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REVIEW ARTICLE

Mannan biotechnology: from biofuels to health

Montarop Yamabhai[1], Suttipong Sak-Ubol[1], Witsanu Srila[1], and Dietmar Haltrich[2]

[1]Molecular Biotechnology Laboratory, School of Biotechnology, Institute of Agricultural Technology, Suranaree University of Technology, Nakhon Ratchasima, Thailand and [2]Food Biotechnology Laboratory, BOKU – University of Natural Resources and Life Sciences, Vienna, Austria

Abstract

Mannans of different structure and composition are renewable bioresources that can be widely found as components of lignocellulosic biomass in softwood and agricultural wastes, as non-starch reserve polysaccharides in endosperms and vacuoles of a wide variety of plants, as well as a major component of yeast cell walls. Enzymatic hydrolysis of mannans using mannanases is essential in the pre-treatment step during the production of second-generation biofuels and for the production of potentially health-promoting manno-oligosaccharides (MOS). In addition, mannan-degrading enzymes can be employed in various biotechnological applications, such as cleansing and food industries. In this review, fundamental knowledge of mannan structures, sources and functions will be summarized. An update on various aspects of mannan-degrading enzymes as well as the current status of their production, and a critical analysis of the potential application of MOS in food and feed industries will be given. Finally, emerging areas of research on mannan biotechnology will be highlighted.

Keywords

Beta-mannanase, biofuels, biorefinery, hemicelluloses, lignocellulose, mannan, mannooligosaccharides, prebiotic

History

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Introduction

The efficient utilization of renewable lignocellulosic biomass as second-generation biofuels has become a global effort for sustainable energy systems and environmental reasons (Lin et al., 2013). In addition, further research is also focused on increasing the value of waste or residual materials through the bio-refinery concept (FitzPatrick et al., 2010). It is anticipated that various biorefinery techniques will greatly reduce the amount of biological wastes produced around the world, as most of them have the potential to be converted into a wide range of value-added products.

Different lignocellulosic plants have a varying composition of macromolecules, but the major components are an average of the following order: glucan > lignin > xylan > mannan > arabinan > galactan. The mannan content is approximately 5%, except for coniferous or softwood which contain more mannan (~10%) than xylan (Lavoie et al., 2011; Wolf et al., 2012). Therefore, lignocellulosic biomass is the most suitable feedstock for biofuel production. Second to cellulose, mannans from softwood are important sources of sugars for the generation of biofuel.

Address for correspondence: Montarop Yamabhai, Molecular Biotechnology Laboratory, School of Biotechnology, Institute of Agricultural Technology, Suranaree University of Technology, 111 University Avenue, Nakhon Ratchasima, Thailand. E-mail: montarop@sut.ac.th

The bioconversion of biomass into monomeric sugars and subsequent fermentation into products such as ethanol can be efficiently conducted by hydrolysis using multiple enzymes (Van Dyk & Pletschke, 2012). Enzyme synergy models for the bioconversion of lignocellulose substrates indicate that pre-treatment is essential for effective hydrolysis of lignocellulosic substrates by enzymes (Alvira et al., 2010). For softwood, mannan-degrading enzymes constitute an important group of enzymes, which can be used both at the pre-treatment step and for total release of all sugars for the production of second-generation biofuels, as well as for the production of potentially health-promoting mannooligosaccharides (MOS) (Do et al., 2009). Endo-β1,4-mannanases or β-mannanases are the main enzymes for complete degradation of mannans (Rodríguez-Gacio Mdel et al., 2012). In recent years, several three-dimensional structures of catalytic domains, as well as carbohydrate-binding modules (CBM) of several microbial β-mannanases, have been elucidated (Gilbert et al., 2008; Guillen et al., 2010). As for plants, LeMAN4 from tomatoes is the only plant β-mannanase whose three-dimensional structure has been determined (Bourgault et al., 2005). This information is crucial for a thorough understanding of the mechanism of substrate recognition and catalysis by these enzymes, as well as for the bioengineering of the recombinant enzymes to suit various biotechnological applications (Wen et al., 2009).

In addition to softwood, mannan can also be found as a non-starch reserve polysaccharide in seed endosperms and vacuoles of a wide variety of plants (Rodríguez-Gacio Mdel et al., 2012; Scheller & Ulvskov, 2010). Mannan extracts from some of these plants are used widely in the food industry

(Gidley & Reid, 2006), while mannan from other sources such as coffee bean, palm kernel or copra meal are food supply chain wastes rich in mannan (Scheller & Ulvskov, 2010), and are therefore also of interest for the biorefinery concept.

Accordingly, in terms of the biorefinery concept (FitzPatrick et al., 2010), mannan biotechnology involves various aspects of technology related to mannan biopolymers. These include pre-treatment and hydrolysis of mannan-rich lignocellulosic biomass, especially softwood, for the production of second-generation biofuels as well as the synthesis of value-added bioactive MOS, all of which will be considered in this review.

Mannan polysaccharides

Sources and functions

Mannans and heteromannans are polysaccharides that are widely distributed in nature as part of hemicelluloses in plant tissue (Capek et al., 2000; Scheller & Ulvskov, 2010) as well as a constituent of glycoproteins in yeast cell walls (Sandin, 1987). In plants, mannans and heteromannans are components of hemicellulose, a term that is used for a part of lignocellulose – a renewable bioresource that comprises lignin, cellulose and hemicellulose (Scheller & Ulvskov, 2010; Van Dyk & Pletschke, 2012). Lignocellulose is widely available in the form of biological wastes from forest industries, energy crops and components of agricultural residues such as straw and grass, coffee bean extracts, palm kernel (Moreira & Filho, 2008) or copra meal (Saittagaroon et al., 1983), to name a few. The term hemicellulose comprises a group of different structural polymers of the plant cell wall consisting of various sugars such as D-xylose, D-mannose, D-glucose, D-galactose, L-arabinose and 4-*O*-methyl-D-glucuronic acid (Braidwood et al., 2014; Scheller & Ulvskov, 2010; Wolf et al., 2012). It constitutes 25–30% of total dry wood weight, and its distribution and constituents vary in softwood (gymnosperms) and hardwood (angiosperms; Moreira & Filho, 2008; Popper et al., 2011). While xylans constitute the predominant hemicellulose of hardwoods and straw, galactomannans represent the largest hemicellulose fraction in softwoods (Puls, 1997). Hemicelluloses are abundant biological wastes from the production of mechanical pulps and wood-containing papers, and hence are available in huge amounts (Scheller & Ulvskov, 2010).

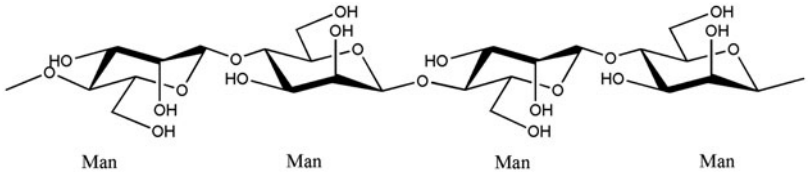
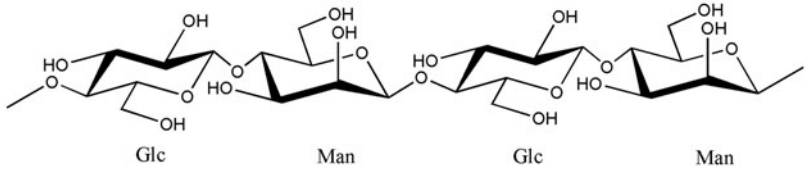
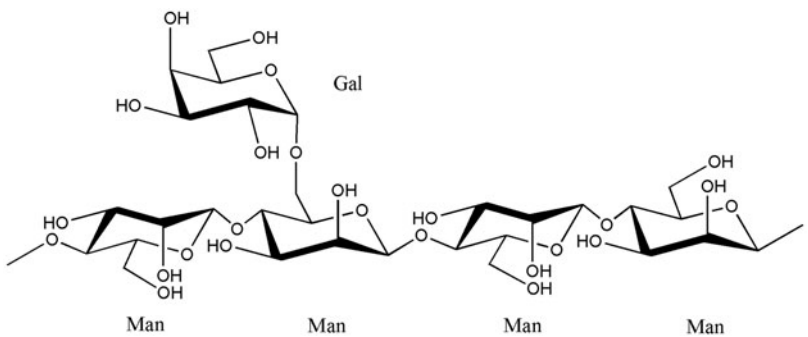
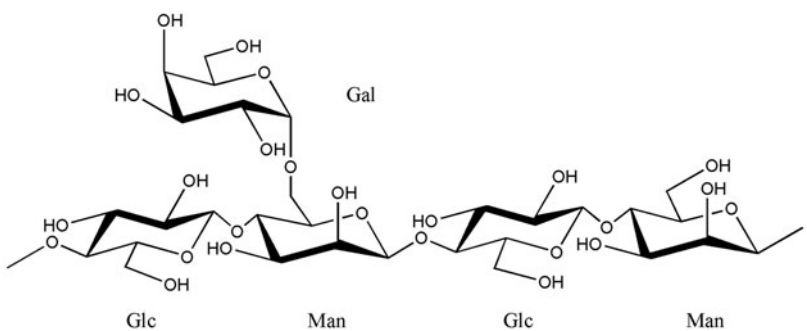
A polysaccharide diversification (including mannans) occurred during the evolution of land plants, which resulted in the structural changes in the cell wall (Lee et al., 2011). Mannans and heteromannans both serve structural elements in plant cell walls and carbohydrate reserves (Rodríguez-Gacio Mdel et al., 2012). Mannan-based polysaccharides exhibit a storage function as non-starch carbohydrate reserve in the endosperm wall of seeds such as coconut (*Cocos nucifera*; Saittagaroon et al., 1983), coffee bean (*Coffea* spp.), locust (carob) bean (*Ceratonia siliqua*) or the vacuole in vegetative tissue of plants such as konjac (*Amorphophallus konjac)*, ivory nut (*Phytelephas spp.)*, guar (*Cyamopsis tetragonoloba*), *Aloe vera*, etc. (Moreira & Filho, 2008). In addition, they also help provide resistance to mechanical damage and retain resistance after exposure to water, due to their water insolubility (Reid & Edwards, 1995). Some of these mannans are well known and widely used as thickening, stabilizing and gelling agents in the food industry, e.g. galactomannan from locust bean gum or glucomannan from konjac (CyberColloids, 2014). In addition to structural and storage functions, mannans have also been suggested to play a role in metabolic networks devoted to various cellular processes (Liepman et al., 2007).

Structure

Mannans differ significantly in their structure according to their origin. Hemicellulosic mannans consist of β-1,4-linked D-mannose (and D-glucose) in the backbone and α-1,6-linked D-galactose as side chains, allowing the formation of various types of linear or branched polysaccharides (Table 1). These polysaccharides can be classified into four subfamilies, namely, linear mannan, glucomannan, galactomannan and galactoglucomannan (Moreira & Filho, 2008). The mannose residues on galactoglucomannans can be acetylated at the C-2 and C-3 positions to various degrees, depending on the source of the polysaccharide, resulting in acetylated galactoglucomannans (Lundqvist et al., 2002). However, it is important to note that the extraction methods can strongly influence the yield, molecular weight and structure of mannans, as observed from studies comparing different methods for preparing galactoglucomannan from spruce (*Picea abies*; Lundqvist et al., 2003). Moreover, it has been shown that acetylation can hinder the detection of mannan by antibodies or CBM (Marcus et al., 2010). A summary of various types of mannans from plants, together with their sources, structures, common and potential applications are shown in Table 1.

In addition to the β-mannans described above, another type of mannan comes from yeast cell walls, which consists of three groups of polysaccharides, i.e. β-glucan, chitin and mannan, the latter being part of the phosphoprotein mannan complex (Nakajima & Ballou, 1974a,b). In *Saccharomyces cerevisiae*, the cell wall comprises 50 and 40% of β-1,3-glucan and mannoprotein, respectively (Lipke & Ovalle, 1998). Two important minor components of yeast cell walls are β-1,6-glucan and chitin, which make up 10% and 1–3% of the total mass of cell walls, respectively (Lipke & Ovalle, 1998). Mannoproteins are highly antigenic and glycosylated polypeptides that carry both *N*-linked and *O*-linked glycans. In many yeasts, *N*-glycans consist of 50–200 additional D-mannose units, while *O*-glycans contain only1–5 mannosyl units. The *N*-linked yeast mannans consist mainly of a long linear polymer of α-1,6-linked D-mannose with short side chains of D-mannosyl units attached to the backbone mainly by α-1,2-linkages, and to each other by both α-1,2 and α-1,3-linkages (Kocourek & Ballou, 1969; Kollar et al., 1997). However, in the yeast *Candida albicans*, in addition to α-1,6-linked branching mannose units, β-1,2-linked mannose residues have also been identified (Shibata et al., 2007). Moreover, an unusual form of mannan, i.e. sulphated (1 → 3)-linked α-D-mannan, has also been reported in seaweed (Perez Recalde et al., 2009). Sulfated polysaccharides are receiving growing interest for biomedical application, especially for tissue engineering and drug delivery approaches (Silva et al., 2012).

Table 1. Typical structures, sources, applications of different subfamilies of mannan polysaccharides.

Subfamily of Mannans	DP	Sources	Ratio: Man:Glc:Gal	Commercial Application	Potential Application
I. Linear mannan (1) 	15–80 (Aspinall, 1959)	Ivory nut, copra meal (Saittagaroon et al., 1983), some algae (Mackie & Preston, 1968), aloe vera, coffee	–	–	Health-promoting effects (Simoes et al., 2009)
II. Glucomannan (2) 	>200 (except eastern white pine; 90, and red wood; 60) (Al-Ghazzewi et al., 2007)	Konjac Hardwood	2:1:0 (Millane & Hendrixson, 1994) 1:1:0 (Liu et al., 2012b) 2:1:0, 3:1:0, 4:1:0 (Ishurd et al., 2006, Northcote, 1972, Willfor et al., 2003)	Gelling, thickening, suspending and film-forming agent –	Prevention of chronic disease (Vuksan et al., 1999), and weight-control agent, pre-biotics (Tester et al., 2012; Al-Ghazzewi et al., 2007)
III. Galactomannan (3) 	n/a	Guar gum Tara gum Locus bean gum Fenugreek gum (Picout et al., 2002)	2:0:1 3:0:1 4:0:1 1:0:1 (Moreira & Filho, 2008; de O. Petkowicz et al., 2001)	Food stabilizer, gel setting, food thickener (Schwartz & Bodie, 1983)	
IV Galactoglucomannan *Galactoglucomannan (4)* 	15–100 (Willfor et al., 2003)	Seed endosperm (Kollarova et al., 2010) Softwood (Lundqvist et al., 2002) Aloe vera bulk water soluble extract (BSW) (Tai-Nin Chow et al., 2005)	3:1:1 3:1:1; 4:1:0.1 15:1:1 (Pu et al., 2008; Timell, 1964; Timell, 1965) 10:1.9–2.6: (Hannuksela & Herve du Penhoat, 2004)	–	Immuno modulation (Tai-Nin Chow et al., 2005) Biofuel resource (Lavoie et al., 2011)

(*continued*)

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Table 1. Continued

Subfamily of Mannans	DP	Sources	Ratio: Man:Glc:Gal	Commercial Application	Potential Application
Acetylated galactoglucomannan (5)	100–150 (Timell, 1967) 10–20 (Lundqvist et al., 2002)	Softwood Hardwood (Teleman et al., 2003)	3:1:1 3:1:0.1 (Timell, 1967) 4:1:0.1 (Lundqvist et al., 2002)		

(1) Linear mannan, a main chain of β-1,4-linked D-mannose (Man) units; (2) Glucomannan, a main chain of β-1,4-linked D-mannose (Man) and D-glucose (Glc) units; (3) Galactomannan, a linear backbone of β-1,4-linked D-mannose (Man) units with α-1,6-linked D-galactose (Gal) units attached to some D-mannose (Man) residues; (4) Galactoglucomannan, a backbone of β-1,4-linked D-mannose (Man) and D-glucose (Glc) units, with α-1,6-linked D-galactose (Gal) residues attached to some D-mannose (Man) residues; (5) Acetylated galactoglucomannan, galactoglucomannan with β-1,4-linked *O*-acetyl groups (Ac) attached to C-2 positions of D-mannose (Man) residue (Scheller & Ulvskov, 2010). (A detailed explanation of the structure of different types of mannans from plants is described in the Supplementary Material I.)

Mannan-degrading enzymes

β-Mannanases and other mannan-degrading enzymes

The two major plant mannan-degrading enzymes are mannan endo-1,4-β-mannosidase or 1,4-β-D-mannan mannanohydrolase (EC 3.2.1.78), commonly known as β-mannanase and β-D-mannoside mannohydrolase or β-mannosidase (EC 3.2.1.25). According to the Carbohydrate Active Enzyme database (www. cazy.org; Cantarel et al., 2009), β-mannanases are classified into various families of glycoside hydrolases (GH; Dhawan & Kaur, 2007), i.e. mostly for GH families 5, 26 and a few to family GH 113 (Zhang et al., 2008); whereas β-mannosidases belong to GH families 1, 2 and 5.

β-Mannanase is an endo-acting enzyme that catalyzes the random hydrolysis of the $(1 \rightarrow 4)$-β-D-mannosidic linkages in mannans, galactomannans and glucomannans via a retaining double displacement mechanism as recently reviewed (Gilbert et al., 2013). The enzymes in this group belong to clan GH-A, comprising the $(\beta/\alpha)_8$ TIM barrel protein fold (Vocadlo & Davies, 2008) and non-catalytic CBMs in certain GH26 mannanases (Zhang et al., 2013). Some β-mannanases from fungi and archaea can perform transglycosylation reactions, in which a carbohydrate hydroxyl group acts as the acceptor molecule instead of water, resulting in the formation of MOS or other mannosides (Dilokpimol et al., 2011; Park et al., 2011). The transglycosylation activity has been found only in GH5 and GH113, but not in GH26 mannanases. Recently, the function of endo-transglycosylase activity of β-mannanases in remodeling of the plant cell wall has been reinterpreted (Schroder et al., 2009). In addition to the catalytic domain, many β-mannanases also contain one or more non-catalytic, CBMs in the family's CBM1, CBM6, CBM10, CBM31 and CBM35 [reviewed by Boraston et al. (2004)]. These CBM modules have been demonstrated to promote the interaction of the enzyme with the substrate, of which the linker between the catalytic and CBM modules is highly flexible, allowing maximum accessibility to structural and storage substrates (Couturier et al., 2013b).

To date, a number of three-dimensional structures of β-mannanases have been reported. These include GH26 β-mannanases from *Cellulomonas fimi* (PDB# 2BVT; Le Nours et al., 2005); *Cellvibrio japonicus* (PDB#1GVY and 2VX4; Cartmell et al., 2008); *Bacillus subtilis* (PDB# 2WHK and 2QHA; Tailford et al., 2008; Yan et al., 2008); *Pseudomonas cellulosa* (PDB# 1J9Y; Hogg et al., 2001); *Podospora anserina* (PDB# 3ZIZ; Couturier et al., 2013b) and GH5 β-mannanases from *Trichoderma reesei* (PDB# 1QNO; Sabini et al., 2000), blue mussel *Mytilus edulis* (PDB# 2C0H; Larsson et al., 2006), tomato fruit *Solanum lycopersicum* (PDB# 1RH9; Bourgault et al., 2005) and *Podospora anserina* (PDB# 3ZM8; Couturier et al., 2013b). These structures indicate a typical active site-cleft containing at least four subsites with the strictly conserved catalytic glutamates on β-strands 4 (nucleophile) and 7 (acid/base; Gilbert et al., 2008). The conserved Trp in subsite-1 contributes to the aromatic platform that interacts with the hydrophobic α-face of the substrate sugar ring. Recently, a GH26 β-mannanase (PaMan26A) from *Podospora anserina*, containing CMB35, with an exceptionally strong-4 subsite has been reported

(Couturier et al., 2013b). This enzyme unusually releases mannotetraose and mannose from mannopentaose, instead of mannotriose and mannobiose. These results indicated that differences in subsite affinities and the presence of CBM may contribute to the differences in catalytic mode of various enzymes, and that many enzymes can act in synergy to degrade mannan-rich polysaccharides. This knowledge is essential for the selection of enzymes to obtain the desired products or to further engineer the enzymes to suit various purposes.

β-Mannosidase is an exo-acting enzyme that catalyzes the hydrolysis of the glycosidic bond of the terminal, non-reducing β-D-mannose residues in β-D-mannosides (Dhawan & Kaur, 2007). This enzyme is used for downstream hydrolysis of manno-oligosaccharides. β-Mannosidases also belong to clan GH-A. Several three-dimensional structures of these enzymes have been reported, indicating diverse structural organization (Dias et al., 2004; Tailford et al., 2007).

Based on the complex structures of various mannans as depicted in Table 1, it can be inferred that other accessory enzymes such as α-galactosidases and acetyl mannan esterases are required to cleave the side chains in order to obtain fermentable sugars as well (Chauhan et al., 2012; Gilbert et al., 2008). However, more details about these enzymes are beyond the scope of this review.

Production of mannan-degrading enzymes

In the past decade, an increasing number of articles have been published on the production and characterization of native and recombinant mannanases from various sources, due to their emerging importance in biotechnological applications. Even though mannanases are found in a wide variety of organisms ranging from bacteria, archaea (Cantarel et al., 2009), thermophiles (Klippel & Antranikian, 2011), fungi (Do et al., 2009; Jagtap et al., 2012; Kote et al., 2009; Liu et al., 2012a; Luo et al., 2009; Saeki et al., 2000), higher plants (Bourgault et al., 2005) and animals (Larsson et al., 2006; Yamaura & Matsumoto, 1993; Yamaura et al., 1996), the main focus of these studies has been on microbial β-mannanases as they can be easily adapted for large-scale production. Most native microbial β-mannanases are extracellular enzymes, and their expression can be induced by various β-mannan-containing substrates such as locust bean gum (LBG), guar gum or copra meal (Kote et al., 2009). However, some β-mannanases have been shown to be intracellular and their expression is constitutive (Dhawan & Kaur, 2007). Despite relatively high yields and interesting properties of several native β-mannanases, the high viscosity of the induction media is troublesome to the biofermentation process, limiting the production of this enzyme on an industrial scale (Do et al., 2009). Therefore, the implementation of genetic engineering techniques for the overexpression of β-mannanases, mainly in *Escherichia coli* (Songsiriritthigul et al., 2010) and *Pichia pastoris* (Do et al., 2009; Mellitzer et al., 2012) expression systems have been reported. The latter systems, in particular, allow high-level secretion of the recombinant enzymes into the culture media and facilitate the affinity purification of both bacterial and fungal β-mannanases for different applications. A comprehensive update on the basic properties and sources of native and recombinant β-mannanases from various microorganisms, encompassing many enzymes that were not reported in previous reviews, can be found in Supplementary Tables S2 and S3, respectively. From these tables, it can be concluded that most of the fungal β-mannanases show their optimum activity at a pH in an acidic range, whereas those of bacteria are in the neutral range. In addition, a number of β-mannanases from alkalophilic *Bacillus* spp. show pH optima between 9 and 10. In general, the optimal temperature of β-mannanase activity varies from 30 to 90 °C, depending on the sources of the enzymes. Both wild-type and recombinant β-mannanases that are active at different pHs and temperatures are appropriate for a wide range of applications. For example, alkalophilic β-mannanases are advantageous for applications in the pulp and paper industry as well as components of detergents (Dhawan & Kaur, 2007), whereas neutral β-mannanases are suitable for bioconversion of β-mannan into MOS (Yamabhai et al., 2011). Highly acidic β-mannanase can be useful for the pre-treatment of lignocellulosic biomass for the production of second-generation biofuel (Do et al., 2009).

Biotechnological application of β-mannanases

The application of mannan-degrading enzymes in biotechnology has gained significant interests during the past decade based on an increasing demand for efficient utilization of renewable bio-resources for sustainable development (Do et al., 2009). In addition to cellulases and xylanases, which are the key enzymes for the hydrolysis of the polysaccharide fraction of lignocellulose, β-mannanases are also required for the production of second-generation biofuels (Van Dyk & Pletschke, 2012). For an efficient bioconversion of lignocellulose biomass to fermentable sugars, thermostable enzymes are essential during the pre-treatment step, followed by simultaneous saccharification and fermentation (SSF) processes (Turner et al., 2007; Viikari et al., 2007). Several wild-type and recombinant β-mannanases that are stable and active at high temperature from thermophilic bacterial, eubacterial (Duffaud et al., 1997; Jiang et al., 2006; Luthi et al., 1991; Talbot & Sygusch, 1990), actinomycetes (Hilge et al., 1998) and fungal sources (Do et al., 2009; Kote et al., 2009; Luo et al., 2009; Sachslehner et al., 2000; Turner et al., 2007) have been characterized. CBMs such as CBM1, naturally fused to β-mannanases, may enhance the hydrolytic efficiency on complex lignocellulosic substrates (Hägglund et al., 2003). Moreover, a successful attempt to improve the hydrolytic capacity of β-mannanase by genetically engineering an additional carbohydrate-binding module (CBM1) to the C-terminus of the enzyme (Pham et al., 2010) or by a directed evolutionary approach (Couturier et al., 2013a) have been reported.

In addition to the pre-treatment of lignocellulosic biomass to generate biofuels, another interesting application of β-mannanase is for the random hydrolysis of mannans into MOS (Songsiriritthigul et al., 2010), which have several possible beneficial effects on health and well-being as described in the next section.

Other applications of β-mannanases include biobleaching of pulp and paper (Gübitz et al., 1997), textile and cellulosic fiber processing (Dhawan & Kaur, 2007), processing of instant coffee by reducing the viscosity of coffee extracts (Sachslehner et al., 2000), extraction of oil from palm kernel (Jorgensen et al., 2010), cleaning composition in laundry detergent and other cleansing reagents (Bettiol et al., 2002; Kirk et al., 2002), improvement of animal feed (Jackson et al., 2003; Wu et al., 2005; Zou et al., 2006), facilitating gas and oil drilling (Gübitz et al., 2001), reduction of the viscosity of thickening agents, clarification of fruits and vegetables and removal and inhibition of biofilm formation (Chauhan et al., 2012; Dhawan & Kaur, 2007; Moreira & Filho, 2008).

Mannooligosaccharides

Mannooligosaccharides (MOS), including both α-MOS and β-MOS, are a rather new class of oligosaccharides that have gained significant interest as a pre-biotic (Gibson et al., 2004). A prebiotic is a ''selectively fermented ingredient that allows specific changes, both in the composition and/or activity in the gastrointestinal microflora that confers benefits upon host well-being and health'' (Roberfroid, 2007). According to this definition, a non-digestible oligosaccharide can only be classified as pre-biotic if it fulfills three criteria (1) resistance to the digestion process of the host, including gastric acids, host hydrolytic enzymes and gastrointestinal adsorption; (2) fermentation by intestinal microflora; and (3) stimulation of the growth and/or activity of selected intestinal bacteria that can potentially contribute to health and well-being (Roberfroid, 2007). These intestinal bacteria include specific groups such as *Lactobacillus* spp. *Enterococcus* spp., *Bifidobacterium* spp., *Bacteroides* spp. and *Eubacterium* (Roberfroid et al., 2010). Only a few established pre-biotics have been described according to these above-mentioned criteria, i.e. inulin, fructo-oligosaccharides (FOS) and galacto-oligosaccharides (GOS). These oligosaccharides all show pre-biotic effects as deduced from *in vivo* studies (Roberfroid, 2007). Despite a lack of *in vivo* evidence, a number of reports suggest pre-biotic effects of both α-MOS and β-MOS, derived from yeast cell wall α-mannan and plant β-mannans, respectively (Charalampopoulos & Rastall, 2012). In addition, accumulating data have suggested that α-MOS can have various other health-promoting effects on both humans and livestock (Heinrichs et al., 2003; Kim et al., 2011; St-Onge et al., 2012; Tester et al., 2012). However, these data are not entirely clear and convincing; therefore, more systematic experimental studies are needed to determine whether α-MOS or β-MOS can be classified unequivocally as prebiotic. Since mannans can be obtained from abundant and inexpensive agricultural wastes, bioconversion of mannan into various types of bioactive MOS and investigation of their actual biological activities are highly attractive areas of research and development.

Preparation of MOS

Mannan polysaccharides can be obtained from two main types of raw materials, i.e. from cell walls of yeast and plants, respectively. Since the cell wall components of plants and yeast are different, it can be expected that the physical and biological properties of their MOS are considerably different. This review will deal with both types of MOS.

α-MOS from S. cerevisiae cell walls

To prepare α-mannan, yeast cell walls are first extracted from *S. cerevisiae* by heating in an autoclave, followed by precipitation with Fehling reagent (Kocourek & Ballou, 1969). In more recent reports on the isolation of cell wall polysaccharides, the cell walls were first separated from the internal components by mechanical cell disruption. The purified polysaccharides were then treated with proteases, which caused protein lysis in the outer cell wall and the release of soluble mannan, which could be separated from insoluble glucans (Kath & Kulicke, 1999). Similar methods using a combination of enzyme and mechanical treatment to improve the extraction yield have been reported recently (Bychkov et al., 2010). Yeast cell walls can also be prepared by autolysis after incubation at pH 5.0 at 50 °C for 24 h (Ganner et al., 2010). In addition to published protocols, several proprietary methods for the preparation of α-MOS, based on the extraction of α-mannan-rich yeast cell walls obtained from yeast cells by autolysis, heating or hydrolysis with alkali or acid, have been reported (Yu et al., 2011). It is important to note that in the yeast *Candida albicans,* a third type of β-1,2-linked mannose units have been identified (Shibata et al., 2007). Since the cell wall architecture of yeast is a defined covalent complex of β-glucans, mannoprotein and chitin (Lipke & Ovalle, 1998), the general yeast cell wall preparations are likely to include both α- and β-MOS as well as other yeast cell wall components.

β-MOS from plant cell walls

Beta-Mannans are commonly prepared from various parts of mannan-rich plants by extraction with hot water or alkaline solutions, followed by precipitation with ethanol. Various methods for the extraction of mannan from well-known sources such as carob and locust bean, guar seeds, konjac, etc., can be found in the cyber colloid website (www.cyber colloids.net/). Coffee mannans, which are comprised mainly of galactomannan and acetylated arabinogalactomannans, can be extracted from roasted coffee beans with hot water (coffee infusions; Nunes & Coimbra, 2001). The amount of extracting galactomannan depends on the origin of coffee and the degree of roasting (Nunes & Coimbra, 2002). Alternatively, mannan can be isolated from green defatted coffee beans by delignification, acid wash and subsequent alkali extraction (Sachslehner et al., 2000). Coconut mannan can be extracted by sequential removal of lipid, carbohydrate, lignin and protein (Saittagaroon et al., 1983).

Biological and physicochemical methods can be used to generate β-MOS from mannans that are extracted from plants. Biological treatments involve enzymatic hydrolysis using a suitable β-mannanase, which randomly cleaves β-1,4-glycosidic linkages in diverse β-mannan substrates. Enzymes that are suitable for bioconversion of mannan into β-MOS, using crude substrates, should display negligible to low activity towards other plant cell wall polysaccharides. *Bacillus licheniformis* ManB has been shown to be appropriate for the bioconversion of soluble and low-substituted

mannan substrates such as konjac glucomannan, locust bean gum galactomannan and β-D-mannan, prepared by controlled hydrolysis of carob galactomannan (Songsiriritthigul et al., 2010). Recently, a physicochemical method for the hydrolysis of mannan to produce β-MOS of various sizes, ranging from mannobiose (M2) to mannoheptaose (M7) has been used (Otieno & Ahring, 2012b). However, β-MOS were only found in small amounts when compared with xylo-oligosaccharides (XOS), which were the main products of this process.

Since both enzymatic and non-enzymatic processes have advantages and disadvantages (Otieno & Ahring, 2012a), depending on the raw material, combining both physiochemical and enzymatic methods could be an interesting approach for the preparation of β-MOS from different sources. More research and development of effective methods for the production of MOS from various mannan-rich bioresources are required.

Biological activities and applications of MOS

Most of the scientific literature on the biological activities of MOS reports the effects of α-MOS from yeast cell walls, especially *S. cerevisiae*, as feed additive. These results propose certain beneficial effects of yeast α-MOS on a wide variety of domestic and farm animals, including dogs (Middelbos et al., 2007), broilers (Iji et al., 2001; Kim et al., 2011), male turkeys (Parks et al., 2001), pigs (Rosen, 2006), calves (Franklin et al., 2005; Heinrichs et al., 2003), lobsters (Sang & Fotedar, 2010) and sea bass (Torrecillas et al., 2007, 2011, 2012). Meta-analysis of the worldwide literature on the studies of the effects of *S. cerevisiae* cell wall mannan on the performance of broilers has suggested beneficial responses in terms of feed intake, live-weight gain, feed conversion ratio and mortality response (Rosen, 2007). These results came from studies of commercially available MOS. In contrast, the effect of feeding diets supplemented with alpha-MOS at 0.1–0.2% did not have significant effects on broiler chickens (Corrigan et al., 2011) or turkeys (Corrigan et al., 2012), except that the composition of the bacterial community in the bird cecal contents changed significantly. More research is needed, therefore, to confirm the beneficial effects of α-MOS from yeast cell walls and α-MOS from a wider group of yeast sources.

Following a ban by the EU on the feeding of all antibiotics and related drugs to livestock in January of 2006, the demand for antibiotic-free meat has been increasing worldwide (Sofos, 2008). Alpha-MOS from yeast cell walls as well as other pre-biotic oligosaccharides has been suggested as an alternative replacement for antibiotic growth promoters (Heinrichs et al., 2003). Since agricultural wastes are rich sources of raw materials for the production of β-MOS, more research on exploring the possibility of using plant β-MOS as feed additives should be performed. Successful application of plant-derived β-MOS from agricultural wastes as feed additive will not only promote the meat industry, but will also support sustainable development of the agricultural sector as well.

In addition to the beneficial effects of yeast α-mannan on livestock, health-promoting effects of β-mannan and β-MOS from other sources have been reported. Coffee β-MOS, prepared from coffee extract by thermal hydrolysis (Asano et al., 2003), have been shown to reduce weight, total body volume, and adipose tissue in men but not women, when consumed as a β-MOS-containing beverage (Salinardi et al., 2010; St-Onge et al., 2012). In animals, coffee β-MOS have been shown to significantly lower the blood pressure of hypertensive rat models (Hoshino-Takao et al., 2008). Coffee mannan prepared with hot water followed by alkali extraction has also been shown to stimulate the expression of the surface lymphocyte activation marker CD69 on B-lymphocytes (Simoes et al., 2009).

Apart from coffee mannan, beneficial effects of mannan-rich plants have been reported. *Aloe vera* L. extracts from inner leaves, prepared by ethanol precipitation, which is rich in galactoglucomannan (Rodríguez Rodríguez et al., 2010), has been shown to promote oral wound healing in rats by stimulating gingival fibroblast proliferation (Jettanacheawchankit et al., 2009), as well as activate proliferation, differentiation, extracellular matrix formation and mineralization of primary human dental pulp cells (Jittapiromsak et al., 2010). Konjac glucomannan has been shown to improve vaginal health recovery after antifungal treatment for *Candida* infection in 14 female patients (Tester et al., 2012). However, the MOS preparations that were used in most of these studies were not a pure mixture with a defined structure, and therefore it is difficult to determine the actual biological activities of MOS. This is because other active ingredients in the preparation, especially from yeast cell walls or aloe extract, could have potent pharmacological effects even in low concentrations. Well-defined MOS products must be obtained to precisely evaluate their biological effects.

Potential mechanisms of action of MOS

Several mechanisms of action have been proposed for the health-promoting effects of α- and β-MOS. The most well known is the potential pre-biotic effect since MOS are non-digestible oligosaccharides. The microbiota or a collection of microbial cells and viruses that reside inside and ouside the host body has been shown to play a fundamental role in health and disease in their hosts (O'Hara & Shanahan, 2006). The host microbiota, especially in the gut, is essential in stimulating the maturation of immune cells as well as promoting the normal development of immune functions (Clemente et al., 2012). The second mechanism of health-promoting effects of α- and β-MOS is related to competitive exclusion of pathogenic bacteria (Callaway et al., 2008; Fernandez et al., 2000; Gaggia et al., 2010). The protection mechanism was thought to be the result of the ability of MOS to bind to mannose-specific lectins of Gram-negative pathogens that express Type-1 fimbriae such as *Salmonella* and *E. coli*, resulting in their excretion from the intestine (Baurhoo et al., 2007).

Another proposed mechanism of action is only specific to α-MOS from *S. cerevisiae* cell walls, which showed the direct interaction with the host immune system (Che et al., 2012). However, this association is not easy to confirm, because it could also be the result of an indirect pre-biotic effect via the alteration of the host microbiota. Recent work in mice suggested that the terminal high-mannose oligosaccharides in secretory IgA (sIgA) are the key responsible agent for innate

immune defense against pathogenic bacteria. The addition of free mannose across a wide dose range could significantly inhibit biofilm formation by *Vibrio cholerae* (Murthy et al., 2011). Therefore, α-MOS may prevent the invasion of pathogens in a similar manner. The role of MOS on the host immune system is likely to be valid only for *S. cerevisiae* mannan because the major bonds in high-mannose proteoglycans are α-linked. Nevertheless, this remains to be established. An experiment that directly compares the function of α- and β- MOS on the host immune system will be useful to clarify this issue.

Conclusions and future perspectives

Mannans are components of lignocellulosic biomass, an abundant renewable resource for the productions of biofuel and high value biomaterials. Pre-treatment of lignocellulosic materials to remove lignin and hemicellulose has been shown to improve the hydrolysis of cellulose and other polysaccharides to produce mixed reducing sugars for fermentation into bioethanol (Sun & Cheng, 2002). β-Mannanases are one of the important polysaccharide hydrolases that act on galactoglucomannans and other mannan-rich hemicelluloses during the pre-treatment process (Gilbert et al., 2008). Despite some progress in cloning and characterization of various microbial β-mannanases that show attractive properties for application in bio-refinery, more understanding of the structure–function relationship and substrate recognition through the analysis of three-dimensional structures and mutational analysis remains to be achieved.

In addition to pre-treatment of lignocellulosic biomass, biotechnological applications of β-mannanases in the food, feed and detergent industries are well established by now. Nevertheless, the costs of these enzymes are still too high and, therefore, more research on the cost-effective production of highly efficient enzymes suitable for diverse applications is still in demand.

A study on the application of MOS as part of nutraceuticals or functional food is a highly attractive area of research. While the utilization of α-MOS from yeast cell walls for health benefits to animals has been fully commercialized, the production of β-MOS from mannan-rich plants is still at the beginning. Various reports on health-promoting effects of α-MOS in animals indicated that they could have benefits for humans as well. Nevertheless, more systematic research on the mechanisms of these beneficial effects as well as their safety for human uses remains to be carried out. Since plants are rich and abundant sources of β-mannans of various structures, β-MOS that are prepared from different species of plants can be expected to have different biological activities. So far, there have been only a few studies on the production β-MOS from different plants, not to mention investigations on their various biological activities. Therefore, a vast area of research on plant β-MOS remains to be explored, ranging from extraction, structure elucidation, bioconversion and systematic analysis of their various biological activities.

Declaration of interest

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Supplementary materials available online:
Supplementary Tables S2 and 3.

Supplementary Material I:

Detailed explanation of the structure of different types of mannnans from plant

2.1.1 Linear mannans or β-1,4 mannans contain only D-mannosyl residues linked via β-(1→4)-bonds in their main chain with less than 5% of galactose residues (w/w) (van Zyl et al., 2010). They are the major mannan components isolated from the seeds of plants including ivory nut, green coffee beans and coconut (copra meal) (Aspinall, 1959, Saittagaroon et al., 1983). The crystal structures of the two types of the mannan microfibrils, i.e., mannan I and II, have been described. Both show different crystalline allomorphs like cellulose, but the packing is different in many aspects (Millane and Hendrixson, 1994).

2.1.2 Glucomannans consist of β-1,4-linked D-mannose and D-glucose in the backbone, with the ratio of mannose to glucose varied from 2:1 to 4:1. They usually show a degree of polymerization higher than 200 (Al-Ghazzewi et al., 2007). The conformations of glucomannan chains are similar to those of cellulose, which occurs as a number of crystalline allomorphs (Millane and Hendrixson, 1994).

2.1.3 Galactomannan comprises β-1,4-linked D-mannose in its backbone and α-1,6-linked D-galactose as side chains with more than 5% of galactose (w/w). The distribution of D-galactosyl residues along the chain of the mannan polymer varies in different sources of this polysaccharide. The D-galactosyl side chains confer hydrophilicity, and therefore the mannose-to-galactose ratio is the key determinant of solubility of this type of polysaccharide in water, as it also helps to prevent the aggregation of the linear heteromannan chains (Dea and Morrison, 1975).

2.1.4 Galactoglucomannans consist of β-1,4-linked D-mannose and D-glucose in their backbone and α-1,6-linked D-galactose on both D-mannose and D-glucose units. They are predominant in softwood (gymnosperms) and can be found in two types, i.e., with a mannose, glucose, and galactose ratio of approximately 3:1:1 and 4:1:0.1, respectively (Lundqvist et al., 2002).

2.1.5 Acetylated galactoglucomannans have a basic structure like the galactoglucomannans with *O*-acetyl groups randomly distributed at the C-2 and C-3 positions of the β-D-(1→4)-mannopyranose units, but not on the β-D-(1→4)-glucopyranose units. On an average, one acetyl group can be found per 3 to 4 hexose units. Acetylated galactoglucomannans have an approximate degree of polymerization (DP) ranging from 100 to 150, which is equivalent to a molecular weight (M_w) of 16–24 kDa. Two types of acetylated galactomannan are found in softwood, i.e., galactose-rich and galactose-poor mannans with the molar ration for mannose:glucose:galactose of approximately 3:1:1 and 3:1:01, respectively (Timell, 1964, Timell, 1965). Since *O*-acetyl-galactoglucomannan or galactoglucomannan can be obtained from

the same source using different extraction procedures (Lundqvist et al., 2003), these two types of mannan polymers were grouped together in this review as shown in the Table 1.

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Supplementary Material II : Properties of microbial native (Table 2) and recombinant (Table 3) β-mannanases

Table 2 : Properties of native β-mannanases

Organism	Mw(kDa)/pI	Optimal pH	Optimal Temperature (incubation period)	Substrate	Reference
Acinetobacter sp. ST1-1	-	6.0	40 (60 min)	copra meal, LBG	(Titapoka et al., 2008)
Aspergillus niger ATCC 20114	-	3.5	70 (5 min)	LBG	(Mohamad et al., 2011)
Aspergillus niger ATCC46890	40/3.7	3.5	- (10 min)	LBG-Galman	(Ademark et al., 1998)
Aspergillus niger FTCC 5003	-	5.3	50 (20 min)	LBG	(Abdeshahian et al., 2010)
Aspergillus niger UAM-GS1	56/4.9	3.0	50 (10 min)	LBR	(Regalado et al., 2000)
Aspergillus niger gr	66	5.5	55 (20 min)	LBG	(Naganagouda et al., 2009)
Aspergillus oryzae CECT2094	110	6.0	40 (10 min)	LBR	(Regalado et al., 2000)
Aspergillus oryzae NRRL 3448	-	5.5	55 (20 min)	LBG	(Abdel-Fattah et al., 2009)
Aspergillu tamari IP 1017-10	53	4.5	- (-)	LBG	(Civas et al., 1984)
Aspergillus flavus gr	-	5.0	60 (20 min)	LBG	(Kote et al., 2009)
Aspergillus fumigatus IMI 385708	60, 63/5.2, 4.9	4.5,4.5	60 (5 min)	LBG	(Puchart et al., 2004)
Bacillus amyloliquefaciens 10A1	-	7.0	50 (30 min)	LBG	(Mabrouk and Ahwany, 2008)
Bacillus circulans M-21	33.4	7.0	50 (30 min)	KG	(Mou et al., 2011)
Bacillus circulans NT 6.7	-	6.0-9.0	50 (30 min)	LBG	(Phothichitto et al., 2006)
Bacillus sp. M50	-	6.0	50 (-)	KGM	(Chen et al., 2000)
Bacillus sp. MG-33	-	6.5	65 (-)	LBG	(Meenakshi et al., 2010)
Bacillus sp. MSJ-5	40.5	5.5	50 (10 min)	LBG	(Zhang et al., 2009)
Bacillus stearothermophilus ATCC 266	162	6.5	70 (5 min)	LBG	(Talbot and Sygusch, 1990)
Bacillus subtilis 168	-	7.0	37 (-)	Galman	(el-Helow and Khattab, 1996)
Bacillus subtilis BM 9602	-	6.0	50 (10 min)	KGM,LBG	(Cui et al., 1999)
Bacillus subtilis NM-39	38/4.8	5.0	55 (10 min)	LBG	(Mendoza et al., 1994)

Bacillus subtilis SA –22	38	6.5	70 (-)	LBG, KGM	(Yu et al., 2003)
Bacillus subtilis WY34	39.6	6.0	65 (10 min)	LBG	(Jiang et al., 2006)
Bacteroides ovatus 0038-1	190/4.8	-	- (10-15 min)	GG	(Gherardini and Salyers, 1987)
Bacillus pumilus ATCC 72	55, 37	5.5-6.9, 6.0	65, 70 (30 min)	Galman	(Araujo and Ward, 1990)
Cellulosimicrobium sp. HY-13	35	7.0	50 (15 min)	LBG	(Kim et al., 2011b)
Clostridium butyricum/beijerinckii	50,53	7.0,8.0	50, 50 (30 min)	KGM	(Nakajima and Matsuura, 1997)
Clostridium tertium KT-5A	53	7.0	30 (20 min)	GG	(Kataoka and Tokiwa, 1998)
Flavobacterium sp. P1	-	7.0	35 (10 min)	KGM, LBG	(Zakaria et al., 1998)
Klebsiella oxytoca CW2-3	-	7.0	50 (60 min)	copra meal, LBG	(Titapoka et al., 2008)
Paenibacillus curdlanolyticus B-6	-	4.0	- (-)	LBG	(Pason et al., 2006)
Paenibacillus sp. DZ3	39	5.0	60 (10 min)	Gulman	(Chandra et al., 2011)
Penicillium occitanis Pol6	18	4.0	40 (30 min)	LBG-Galman	(Blibech et al., 2010)
Penicillium oxalicum SO	29	5.0	60 (10 min)	GG	(Kurakake et al., 2006)
Sclerotium rolfsii	61.2, 41.9/3.5	2.9. 3.3	74, 72 (5 min)	LBG	(Gübitz et al., 1996)
Scopulariopsis candida LMK004	41	5.0	50 (10 min)	LBG	(Mudau and Setati, 2008)
Scopulariopsis candida LMK008	28	6.0	40 (10 min)	LBG	(Mudau and Setati, 2008)
Streptomyces galbus NR	-	6.5	40 (30 min)	Galman	(Kansoh and Nagieb, 2004)
Streptomyces sp. PG-08-03	-	8.0	75 (-)	LBG	(Bhoria et al., 2009)
Thermotoga neopolitana 5068	65/5.1	6.9	90-92 (30 min)	Azo-CGM	(Duffaud et al., 1997)
Trichoderma harzianum T4	32.5	3.0	55 (30 min)	LBG	(Ferreira and Filho, 2004)
Trichoderma reesei C30	46/5.2	5.0	75 (10)	LBG	(Arisan-Atac et al., 1993)
Trichoderma reesei	53, 51/5.4, 4.6	3.5, 3.5	70, 70 (-)	LBG	(Stalbrand et al., 1993)

LBG: locust bean gum; KGM: konjac glucomannan; GG: guar gum; Galman: galactomannan; Gulman: glucomannan; CGM: Carbo galactomannan; pNp-Man: *p*-nitrophenyl β-D-mannopyranoside; *o*NPG: *o*-nitrophenyl-β-D-galactopyranoside; -: Not reported

Table 3 : Properties of recombinant microbial β-mannanases

Organism	Mw(kDa)/pI	Optimal pH	Optimal Temperature (incubation period)	Substrate	Reference
Agaricus bisporus C54-*carb8*	-	-	- (-)	LBG	(Tang et al., 2001)
Aspergillus awamori K4	-	3.0	80 (10 min)	Gulman	(Kurakake and Komaki, 2001)
Aspergillus aculeatus CGMCC0608	45/4.5	5.0	60-70 (-)	-	(Christgau et al., 1994)
Aspergillus aculeatus MRC11624	50	3.0	50 (10 min)	LBG	(Setati et al., 2001)
Aspergillus aculeatus VN	54	2.5-3.0	70-75 (30 min)	LBG	(Pham et al., 2010)
Aspergillus fumigatus IMI 385708	60, 60	4.5, 5.2	60, 45 (5 min)	LBG	(Duruksu et al., 2009)
Aspergillus nidulans FGSC A4	56, 56	5.5, 5.5	50, 50 (5 min)	KGM, LBG, GG	(Dilokpimol et al., 2011)
Aspergillus niger BK01	53	4.5	80 (10 min)	LBG	(Do et al., 2009)
Aspergillus niger CBS 513.88	45	5.0	45 (5 min)	LBG	(Zhao et al., 2011)
Aspergillus niger LW-1	52	3.5	70 (10 min)	LBG	(Li et al., 2011)
Aspergillus sulphureus	48/4.8	2.4	50 (30 min)	LBG	(Chen et al., 2007)
Aspergillus terrus	-	7.5	55 (-)	-	(Huang et al., 2007)
Bacillus agaradhaerens	38	8-10	60 (20 min)	AZCL-CGM	(Bettiol and Showell, 2000)
Bacillus sp. AM001	55, 38	9.0, 8.5	60, 65 (10 min)	KM	(Akino et al., 1989)
Bacillus circulans CGMCC 1416	31	7.6	58 (10 min)	LBG	(Li et al., 2008)
Bacillus circulans CGMCC1554	32	7.6	60 (10 min)	LBG	(Yang et al., 2009)
Bacillus circulans K-1	62	6.9	65 (-)	-	(Yoshida et al., 1998)
Bacillus licheniformis DSM13	45	6.0-7.0	50-60 (10 min)	LBG	(Songsiriritthigul et al., 2010)
Bacillus sp. JAMB-750	-	10.0	- (-)	-	(Hatada et al., 2005)
Bacillus sp. N 16-5	55/4.3	9.5	70 (10 min)	LBG	(Ma et al., 2004)
Bacillus sp.1633	34	-	50 (20 min)	AZCL-CGM	(Markus et al., 2003)
Bacillus subtilis	41	6.0	60 (5 min)	LBG	(Yamabhai et al., 2008, Yamabhai et al., 2011)

Bacillus subtilis B23	-	6.8	50 (-)	CGM	(Zhou et al., 2011)
Bacillus subtilis B36	38	6.4	50 (10 min)	LBG	(Li et al., 2006)
Bacillus subtilis BCC41051	38/5.3	7.0	60 (20 min)	LBG	(Summpunn et al., 2011)
Bacillus subtilis G1	45	6.5	45 (5 min)	LBG	(Vu et al., 2012)
Bacillus subtilis HB002	-	6.0	55 (15 min)	KGM	(Yang et al., 2009)
Bacillus subtilis MA139	38	6.0	50 (20 min)	Galman	(Qiao et al., 2010)
Bacillus subtilis WL-3	38	6.0	60 (15 min)	LBG	(Yoon et al., 2008)
Bispora antennata CBS 126.38	45	6.0	70 (10 min)	LBG	(Liu et al., 2012)
Bispora sp. MEY-1	80	1.0-1.5	65 (10 min)	LBG	(Luo et al., 2012)
Caldibacillus cellulovorans	30.7	6.0	85 (15 min)	LBG	(Sunna et al., 2000)
Caldicellulosiruptor Rt8B.4	-	5.5	75 (15 min)	LBG-Galman	(Sunna, 2010)
Caldocellum saccharolyticum	34	6.0	80 (10-15 min)	LBG	(Luthi et al., 1991)
Caldocellum saccharolyticum	-	6.0	80 (-)	LBG	(Morris et al., 1995)
Cellulomonas fimi ATCC 484	100	5.5	42 (-)	LBG	(Le Nours et al., 2005, Stoll et al., 1999)
Cellulosimicrobium sp. HY-13	44	6.0	50 (15 min)	LBG	(Kim et al., 2011a)
Cellvibrio japonicus	-	8.0	50 (30 min)	KGM	(Cartmell et al., 2008)
Ceriporiopsis subvermispora CS-1	-	4.5	60 (10 min)	LBG	(Heidorne et al., 2006)
Chaetomium sp. CQ31	50	5.0	65 (10 min)	LBG	(Katrolia et al., 2012)
Clostridium cellulolyticum ATCC 35319	45	-	- (-)	-	(Perret et al., 2004)
Clostridium cellulovorans ATCC 35296	70	7.0	40 (2 h)	LBG	(Jeon et al., 2011)
Clostridium josui	-	6.5	50 (10 min)	KGM,CGM	(Sakka et al., 2010)
Clostridium thermocellum YS	70	6.5	65 (10 min)	plant polysaccharides	(Halstead et al., 1999)
Clostridium thermocellum F1	55	7.0	75 (10 min)	KGM	(Kurokawa et al., 2001)
Dictyoglomus thermophilum Rt46B.1	40	5.0	80 (15 min)	LBG	(Gibbs et al., 1999)
Erwinia carotovora CXJZ95-198	42	7.5	55 (10 min)	KGM	(Zhang et al., 2007)
Humicola insolens Y1.	47	5.5	70 (10 min)	LBG	(Luo et al., 2012)

Paenibacillus sp. BME-14,	50	4.5	60 (30 min)	LBG	(Fu et al., 2010)
Paenibacillus polymyxa GS01	-	5.0	50 (30 min)	LBG	(Cho et al., 2006)
Pantoea agglomerans A021	38.5	6.0	55 (20 min)	LBG	(Wang et al., 2010)
Penicillium freii F63	72	4.5	60 (10 min)	LBG	(Wang et al., 2012)
Penicillium pinophilum C1	65	4.0	70 (10 min)	LBG	(Cai et al., 2011a, Cai et al., 2011b)
Penicillium sp. C6	39	4.5	70 (10 min)	LBG	(Cai et al., 2011b)
Phanerochaete chrysosporium RP78	65	4.0-6.0	60 (15 min)	LBG	(Benech et al., 2007)
Phialophora sp. P13	45/4.5	1.5	60 (10 min)	LBG	(Zhao et al., 2010)
Piromyces sp.	68	-	- (-)	-	(Fanutti et al., 1995)
Pseudomonas fluorescens subsp. *cellulosa*	46	7.0	- (10 min)	plant polysaccharides	(Braithwaite et al., 1995)
Rhodothermus marinus ATCC 43812	113	5.4	85 (15 min)	Azo-CGM	(Politz et al., 2000)
Sphingomonas sp. JB13	48	6.5	40 (10 min)	LBG	(Zhou et al., 2012)
Streptomyces lividans 66	36/3.5	6.8	58 (5 min)	Galman	(Arcand et al., 1993)
Streptomyces sp. S27	38	7.0	65 (10 min)	LBG	(Shi et al., 2011)
Streptomyces thermolilacinus NBRC14274	-	6.0	55 (10 min)	Azo-CGM, LBG	(Kumagai et al., 2011)
Thermotoga maritime DSM 3109	76.9	7.0	90 (-)	Azo-LBG	(Parker et al., 2001)
Vibrio sp. MA-138	73	7.0	50 (10 min)	KGM	(Tanaka et al., 2009)
Xanthomonas campestris pv. *campestris*	42	7.0	37 (30 min)	LBG	(Hsiao et al., 2010)

LBG: locust bean gum; KGM: konjac glucomannan; GG: guar gum; Galman: galactomannan; Gulman: glucomannan; CGM: Carbo galactomannan; pNp-Man: *p*-nitrophenyl β-D-mannopyranoside; *o*NPG: *o*-nitrophenyl-β-D-galactopyranoside; -: Not reported

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