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Mannan degrading enzymes with special reference to β-Mannanase: A review

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Abstract

Mannans are widely distributed as the main component of the hemicellulose fraction in softwoods, seeds and yeast cell wall. β-mannanases, β-mannosidases, and β-glucosidases are the main enzymes that break down mannan. To eliminate the side chain substituents, additional enzymes like α-galactosidases and acetyl mannan esterases are needed. Numerous bacteria, fungi, actinomycetes, plants, and mammals are known to produce mannanases. Due to their ability to function throughout a broad pH and temperature range and their primary extracellular nature, microbial mannanases have found usage in the pulp and paper, pharmaceutical, food, feed, oil, and textile sectors. The studies on mannanases that have been published recently are compiled in this review with respect to significant microbiological sources, synergistic interaction, production conditions, enzyme characteristics, and possible industrial uses.

Keywords: Mannans, β-mannosidases, enzyme, β-glucosidases and microbiological

Introduction

Mannan polysaccharides are a type of complex carbohydrate primarily composed of the sugar mannose. They are a major component of hemicellulose, a structural component found in plant cell walls, particularly in softwoods. Mannans can be linear or branched, and can also incorporate other sugars like galactose and glucose. Mannans occur primarily in the hemicelluloses of softwood as well as plant seeds like coffee beans, soy beans, alfalfa seeds, ivory nuts and cell walls of yeasts (Olaniyi *et al.,* 2013; Singh *et al.,* 2018) [50, 101]. Mannans are made up of a linear backbone of mannose residues connected by β-1, 4-mannosidic linkages. Depending on the backbone's acid or carbohydrate substitutions, they can also be classified as glucomannan, galactomannan, or galacto-glucomannan (Olaniyi *et al.,* 2013) [50].

Degradation of mannan to its monomer sugars is performed by acid and enzymatic hydrolysis. Acid hydrolysis of mannan is environmentally unfriendly and produces toxic byproducts, whereas enzymatic depolymerization uses mild conditions without the formation of toxic byproducts (Chauhan *et al.,* 2012). Microbial enzymes are preferred for industrial application because of their easy and economical production and novel properties such as activity in a wide range of temperature and pH (Dawood and Ma, 2020) [95]. Commercially important mannan degrading enzymes from fungi and thermophilic bacteria usually resist robust conditions such as extreme temperatures and pH (Kumar *et al.,* 2008) [102].

The heterogenous nature of mannan does not allow accessibility of a single enzyme for all bonds present in it. Complete degradation of hemicelluloses requires the collective action of many enzymes. The mannan-degrading enzymes are a group of enzymes having β- mannanase, β-mannosidase, and β-glucosidase as the main chain degrading enzyme. Accessory enzymes such as α-galactosidase and acetyl mannan esterase are required to remove side-chain substituents from mannan polysaccharide. (Dhawan and Kaur, 2007).

An endo-type enzyme, β- Mannanase, is responsible for the breaking of β-1,4-linked internal linkages of the mannan backbone to produce mannooligosaccharides. β-mannosidase, which acts as an exo-type enzyme, cleaves β-1,4-linked mannosides, releasing mannose from the nonreducing end from mannans and mannooligosaccharides. β-Glucosidase, an exo-type enzyme, hydrolyze 1,4-β-D-glucopyranose at the nonreducing end of the oligosaccharides released from glucomannan and galacto-glucomannan by β-mannanase. α-Galactosidase, a debranching enzyme, catalyzes the hydrolysis of α-1,6-linked D-galactopyranosyl side chains of galactomannan and galacto-glucomannan. Acetyl mannan esterase, a debranching enzyme, releases acetyl groups from galacto-glucomannan (Chauhan *et al.,* 2012). Recently β-mannanases have attracted significant attention from both industry as well as academia because of their potential applications in many important industries including pharmaceutical, oil drilling, textile, detergents, food, animal feed, and production of bioethanol (Dawood and Ma, 2020) [95]. This paper focuses on microbial sources, production, purification, characterization, synergistic interaction and application of mannan degrading enzymes.

Microbial Mannolytic Enzymes

Mannolytic enzymes have been isolated from plants, animals and microorganisms (Kim *et al.,* 2013; Jana *et al.,* 2018 [103, 104]; Favaro *et al.,* 2020 [118]; Chourasia and Gaherwal, 2024b) [112]. These enzymes performed many important metabolic functions in various organisms. Mannan degrading enzymes have been produced from microbes due to their low cost, higher stability, large scale production in less time and space, and ease of genetic manipulation. These qualities increase their market desirability and make them suitable candidates in various industries (Dawood and Ma, 2020) [95]. Numerous microbes possess the ability to hydrolyse mannan efficiently. Most of the mannan degrading microorganisms are gram positive bacteria such as *Bacillus species* (David *et al.,* 2018) [67]. But there are also some gram-negative bacteria like *Klebsiella*

Oxytoca that also efficiently degrades mannan (Tuntrakool and Keawsompong, 2018) [106]. β-mannanase from Gram-negative bacterium *Klebsiella grimontii* was identified by Chen *et al.* (2023a) [93]. β-mannanases from fungi are primarily derived from *Aspergillus, Penicillium,* and *Trichoderma*. In addition, there have been reports on the β-mannanases of *Chaetomium* and *Rhizomucor.* β-Mannanases from *Lichtheimia ramosa*, *A. oryzae RIB40, P. pinophilum* were isolated (Cai *et al.,* 2011a; Tang *et al.,* 2016 [90, 92]; Xie *et al.,* 2019). Soni *et al.* (2017) [89] screened soil fungi capable of producing β-mannanase, and six of them with high β-mannanase activity were studied. A neutral thermophilic β-mannanase was isolated from *Malbranchea cinnamomea* (Li *et al.,* 2022) [88]. Among actinomycetes *Streptomyces sp.* and *Nocardiopsis sp.* have shown appreciable mannan degrading ability (Gohel and Singh, 2015; Pradeep *et al.,* 2016) [33, 111].

Enzymes Involved in the Mannan Hydrolysis

Hydrolysis of mannans requires several glycoside hydrolase (GH) enzymes cooperatively acting together. The CAZy system of annotation (www.cazy.org) classifies these enzymes into GH families based on amino acid sequence, structural and mechanistic similarity rather than catalytic activity as used in the Enzyme Commission (EC) classification system. Organisms that express these plant cell wall hydrolases (mannanolytic enzymes) can possess large numbers of closely related enzymes (same EC classification/enzyme activity, but different GH families). This probably indicates the evolutionary pressure to adapt to the slight variations in the composition of cell wall polysaccharides that are present both among different species and within a single organism, in a manner that corresponds to tissue differentiation (Tailford *et al.,* 2009) [87].

β-Mannanases

Four CAZymes families have been reported with β-mannanase activity among their members: GH5, GH26, and GH113 and more recently, the most distinct of them, GH134 (Sharma *et al.,* 2018) [82]. GH5 is one of the largest families of CAZymes, having different activities and has been further divided into several subfamilies. GH5 enzymes are quite diverse in the substrate recognition, being active both against linear mannan and branched mannan (Tailford *et al.* 2009; Aspeborg *et al.,* 2012) [81, 87]. GH26 family of CAZymes behold mainly β-mannanases and β-mannosidases from bacteria, although endo-glucanases, xylanases, xyloglucanases, and a few fungal mannanases are also found in the group. Recently, GH26 mannanases have been identified in rumen as part of the ruminant's complex enzymatic system for lignocellulose degradation (Mandelli *et al.,* 2020) [80]. GH113 is a relatively new glycosyl hydrolase family that comprises only mannanases. In this family, both endo and exo-acting enzymes are found, and transglycosylation activity has also been observed for its members (Zhang *et al.,* 2008) [79].

The first member of GH134 family has been reported from the filamentous fungus *A. nidulans* in 2015. This enzyme has an endo-mannanase activity and generates mannobiose, mannotriose and mannotetrose as the main products of mannan hydrolysis. The most abundant product obtained was mannotriose. The enzyme has a neutral optimum pH and has been more active against MOS than a GH5 mannanase from the same organism. Furthermore, synergistic effects has been reported while employing the combination of GH134 with GH5 mannanases to perform mannan deconstruction (Shimizu *et al.,* 2015) [78]. The majority of GH134 enzymes described have originated from fungi sources. However, an exception has been identified from *Streptomyces sp.* (SsGH134), which is also thermostable and optimally active at acidic pH (Sakai *et al.,* 2018) [31].

β-Mannosidases

β-mannosidases (EC 3.2.1.25) play an important role in the generation of mannose, the final product of mannan degradation. This enzyme acts as exo-hydrolases and catalyzes the hydrolysis of nonreducing ends of mannobiose and mannotriose. β-mannosidases are found in glycoside hydrolase families GH1, GH2, and GH5, which are part of clan A and feature β-barrel tertiary structures. These enzymes may also include carbohydrate-binding modules alongside their catalytic domains to enhance substrate binding. (Costa and Filho, 2019) [86].

α-Galactosidases

α-Galactosidases (EC 3.2.1.22) are enzymes that act as debranching agents, facilitating the hydrolysis of nonreducing terminal α-galactose residues found in galactomannan or galactoglucomannan, thereby creating additional sites for further hydrolysis by β-mannanases. These enzymes are classified within several families of glycoside hydrolases: GH4, GH27, GH36, GH57, GH97, and GH110.44 (Aulitto *et al.,* 2019) [85].

β-Glucosidases

Another exo-acting enzyme required for mannan degradation are the β-glucosidases (EC 3.2.1.21). They hydrolyse β-1,4-D-glucopyranose at the nonreducing ends of manno-oligosaccharides released after action of β-mannanases on glucomannan and galactoglucomannan. Monosaccharides like mannose and glucose have been released after hydrolysis (Michalak, 2020) [83].

Acetyl mannan esterases

Acetyl mannan esterases (EC 3.1.1.-), together with α-galactosidases are debranching enzymes as they remove side-chain substituents. Specifically, acetyl mannan esterases remove acetyl groups from galactoglucomannan and glucomannan.These polymers may contain 2-O-, 3-O-, and 6-O-acetylations on any mannose residue in the chain. Acetylations can influence a polymer enzymatic degradability, thus the action of acetyl mannan esterases is crucial for the use of galactoglucomannan and glucomannan (Michalak, 2020) [83].

Synergistic Interaction of Mannan Degrading Enzymes

The cell walls of plants and algal polysaccharides play a crucial role in the advancement of the bioeconomy. This significance arises from the fact that polysaccharides are the most prevalent organic molecules in nature, possessing intricate chemical structures that necessitate a diverse array of enzymes for their breakdown. Microorganisms generate enzymes that degrade polysaccharides, which work together synergistically to achieve the complete hydrolysis of complex carbohydrates. Despite being known for many years, the concept of enzyme synergy remains inadequately understood at the molecular level, making it challenging to utilize and optimize effectively. Recently, there has been an increased focus on enhancing and characterizing enzyme synergy for the hydrolysis of polysaccharides (Ahmed Khamassi and Dumonn, 2023) [94].

The heterogenous nature of mannan requires the collective and synergistic action of many enzymes for its complete degradation. Due to insoluble rigid structure of the plant cell wall hydrolysis process is very slow (Chauhan *et al.,* 2012). The level of synergy has been described as "the ratio of the product yield or rate produced by enzymes when combined to the total yield or rate of these products when the enzymes are applied individually in the same quantities as they were utilized in the mixture" (Kumar and Wyman, 2009) [116]. Synergy relies on the proportion of carbohydrate-degrading enzymes present as well as the particular traits of the enzymes and substrate involved. Synergy elucidates the distinct mechanisms by which specific enzymes operate and how they interact with one another. This is typically done with pure enzymes on specific substrates (Beukes and Pletschke, 2011) [99]. A synergistic association is present when the degree of synergy (DS) is greater than 1.0. If the DS is less than or equal to 1.0, then no synergy has taken place between the enzymes (Maglas *et al.,* 2015). Researchers have tried to predict the optimal ratios of enzymes to determine optimal synergistic combinations for complete degradation of complex polysaccharide (Banerjee *et al*., 2010) [117].

Homeosynergy and heterosynergy have been identified with respect to hemicellulases degradation. Homeosynergy occurs between main-chain cleaving enzymes, while heterosynergy occurs between main-chain cleaving and debranching enzymes. (Kovacs, 2009 [96]; Maglas *et al.,* 2015). It is proclaimed that a main-chain cleaving enzyme will have enhanced activity if substituents are first removed through debranching enzymes (Vardakou *et al.,* 2004) [98]. Based on this information, certain studies have employed the debranching enzyme as a form of pretreatment prior to the sequential addition of the main-chain cleaving enzyme. In some instances, this approach has proven effective, while in others it has not. The effectiveness is contingent upon the specificity of the enzymes involved in the reaction, as certain main chain cleaving enzymes necessitate the presence of the substituent for their activity. (Sorensen *et al.,* 2007; Vardakou *et al.,* 2004) [97, 98].

The two-novel galactomannan-active enzymes, Man113A and Gal27A, encoded by the mannan utilization gene cluster of Bacillus sp. N16-5. rGal27A has a synergistic interaction with ManA/Man113A in galactomannan degradation. The synergy degree of rGal27A and rManA on hydrolysis of locust bean gum and guar gum dramatically increased the yields of mannose, mannobiose, and mannotriose (Song *et al.,* 2018). Aulitto *et al.* (2018) [19, 45] has identified synergistic association between the thermophilic enzymes for galactomannans degradation. They used two recombinant thermophilic enzymes β-mannanase from *Dictyoglomus turgidum* and α-galactosidase from *Thermus thermophilus.* They assess their hetero synergistic association on galactomannans degradation at 80 ºC. The most efficient synergy has been observed using Locust bean gum as substrate. Xie *et al.* (2020) [46] reported the synergistic effect of mannanase and α-galactosidase using palm kernel meal, showing that the reducing sugar release significantly increased by 21%.

Production conditions and Properties of Mannan Degrading Enzymes

Microbial mannanases are secreted extracellularly and induced by galactomannan-rich substrate such as locust bean gum (LBG). Other substrates like eichhornia stem powder, palm kernel cake, konjac powder, copra meal and wheat bran have also been practiced for the same purpose, since they offer significant benefit due to their cheaper cost and abundant availability. β-mannanase are mostly produced by using submerged fermentation. However, β-mannanases have also been produced in solid state fermentation using fungi. Both SSF and SmF are viable methods for mannanase production. The choice between the two depends on the specific requirements of the process and the resources available. (Chauhan *et al.,* 2012; Dawood and Ma, 2020; Chourasia *et al.,* 2025) [95, 114].

A number of nutritional and physico-chemical factors like temperature, incubation time, moisture content, particle size, pH, carbon source, and nitrogen content affect the production of β-mannanase. These factors are different for different microorganisms. The optimum temperature for mannanase production has been reported in the mesophilic range in most of the cases, and it corresponds with the growth temperature of the respective microorganism. In general, for best growth and mannanase production, bacteria prefer neutral to alkaline pH and fungi acidic pH (Chauhan *et al.,* 2012). Various studies have shown increased production of β-mannanase through process optimization. One factor at a time approach has been employed to improve mannanase production (Olaniyi *et al.,* 2013; Khattab *et al.,* 2020) [50, 51]. Statistical methods like Box Behnken, central composite design, and placket Burman or their combination have also been used to increase the production of mannan degrading enzymes (Yatmaz *et al.,* 2016; Jana *et al.,* 2018; Blibech *et al.,* 2020; Basmak and Turhan, 2024) [47, 48, 49, 103]. The table- 1 summarizes some of the production of mannanase studies that have been reported in literature.

Different industrial productions have varying requirements for the optimal temperature of β-mannanase activity. For instance, juice clarification is typically carried out at low temperatures, while β-mannanase is required to exhibit its catalytic activity at higher temperatures during oil drilling operations. Microbial β-mannanase generally showed highest activity between 40 and 65°C, while enzyme activity gradually decreased beyond this range. Some β-mannanases have the properties of high temperature resistance, such as β-mannanase from the extremely thermophilic B. subtilis isolated from hot springs, the optimal temperature is 60 °C, and it can tolerate high temperature of 90°C (Luo *et al.* 2017) [55]. According to Chourasia and Gaherwal (2024a) [112], the ideal temperature for mannanase activity derived from *Aspergillus niger* is 75°C. Certain psychrophilic enzymes exhibit significant activity at temperatures as low as 20°C, with their optimal performance observed at 40 °C (Parvizpour *et al.* 2014) [54].

The optimal pH range for microbial β-mannanases activity is typically between 4.0 and 7.0. Bacteria and fungi have different optimal pH ranges for mannanase activity. Bacterial β-mannanase exhibits alkaline activity and remains stable between pH range 6.0–9.0. Some bacterial β-mannanases have an optimal pH value as high as 9.5, which remain stable in an alkaline environment (Zhou *et al.,* 2018) [53]. In contrast, β-mannanase from fungi shows acidic optimal pH values, generally between pH 4.5–5.5. However, some fungal β-mannanase can maintain high activity around pH 3.0–7.0, indicating their strong acid adaptability (Chourasia and Gaherwal, 2024a) [112].

Various chemical reagents and metal ions have shown distinct effects on β-mannanase derived from diverse microbial sources. β-Mannanase from B. subtilis BE91 is significantly activated by Al $^{3+}$, NH_4^+, and divalent metal ions including Mn $^{2+}$, Mg $^{2+}$, Ca $^{2+}$, Zn $^{2+}$, and Cu $^{2+}$. However, K $^{+}$ and Fe $^{3+}$ have minimal impact on enzyme activity. Conversely, Ba $^{2+}$ and Pb $^{2+}$ exert significant inhibitory effects on enzyme activity (Cheng *et al.,* 2016) [52]. Soni *et al.* (2016) reported that activity of β-mannanase from *Aspergillus terreus FBCC 1369* was stimulated by β-mercaptoethanol and strongly inhibited by Hg $^{2+}$. The purified mannanase from *Enterobacter ludwigii* MY271 has been greatly enhanced by several metal ions and chemical reagents, such as Mg $^{2+}$, L-cysteine, glutathione and β-mercaptoethanol. Whereas the enzyme was strongly inhibited by Hg $^{2+}$, Cu $^{2+}$, N-bromosuccinimide, 1-ethyl-3-(3- dimethyl-amino-propyl)-carbodiimide, PMSF and SDS (Yang *et al.,* 2017). The table 2 summarizes some of the characteristics of mannanase that have been reported in literature.

Table 1: Production of Mannan Degrading Enzymes

Enzyme	Microorganism	Fermentation	Fermentation substrate	Enzyme Yield	References
β- mannanase	*Aspergillus niger*	Smf	LBG	39.89	Chourasia and Gaherwal, 2024a [112]
	Bacillus nealsonii PN- 11	Smf	LBG	55	Chauhan *et al.,* (2014) [2]
	Paenibacillus thiaminolyticus.	Smf	Wheat bran	1100	Dhawan *et al.,* (2016) [4]
	Bacillus subtilis ATCC 11774	Semi solid fermentation	Palm kernel cake	805.12	Norizan *et al.,* (2020) [3]
	Fusarium equiseti NFCCI 3284	SSF	PKC	5945 nkat/gds	Soni *et al.,* 2016 [5]
	Acrophialophora levis NFCCI 3286	SSF	PKC	4726 nkat/gds	Soni *et al.,* 2016 [5]
	Malbranchea cinnamomea NFCCI 3724	SSF	Palm kernel cake	599	Ahirwar *et al.,* (2016) [5]
	Aspergillus oryzae	SSF	copra meal	434	Jana *et al.,* (2018) [103]
	Aspergillus niger	SSF	Water hyacinth	378	Chourasia *et al.,* 2025 [114]
β-Mannosidase	*Bacillus sp. 3A*	Smf	LBG	22.62	Onilude *et al.* (2012) [12]
	Phlebia radiate Fr. 79	Smf	ADMS-LNMo supplemented with LBG	—	Prendecka *et al.* (2007) [13]
	Aspergillus awamori K4	SSF	Coffee waste and wheat bran	—-	Kurakake & Komaki (2001) [14]
	Aspergillus oryzae PT4	SSF	Copra meal	87.55	Antia *et al.,* 2023 [1]
α-Galactosidase	*Lichtheimia ramosa*	SmF	BMGY medium	953.6	Xie *et al.,* 2020 [46]
	Rhizomucor miehei	SmF	Soy molasses	121.6	Wang *et al.,* 2019 [8]
	Trametes versicolor	SmF	Soybean cake powder + Galactose	300	Liu *et al.,* 2020a [9]
	Chrysoporthe cubensis	SSF	Sugarcane bagasse +wheat bran + Locust bean gum	2.4	Dutra *et al.,* 2017 [7]
	Fusarium moniliforme NCIM 1099	SSF	Wheat bran	207.33	Gajdhane *et al.,* 2016 [11]
	Trichoderma sp. (WF-3)	SSF	Guar gum + Soybean meal + Wheat straw	176.73	Chauhan *et al.,* 2015 [10]

Table 2: Biochemical Characteristics of Mannan Degrading Enzymes

Enzyme	Micro organisms	Opt. pH	pH Stability	Opt. Temp.	Temp. Stability	Inhibitor	Activator	References
β-Mannanase	**Bacteria**							
	P.polymyxa KF-1	6.0	60%/pH6.0–9.0/24 h	45	70%/50°C/1 h	NR	NR	(Gao *et al.,* 2023) [76]
	B.clausii S10	9.5	50%/pH7.0–11.5/6 h	75	80%/80°C/1 h	NR	NR	(Xu *et al.,* 2022)
	B.nealsonii PN-11	8.8	85%/pH5.0–10.0/3 h	65	100%/60°C/3 h	NR	NR	(Yang *et al.,* 2016) [36]
	K.pneumoniae SS11	9.0	70%/pH7.0–10.6/30 min	70	100%/60°C/60 min	NR	NR	(Singh *et al.,* 2019) [37]
	Bacillus sp. MK-2	6.0	85%/pH 4.0–5.0/30 min	55	85%/50°C/30 min	NR	NR	(Zhang *et al.,* 2019) [8]
	Fungi							
	Aspergillus niger	3.8	85%/pH3-7/60min	75	90%/50°C/60min	NR	NR	(Chourasia and Gaherwal, 2024) [112]
	Coprinopsis cinerea	8.0–9.0	90%/pH8.0–9.0/1 h	70	80%/20–50 °C/1 h	NR	NR	(Yan *et al.,* 2023) [34]
	A.oryzae	6.0	75%/pH5.0–	30	50%/90°C/30 min	NR	NR	(Sakai *et al.,*

			10.0/90 min					2017) [30]
	R.miehei	7.0	pH4.0–10.0/30 min	65	90%/60°C/30 min	NR	NR	(Li *et al.,* 2017)
	Actinomycetes							
	Streptomyces sp.NRRL B-24,484	4.0-6.5	80%/pH3.0–10.0/90 min	40	30%/100°C/2 h	NR	NR	(Sakai *et al.,* 2018) [31]
	Streptomyces sp. CS428	12.5	pH5.0–12.5/24 h	60	100%/60°C/1 h	NR	NR	(Pradeep *et al.,* 2016)
β-Mannosidase	Bacteria							
	Paenibacillus polymyxa	7.0	NR	35	NR	Zn2+, Cu2+, Hg2+	K+, Ca2+, Mn2+, and Mg2+	(Bai *et al.,* 2014) [26]
	Streptomyces sp.	7.0	NR	50	NR	Hg2+, Ag2+, Fe2+	NR	(Shi *et al.,* 2011) [25]
	Thermotoga maritima	7.0	5-9	95	Up to 85°C	Cu2+, Hg2+, Ag2+	NR	(Zhang *et al.,* 2009) [24]
	Fungi							
	Myceliophtora thermophila	5.3	NR	40	NR	NR	NR	(Dotsenko *et al.,* 2012) [27]
	Phlebia radiata	5.5	NR	50	NR	NR	NR	(Prendecka *et al.,* 2007) [13]
	Thermoascus aurantiacus	3.0	NR	76	NR	NR	NR	(Gomes *et al.,* 2007) [29]
α-Galactosidase	Bacteria							
	Bacteroides thetaiotaomicron	7.0	NR	60	Below 40 ■C	Ca2+, Fe2+, Zn2+	NR	Shin *et al.,* 2020 [16]
	Bacillus coagulans	6.0	5.0 – 10.0 (>70 %, 30 min)	55	T1/2 30 min (60 ■C)	Ag+,Hg2+, SDS, Galactose	NR	Zhao *et al.,* 2018 [15]
	Bacillus megaterium	6.8	6.0 – 7.4 (>60%, 24 h)	37	Below 45 ■C (>80%, 2 h)	Hg2+, Ag+, Co2+, Cu2+, SDS, β- ercaptoethanol, Xylose, Glucose, Galactose	Ca2+, Mn2+, Fe3+	Huang *et al.,* 2018 [18]
	Thermus thermophilus	6.0	5.0 – 8.0	90	T1/2 60 min (90 ■C), 30 h (70 ■C)	EDTA, SDS, Tween 20, Triton X- 100, Galactose, Saccarose, Arabinose, Urea, Guanidine chloride	Co2+, Mn2+, Zn2+	Aulitto *et al.,* 2017 [17]
	Hermetia illucens metagenome	7.0	4.0 – 11.0 (15 h)	40	Below 40 ■C (>85%, 4 h)	Co2+, Fe2+, Zn2+, Cu2+, Cd2+, EDTA	Mg2+, Ca2+	Lee *et al.,* 2018 [19]
	Fungi							
	Aspergillus oryzae YZ1	4.6	3.0 – 8.0	50	>60% at 40 – 45 ■C (40 min), 28.7% at 50 ■C (40 min)	Cu2+, Pepsin	Ca2+, Trypsin	Wang *et al.,* 2020 [9]
	Paecilomyces thermophila	5.0	4.5 – 11.5 (>90%, 30 min)	60	T1/2 533.2 min (50 ■C), 115.5 min (55 ■C), 4.8 min (60 ■C)	Hg2+, Ag+, Fe2+, EDTA	Triton X-100	Liu *et al.,* 2020 [9]
	Talaromyces leycettanus JCM12802	4.0	3.0 – 11.0	70	>60% at 65 ■C, 60 min	Ag2+, SDS, Galactose	NR	Wang *et al.,* 2016 [22]
	Rasamsonia emersonii	4.0	NR	80	100% at 70 ■C (60 h), 80% at 80 ■C (3 h)	Ag2+	NR	An *et al.,* 2019

Applications

Production of Manno-oligosaccharides

Mannooligosaccharides (MOS) are small chains of mannose sugar monomer that act as prebiotic and confer health benefits to the consumers. MOS are also synthesized by the physicochemical or enzymatic treatment of naturally occurring mannans such as yeast cell wall, seeds, softwood etc. These oligomers modulates beneficial gut microbiota of animals and have numerous health benefits, including antineoplastic, immunomodulatory, and hypolipidemic effects, indicating that they have immense potential as a functional food ingredient (Kango *et al.,* 2022) [43]. The β-mannanase of *A. kawachii* IFO 4308 was modified to produce the acid-resistant and heat-resistant mutant ManAK, which was expressed in *P. pastoris* efficiently. ManAK efficiently degrades locust bean gum, konjac gum, and guar gum. These substrates can be degraded to MOS with Mw lower than 2000 Da even at high initial concentrations (10%), and the end products show different molecular weight distributions (Liu *et al.,* 2020) [9]. The expression of β-mannanase gene from *Rhizomucor miehei* in *Pichia pastoris* produced recombinant mannanase showed maximum activity at pH 4.5 and 65°C, and exhibited high specific activities towards mannans. They produce manno-oligosaccharides from pretreated palm kernel cake. Using steam explosion pretreatment and recombinant β-mannanase, 80.6% of total mannan in PKC has been hydrolyzed (Li *et al.,* 2018) [44]. Multi-tolerant β-mannanase from *Aspergillus oryzae* hydolysed low-cost agro waste copra meal. Evaluation of various thermodynamic parameters indicated high-efficiency of mannanase towards LBG and konjac gum. Fluorescence assisted carbohydrate electrophoresis (FACE) revealed the generation of sugars from DP 1- 4 with some higher DP MOS from different mannans using mannanase (Jana *et al.,* 2018) [103]. The GH26 β-mannanase PpMan26A from *P. polymyxa* hydrolyzed konjac gum to MOS with a degree of polymerization of 3–8 (Gao *et al.,* 2023) [76].

Application in detergent additives

Mannan-rich guar gum, locust bean gum, and konjac gum are commonly utilized as thickening agents in various products such as shampoo, hair gel, chewing gum, and toothpaste to enhance viscosity. However, due to the strong affinity between mannan and cellulose molecules, it is challenging to remove mannan stains from clothing once contaminated (Chouhan *et al.,* 2012). β-mannanases in combination with detergents can be used for cleaning or preparation of fibers in textile and cellulosic processing industries. To prepare the material that is ready for garment manufacture the cellulosic material is processed through several steps: singing, desizing, scouring, bleaching, dyeing, and finishing (Mojsov, 2011) [59]. The efficacy of *Bacillus CFR1601* β-mannanase in removing stains from cotton fabric contaminated with chocolate ice cream and ketchup was evaluated. The results indicated that the combination of detergents and β-mannanase showed better decontamination ability than detergents alone (Srivastava *et al.,* 2016). David *et al.* (2018) [67] investigated the potential of protease and β-mannanase secreted by *B. nealsonii strain PN-11* as detergent additives. The use of a single enzyme exhibited favorable compatibility with the detergent, thereby enhancing the detergent’s efficacy against various types of stains (Kaira *et al.,* 2016) [69].

Pharmaceutical and food industry

Mannose is a monosaccharide that has demonstrated important benefits for the immune system, being active against metabolic syndrome, diabetes, intestinal diseases, urinary tract infections, and other conditions. In the food sector, mannose serves as a texture enhancer in products such as ice creams, salad dressings, and processed fruits. In the pharmaceutical sector, beyond the previously mentioned uses, mannose acts as a foundation for the development of immunostimulant and antitumor compounds, vitamins, and mannitol, and is also utilized as an excipient in rapidly dissolving tablets. The worldwide market for mannitol, which is utilized in drug delivery systems, is projected to reach 100 million dollars in global sales. In the cosmetics sector, mannose is additionally employed as a moisturizing agent, offering the benefit of a "dry touch." (Hu *et al.,* 2016).

Currently, most commercially available mannose is produced by extraction from yeast cell walls, and plants using various pretreatment and extraction techniques (Zhang *et al.,* 2009) [24]. Another way to produce mannose is through chemical processes, but it is not economically viable. This makes using mannanases a safer and more environmentally friendly choice (Hu *et al.,* 2016). Mannans are present in fruit juice and coffee extracts, and the high viscosity of these polymers is undesirable for the industrial processes. To solve this problem, mannanases can be employed to reduce the viscosity and turbidity of the liquids, making the products clearer and more attractive to consumers (Srivastava and Kapoor, 2017; Dawood and Ma, 2020) [64, 95].

Biobleaching of pulp and paper

Biobleaching utilizing mannanase involves the application of the enzyme to decompose hemicellulose mannan in pulp, which results in the loosening of pulp fibers, the exposure of lignin, and the enhancement of subsequent chemical bleaching processes. This enzymatic treatment not only improves the brightness and whiteness of the pulp but also significantly decreases the requirement for harsh chemicals such as hypochlorite during the process. Mannanase operates in synergy with xylanase, another type of hemicellulase, thereby enhancing the overall properties of paper by diminishing lignin-carbohydrate complexes and eliminating chromophores (Angural *et al.,* 2021) [42]. The predominant source of pulp is softwood, which contains approximately 15–20% hemicellulose in the form of galactomannan. Consequently, β-mannanase enzymes that exhibit high specificity for galactomannan substrates are considered excellent candidates for application in the pulp and paper sector (Chauhan *et al.,* 2012). Angural *et al.,* (2021) [42] has studied a cocktail of thermo-alkali stable laccase, xylanase and mannanase from *Bacillus tequilensis* LXM 55 for pulp biobleaching. After optimization, the cocktail now contains larger levels of the enzyme’s laccase, xylanase, and mannanase. Treatment of pulp with an enzyme cocktail significantly improved the pulp's brightness, whiteness, and other characteristics. In this process 40% less chlorine has been required to obtain the paper of the same quality unlike traditional methods having 100% chlorine consumption.

Biofuel industry

Mannanase is used in the biofuel industry to enhance the breakdown of lignocellulosic biomass, particularly the mannan components, into fermentable sugars. This process is critical for producing next-generation biofuels like bioethanol and biobutanol from non-food, renewable resources, improving efficiency and sustainability. Mannanase, specifically endo-β-1, 4-mannanase, is a key enzyme that works synergistically with other enzymes to deconstruct plant material. The biofuel industry can employ recombinant β-mannanase enzymes depending on the feedstock. Mannanase can be used to process a variety of mannan-rich agricultural wastes like palm kernel cake, locust bean gum, guar gum,konjac powder, water hyacinth powder, orange peel etc., into fermentable sugars (Dawood and Ma, 2020; Chourasia *et al.,* 2025 [95, 114]).

In Animal Feed Industry

β-Mannan is a complex carbohydrate commonly found in feed ingredients such as soybean meal (SBM), palm kernel cake, copra meal, konjac powder and guar gum. All these meals have very limited utilization in the intestine. Incorporation of β- mannanase into these diets results in decreased intestinal viscosity, thus improving both the weight gain of chicks and their feed conversion efficiency (Dhawan and Kaur, 2007). β-mannanase supplementation in diet especially in high fiber diets has benefited the animals in many different ways. β-Mannanase increases growth performance and ileal digestible energy (IDE) and decreases intestinal viscosity in broilers fed diets with varying levels of galactomannan (Latham *et al.,* 2018) [44]. Dietary β-mannanase supplementation significantly improves growth performance, such as weight gain and survival, and enhances nutrient digestibility in common carp (Cyprinus carpio) fed plant protein-rich diets. This enzyme also positively impacts gut health by reducing digesta viscosity and modulating the gut microbiota. Furthermore, it influences gene expression, upregulating genes related to muscle development (like MyoD) and the liver's immune response (like TNF-α) (Dawood and Shi, 2022) [41]. Supplementing African catfish diets with β-mannanase at an optimum dose, improves growth, enhances digestive enzymes, gut morphology, and antioxidant capacity, and boosts immunity. It protects the fish against bacterial infections like *Aeromonas hydrophila,* reducing mortality in challenged fish (Adeshina *et al.,* 2024 [39]). Soybean meal based (SBM) diets with β-mannanase supplementation showed multiple beneficial effects on juvenile *Nile tilapia* growth performance, energy and nutrient utilization, and gut health, promoting improved gut histomorphometry and abundance of beneficial bacteria and reducing potentially harmful bacteria (da Cruz *et al.,* 2024) [40].

Conclusion

A review of mannan-degrading enzymes, primarily focusing on β-mannanases, reveals their widespread presence across various life forms and their growing importance in numerous industries like pharmaceuticals, detergent industry, food and feed, bioethanol etc. These enzymes effectively hydrolyze mannans, complex polysaccharides found in softwood, seed and other biological material, into simpler sugars and oligosaccharides. Combining β-mannanase with accessory enzymes can significantly enhance the efficiency of mannan degradation and the release of target products like MOS. Considerable work is underway in bioengineering β-mannanases to improve their activity, thermostability, pH tolerance, and resistance to chemicals, making them more suitable for industrial conditions. In order to replace the use of toxic chemicals in the industrial sector with environmentally acceptable biocatalysts, it is urgently necessary to develop β-mannanases that are more affordable and better adapted to the needs of the industrial sector in order to lower the danger of environmental pollution.

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