analysis on two different Brazilian mangroves, a preserved mangrove in Rio de Janeiro state, Ilha Grande and peri-urban mangrove area, Bahia state, Porto Seguro were conducted, by Thompson and colleagues, and many endo-1,4-D-glucanase, 1,4-β-cellobiosidase and β-glucosidase genes were found (Thompson *et al.* 2013). Our group also conducted functional metagenomic analysis on the best sustainably-managed mangrove forest, Matang Mangrove Forest Reserve (MMFR) in Malaysia (Priya *et al.* 2018). In this study, we focused on two sites, Virgin Jungle Forest (VJF) and Productive Zone (PV). A numerous number of endo-1,4-D-glucanase (cellulase) and β-glucosidase genes were found in both sampling sites (Priya *et al.* 2018). Furthermore, 1,4-β-cellobiosidase and 1,4-β-glucosidase were also detected (Priya *et al.* 2018). These results of functional metagenomic analyses indicate that numerous cellulose-degrading bacteria are present in mangrove soils.

## HEMICELLULOSE-DEGRADING BACTERIA AND ITS ENZYMES

Xylanases play an important role in primary degradation of hemicellulose, such as xylan. Wang and co-researchers reported that xylanases are distributed in various soil environments, mangrove swamp, hot spring, pond, farmland, snow lotus and glacier (Wang *et al.* 2012). Several xylan-degrading bacteria were isolated from mangrove soils. A *Streptomyces* sp., which is able to produce a highly alkaline and thermotolerant xylanase, was isolated from mangrove forest of Kadalundi, Kerala, India (Thomas *et al.* 2013). Fifteen xylan degrading bacteria were isolated from mangrove sediment of Kuantan, Malaysia by Omar and co-researchers (Omar *et al.* 2017). A highest extracellular xylanse producing strain, K2-04, was identified as *Verrucosispora* sp. through 16S rRNA analysis (Omar *et al.* 2017). *V. wenchangensis* isolated from mangrove soil of Wenchang, Hainan, China, also degraded xylan (Xie *et al.* 2012). It was reported that *B. subtilis* cho40 isolated from the mangrove area of Mandovi estuary, India, can produce a novel halotolerant xylanase (Khandeparker *et al.* 2011). Haldar and Nazareth (2018) isolated 11 xylan-degrading bacteria belonging to *B. toyonensis*, *L. macroides* and *S. pasteuri* from Mandovi estuary and three strains, *B. toyonensis*, *L. macroides* and *S. hominis* from Zuari esturay, Goa, India. Our team also isolated two xylan-degrading bacteria, *Mangrovimonas*-like bacterium TPBH4 and *M. xylaniphage* ST2L12 from two mangrove sediments, Taman Paya Bakau and Matang Mangrove Forest, Malaysia, respectively (Dinesh *et al.* 2017; 2016). The genome information of both TPBH4 and ST2L12 demonstrated that TPBH4 possesses ten endoxylanases, two β-D-xylosidases and two α-L-arabinofuranosidases and ST2L12 possesses eight endoxylanases, two β-D-xylosidases and two α-L-arabinofuranosidases (Dinesh *et al.* 2016). In addition, *Micobulbifer chitinilyticus* isolated from mangrove forest in Okinawa, Japan, exhibited xylan degradation activity (Baba *et al.* 2011). Other *Microbulbifer* species, *M. mangrove* also exhibited xylan degradation (Vashist *et al.* 2013). Lee and co-researchers isolated two xylan-degrading bacteria, *Microbacterium mangrove* and *Novosphingobium malaysiense* from mangrove sediments of the Tanung Lumpur River in Pahang, Malaysia (Lee *et al.* 2014a; 2014b).

Functional metagenomic analysis by Thompson and colleagues revealed that endoxylanase, β-D-xylosidase, acetylxylan esterase, α-galactosidase, α-glucuronidase and α-mannosidase were found in Brazilian mangroves (Thompson *et al.* 2013). In our mangrove metagenomic datasets, surprisingly, endoxylanase were found in 12 phyla, and the most abundant phylum was *Proteobacteria*, accounting for 31.7% of the total hits for bacteria, followed by *Actinobacteira* (21.6%), *Firmicutes* (15.0%), *Bacteroidetes* (12.6%) and *Acidobacteria* (7.9%) (Priya *et al.* 2018). Many anaerobic bacteria were found in these groups. For example, the genera *Thermotoga*, *Petrotoga* and *Marinitoga* belonging to the phylum *Thermotoga* were detected. In phylum Firmicutes, several anaerobic bacteria, such as *Holdemania filiformis*, *Caldicellulosiruptor saccharolyticus*, *Eubacterium rectale*, and *Clostridum* spp. were also fund in the metagenome datasets. It was known that the genus *Clostridium* possesses cellulolytic enzyme

complex called cellulosome (Felix & Ljungdahl 1993; Gal *et al.* 1997; Sabathé *et al.* 2002). The cellulosome has high activity on crystalline cellulose. In addition, xylan-degrading enzymes were also detected from cellulosome (Blouzard *et al.* 2010; Kosugi *et al.* 2002; Mohand-Oussaid *et al.* 1999), indicating that the genus *Clostridium* is crucial for decomposition of cellulose and hemicellulose in anaerobic environments. Anaerobic bacteria *Dictyoglomus thermophilum* and *D. turgidum* belonging to the phylum *Dicyoglomi* known as xylan-degrading bacteria (Brumm *et al.* 2016; Gibbs *et al.* 1995) were also detected. Besides that, *Opitutus terrae* belonging to the phylum *Verrucomicrobia* was also found. In our study, the phylum *Acidobacteria* is one of abundant in endoxylanase producing bacteria (Priya *et al.* 2018). The phylum is abundant in soils and sediments, and the majority of the phylum is considered aerobic heterotrophs (Ward *et al.* 2009). However, the bacteria have been difficult to isolate and culture in the laboratory (Ward *et al.* 2009). Accordingly, these bacteria were not isolated by traditional culture-based methods.

β-D-xylosidase were found in ten phyla, and the most abundant phylum was *Proteobacteria* (33.8%), followed by *Firmicutes* (22.4%), *Bacteroidetes* (13.0%), *Actinobacteira* (12.4%), and *Chloroflexi* (5.7%). α-L-arabinofuranosidase were also found in 10 phyla, the most abundant phylum was *Actinobacteira* (28.8%), followed by *Proteobacteria* (22.9%), *Bacteroidetes* (16.6%), *Firmicutes* (15.3%) and *Verrucomicrobia* (5.4%). Based on the results, hemicellulose degradation in Matang mangrove sediment are represented by the phyla *Proteobacteria*, *Actinobacteria*, *Firmicutes* and *Bacteroidetes*. In addition, the results suggested that a huge variety of bacterial species involve in hemicellulose degradation in mangrove ecosystems.

## PECTIN-DEGRADING BACTERIA AND ITS ENZYMES

Many pectin-degradation enzymes were found in plant pathogenic bacteria, such as the genera *Agrobacterium*, *Burkholderia*, *Bacillus*, *Erwinia*, *Klebsiella*, *Pseudomonas* and *Xanthomonas* (Prade *et al.* 1999). However, pectin-degradation bacteria isolated from mangrove areas are still scare. Arijit and co-researchers isolated pectinolytic actinomycete, *Streptomyces* sp.GHBA10, from Valapattanam mangrove forest in Kerala, India and purified pectinase from the culture supernatant (Arijit *et al.* 2013). *Microbulbifer mangrovi* also exhibits pectin degradation activity (Vashist *et al.* 2013), and three pectate lyase were found in the genome sequence of the strain (Imran *et al.* 2017).

Several pectin esterases and pectin lyases were found in metagenome data sets of Brazilian mangroves (Thompson *et al.* 2013). Our previous study demonstrated that pectin methylesterase endo- and exo-polygalacturonases, pectin lyases, pectate lyase and oligogalacturonide lyases were found in Malaysian mangrove metagenome (Priya *et al.* 2018). However, a number of genes encoding pectin-degrading enzymes are obviously less than that of cellulose-degrading and hemicellulose degrading enzymes (Priya *et al.* 2018).

## CONCLUSION

The aim of this review is to describe cellulose, hemicellulose and pectin-degrading bacteria found and isolated from mangrove areas. Cellulose-degrading bacteria isolated by culture-based methods were classified into four phyla, *Proteobacteria*, *Firmicutes*, *Actinobacteria* and *Bacteroidetes*. Especially, the genus *Bacillus* belonging to the phylum *Firmicutes* was dominant genus. In addition, several thermostable cellulases were also isolated (Kalaiselvi *et al.* 2013; Pandey *et al.* 2013; Naresh *et al.* 2019). Meanwhile, based on metagenomic approaches, bacteria belonging to three phyla, *Proteobacteria*, *Firmicutes* and *Actinobacteria* were detected as cellulose-degrading bacteria, and a novel β-glucosidase and a endoglucanase were cloned and characterized (Li *et al.* 2012; Mai *et al.* 2014; Thompson *et al.* 2013; Ottoni *et al.* 2017). Besides that, Numerous genes encoding cellulose-degrading enzymes, such as, endo-1,4-$_{D}$-glucanase (cellulase) and β-glucosidase were found in metagenome datasets from Matang Mangrove Forest Reserve (Priya *et al.* 2018).

In hemicellulose, although bacteria belonging to four phyla, *Proteobacteria*, *Firmicutes*, *Actinobacteria* and *Bacteroidetes* were isolated by culture-dependent methods, taxonomic analysis of metagenome datasets from Matang Mangrove Forest Reserve, Malaysia revealed that bacteria belonging to 10 out of 12 phyla involve hemicellulose degradation (Priya *et al.* 2018). In addition, various anaerobic bacteria belonging to the phyla *Firmicutes*, *Dicyoglomi*, *Thermotoga* and *Verrucomicrobia* were detected in the datasets. Mangrove sediments under aerobic surface layer are predominantly anaerobic condition, and anaerobic biochemical processes are catalysed by microbial communities consisted of anaerobic bacteria (Lyimo *et al.* 2009). Therefore, anaerobic bacterial communities may play an important role in degradation of plant polysaccharides in mangrove sediments.

In pectin, information of pectin-degrading bacteria and its enzymes in mangrove ecosystems are still scarce. However, a few genes encoding pectin-degrading enzymes were found in mangrove metagenomes (Thompson *et al.* 2013; Priya *et al.* 2018).

In summary, further metagenomic approach will lead to a better understanding of the taxonomic and functional biodiversity of the bacterial communities related to the plant polysaccharides in mangrove ecosystems.

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