Chapter 4
Fungal Biodiversity Producing Xylanase Enzymes Involved in Efficient Uses of Xylanolysis

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Abbreviations

AGX	Arabino(glucurono)xylan
Araf	Arabinofuranose
AX	Arabinoxylan
DTT	Dithiothreitol
GAX	Glucurono(arabino)xylans
GlcA	Glucuronic acid
HX	Heteroxylan
MeGlcA	4-*O*-methyl-D-glucuronosyl
MLG	Mixed-linkage glucan
SbmF	Submerged fermentation
SSF	Solid-state fermentation
Wis	Water-insoluble
X	Homoxylan
Xyl	Xylanase

1 Introduction

Xylan is among the most common hemicellulose which can be found in nature and comes second among the world's most widely available biopolymer in plants (Muchlisyam et al. 2016). Xylanases are hydrolytic enzymes that depolymerize the plant cell component xylan, by cleaving the β-1,4 backbone of xylan. Fungal sources

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are among the widely used producers of xylanase. But xylanases can also be produced by other species like marine algae, bacteria, yeast, snails, protozoans, crustaceans and insects (Bajpai 2014).

Many fungal species like *Aspergillus*, *Trichoderma* and *Fusarium* species are active xylanase producers. Xylanases have various biotechnological and industrial applications such as in the animal feed industry, processing of bread, food industry, cellulose pulp bleaching and textile manufacturing (Bajpai 2014).

Due to the increasing interest in the biotechnological applications of xylan, intensive research is being carried out mainly focussing on xylanolytic enzymes that are derived from microbial sources majorly mesophilic fungi. This review highlights the occurrence, structure, property of xylans and the production and application of xylanases.

2 Structure of Xylan

Hemicellulose residues were known to be first extracted from plant using dilute alkali. They are found to be of lower molecular weight than cellulose. They can have D-xylose, D-mannose, L-arabinose or D-galactose as their principal monomeric unit. Xylan contains close to or more than 90% of D-xylose as monomer and also traces of L-arabinose. Xylan homopolymer consisting of only D-xylose are very difficult to isolate and are normally found to contain 2–4 sugar monomers. In the initial broad classification, polysaccharide such as chains of D-xylose, D-galactose residues and D-mannose (either alone or in association with D-glucose) (Sunna and Antranikian 1977) can be recognized.

Xylan contains the same backbone structure of D-xylose but differences occur because of the sugar substituents present. These contain acetyl, arabinose and glucuronosyl residues. The xylan isolated from esparto grass is found to be made of the chains of (1 3 4)-P-D-xylopyranose residues. Similarly, xylan isolated from land plants are found to contain the same backbone but show the difference in the arrangement of sugar substitutes. Substitutes found were D-glucuronic acid and L-arabinose, and 4-methyl ether was also found attached (Jayme and Sätree 1942).

2.1 Backbone (D-Xylose)

Xylan that was isolated from plants and grass have found to contain the same backbone of β-(1 → 4)-linked xylose remnant. The main chain of xylan is composed of fl-(1 → 4)-linked β-xylopyranose residues. The presence of β-(I → 4) linkages was also found established between two xylose residues adjacent to each other (Biely 1985) (Fig. 4.1).

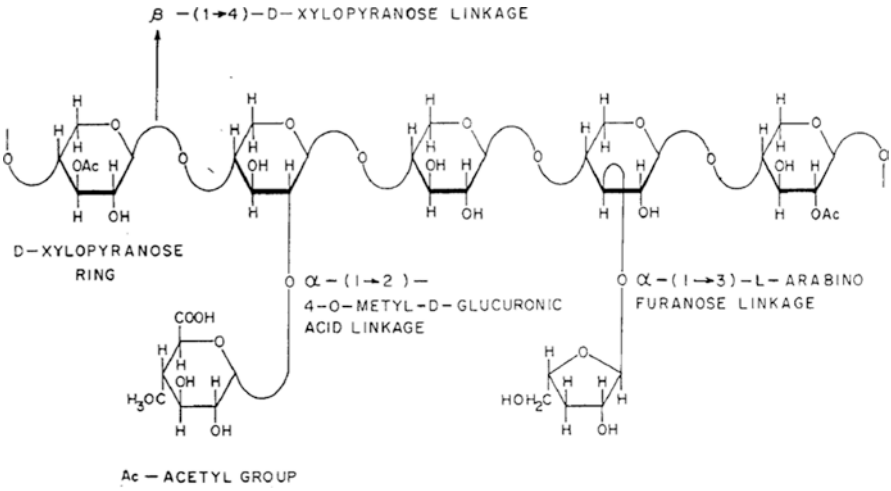

Fig. 4.1 Xylan structure with side chains (Biely 1985)

2.2 Side Chains

Common substituents like acetyl, glucuronosyl and arabinosyl residues are commonly found in the xylan backbone (Biely 1985).

3 Properties of Xylan

3.1 Solubility

Microbial and fungal sources need to secrete an enzyme complex to hydrolyze heteropolymers such as xylan to simple sugars. These enzymes, having different substrate specificity and catalytic activity, are capable of depolymerization of hemicellulose. Xylan varies insolubility. They can be either found to be soluble or non-soluble. Also, it has been shown that the solubility of the xylan structure directly depends upon the degree of substitution in the xylan structure. Another factor determining the degree of solubility is the degree of polymerization of the xylan molecule (Izydorczyk and Biliaderis 1992).

3.2 Characteristics of Xylan Extracted from Different Sources (Table 4.1)

Table 4.1 Xylanases from different microbial strains along with their distinct characteristics (Bastawde 1992)

Microorganism	Characteristics
Aspergillus fumigates	Molecular weight is 19, 8.5 kDa. Optimum temperature and pH is at 55 °C and 5.5, respectively. Its stability ranges from pH 5.0 to 9.0 and temperature of 50 °C
Aspergillus fischeri	Molecular weight is 31 kDa. Optimum temperature and pH is at 60 °C and 6.0, respectively. Its stability ranges from pH 5.0 to 9.5 and temperature of 55 °C
Streptomyces sp.	Molecular weight ranges from 42 to 44 kDa. Optimum temperature and pH is at 55 °C and 5.5, respectively. Its stability ranges from pH 4.0 to 9.0 and temperature of 50 °C
Aspergillus sojae	Molecular weight is 33, 36 kDa. Optimum temperature and pH is at 50, 60 °C and 5.0, 5.5, respectively. Its stability ranges from pH 5.0 to 9.0 and temperature of 50 °C
Aspergillus nidulans KK-99	Optimum temperature and pH is at 55 °C and 8.0, respectively. Its stability ranges from pH 4.0 to 9.5
Acrophialophora nainiana	Molecular weight is 22 kDa. Optimum temperature and pH is at 55 °C and 7.0, respectively. It's thermostable up to 55 °C
Bacillus sp	Molecular weight is 99 kDa. Optimum temperature and pH is at 75 °C and 6.0, respectively
Myceliophthora sp	Molecular weight is 53 kDa. Optimum temperature and pH is at 75 °C and 6.0, respectively. It's stable at pH 9.2 and temperature of 60 °C
Penicillium capsulatum	Molecular weight is 22 kDa. Optimum temperature and pH is at 48 °C and 3.8, respectively. It's thermostable at pH 5.0 and temperature of 50 °C
Thermomyces lanuginosus	Molecular weight is 24.7 kDa. Optimum temperature and pH is at 70 °C and in the range of 6.0–6.5, respectively. Its stability ranges from pH 5.5 to 10 and temperature of 60 °C

4 Enzyme Complex Involved in the Hydrolysis of Xylan

4.1 Endoxylanase

The enzyme 4-endoxylanase having the structure 1,4-p-o-xylan xylohydrolase is one of the enzymes responsible for xylan degradation. The substrate acts at the specific site and not randomly. The site of attack depends on the nature of the substrate and also on the presence of substituents. They are responsible for cleaving the glycosidic linkages of the xylan backbone. This converts the main products into oligosaccharides and further hydrolysis converts them into xylose, xylobiose and xylotriose (Reilly 1981).

4.2 p-Xylosidase

These are exoglycosidases having the formula p-D-xylosidexylo hydrolase and molecular weight in the range of 60 and 360 kDa. Short xylooligosaccharides and xylobiose are hydrolyzed to liberate xylose by this substrate (Wong et al. 1988). These are reported to be found in bacteria and fungi and also among cell associated with yeast and bacteria. The purified form of P-xylosidases are not capable of hydrolyzing xylan. However, some reports show that they attack xylan slowly producing xylose (Sunna and Antranikian 1977).

4.3 L-Arabinofuranosidases

This substrate plays an important role in hydrolyzing xylan despite the fact that only a few such enzymes have been isolated. The two types are only existence-exo-acting and endo-acting. Exo-acting are found to be active against branched arabinans, whereas endo-acting are found only active towards linear arabinans. Such endoarabinases are found to be present in *Bacillus subtilis*, *Clostridium felsineum* and various fungi sources. Most enzymes studied that degrade arabinan are exo-acting (Kaji and Saheki 1975; Van der Veen et al. 1994; Kaji 1984).

5 Occurrence and Isolation of Xylan

5.1 Occurrence

Xylanases occur in both prokaryotes and eukaryotes and are found to occur widely. They are found among higher eukaryote-like snails, insects, protozoa, etc. Among prokaryotes, bacteria and cyanobacteria are found to produce xylanase in the marine environment. Among two types of xylanase (extracellular and intracellular), intercellular xylanases are found in bacteria and protozoa from tureen sources (Dekker and Richards 1976).

Terrestrial plants and algae are known to have xylan-type polysaccharides. These are also found in different tissues of the same plant at different sites. The structural diversity in plants can be due to the fact that structural diversity is related to the functionality in the plant and hence can show the relation between the distribution of particular classes of xylan.

Xylan can also be found in the botanically oldest plant families. In green algae, Homoxylans (X) having b-(1e3) glycosidic linkages have been found to function as substitute cellulose in the cell wall architecture. Also, red seaweeds in the Palmariales and Nemaliales have cell wall comprising of homoxylans having mixed b-(1e3 and 1e4) glycosidic linkages (Painter 1983).

6 Naturally Occurring Xylans

6.1 In Plant Material

Different agricultural crops like corn stalks, sorghum, corn cobs, sugar cane, straw, hulls of fruits and dry husks of fruits and vegetable are known to be very rich sources of xylan. Other sources include forest and pulping waste products from hardwoods. Glucuronoxylan, arabinoglucuronoxylan and arabinoxylan are other structural forms of xylan produced from certain plant sources. Wheat flour xylan consists of 30–40% arabinose which are irregularly attached to the xylose backbone. A distinguishing feature of wheat bran xylan is that it has a large number of side groups attached with glucuronic acid on every 7–8 xylose positions (65% of xylose has attached arabinose). The barley husk xylan are found to contain glucuronic acid and xyloarabinose groups attached to it. Hardwood xylan are found to have 4-*O*-methylglucuronic acid on each tenth xylose. Softwood xylan along with arabinose side group contains more side groups as 4-*O*-methylglucuronic acid are found in each sixth xylose (Ebringerova and Heinze 2000) (Table 4.2).

6.2 In Cell Wall

Xylan is a hemicellulose found in the grass cell wall. The type II grass walls are found to be rich in β-(1,3/4) glucan (also called mixed-linkage glucan) and GAXs (glucurono(arabino)xylans). Grass xylans are found to contain similar general

Table 4.2 Structural features of xylans found in various plant tissues which are found within *Zea mays* and *Oryza sativa* (Ebringerova and Heinze 2000)

Plant source	Xylan type
Corn	*Mature leaves* GAX I GAX II
	Bran HX
	Coleoptile GAX I GAX II
Rice	*Cobs* wis-AGX ws-AGX
	Endosperm AX GAX
	Bran AX GAX

xylans structure (i.e. substitution with MeGlcA or α-Ara*f*, GlcA residues). In addition to it, it also contains some unique features like the presence of Xyl-arabinofuranosyl side chains and the presence of feruloyl groups at the C-5 position of Ara*f* residues. The grass xylans are of two main groups-GAX, making up to 35% of vegetative cell wall that is found to contain GlcA/MeGlcA and Ara*f* remnants; also the cell wall of cereals containing AX, lacking GlcA (Faik 2010).

7 Xylanase from Thermophilic Fungal Source

The enzymes produced from extremophilic and thermophilic microorganism show greater stability. Recently, a lot of efforts has been put in the isolation from such sources. The common thermophilic fungi involved in xylanase production includes *Chaetomium thermophile, Humicola insolens, Humicola lanuginosus, Humicola grisea, Melanocarpus albomyces, Paecilomyces variotii, Talaromyces byssochlamydoides, Talaromyces emersonii, Thermomyces lanuginosus* and *Thermoascus aurantiacus.* These xylanases are usually glycoproteins and can withstand optimum temperatures between 60 and 80 °C. They show the highest activity at an acidic pH of about 4.5–6.5 and exhibit variable molecular weights in the range of 6–38 kDa (Polizeli et al. 2005).

8 Xylanase from Mesophilic Fungal Source

The genera *Aspergillus* and *Trichoderma*, belonging to the class of mesophilic fungi, are leading in xylanase production.

8.1 Aspergillus Species

The production of xylanase from soybean residues by *Aspergillus foetidus* was optimized with the production level of 13.98 U/mL occurring at fermentation for 168 h, pH 7.0, 28 °C and 120 rpm. The specific xylanolytic activity of *Aspergillus fumigatus* was found to be 1055.6 U/g and 558.3 U/g, after 5 days of solid-state fermentation (SSF) in wheat bran and soybean, respectively, by Delabona et al. (2013). In the same work, he found that *Aspergillus niger* showed a specific xylanolytic activity of 1285.0 U/g, 484.2 U/g and 1050.0 U/g using the residue of wheat bran, soybean and wheat bran with sugarcane bagasse, respectively. De Souza Moreira et al. (2013) found that xylanases could be produced by *A. terreus* under submerged fermentation at an optimum pH and temperature of pH 6.0 and 50 °C at 120 rpm and 5.0 and 45 °C at 120 rpm, respectively. Guimaraes et al. (2013) found a xylanolytic activity of 10.50 and 11.92 U/mL, respectively, for *Aspergillus niger* and *Aspergillus flavus*,

Table 4.3 Details about the production of xylanase from different fungal sources (adopted from Delabona et al. 2013; Souza Moreira et al. 2013)

Aspergillus species	Production level	Fermentation details
Aspergillus foetidus	13.98 U/mL	Time 168 h, pH 7, 28 °C and 120 rpm
Aspergillus fumigatus	1055.6 U/g	After 5 days of SSF
Aspergillus niger	1285.0 U/g	Using wheat bran residue
Aspergillus terreus	Unknown	Under submerged fermentation at pH 6.0, 50 °C at 120 rpm
Aspergillus flavus	11.92 U/mL	Using 0.5% corn cob
Aspergillus awamori	Unknown	SSF at pH 5 and 50 °C

using wheat bran 0.5% and corn cob 0.5% as residues. Based on the data obtained from different literature, it was found that the xylanase from *A. foetidus* was more effective in comparison to xylanase from *A. niger, A. flavus and A. fumigatus.* (Cunha et al. 2018). The SSF of tomato pomace by *Aspergillus awamori* was known to produce hydrolytic enzymes like xylanase. At pH 5, the enzyme shows optimum activity and temperature of 50 °C. Hg^{2+} and Cu^{2+} could strongly inhibit the enzyme, whereas the enzyme can be activated by Mg^{2+}. The enzymatic activity was observed to be quite high when the extract was preserved at a pH of 3–10 and a temperature range of 30–40 °C (Umsza-Guez et al. 2011).

Xylanase can be produced by *Aspergillus* species on fermentation of soybean residues, wheat bran, residues of wheat bran with sugarcane bagasse, corn cob and tomato pomace. Based on the data obtained from different literature, it was found that the xylanase from *A. foetidus* was more effective in comparison to xylanase from *A. niger, A. flavus* and *A. fumigatus* (Cunha et al. 2018). Hg^{2+} and Cu^{2+} could strongly inhibit the enzyme, whereas the enzyme can be activated by Mg^{2+} (Table 4.3).

8.2 Trichoderma Species

Ascomycetes filamentous fungi *Trichoderma reesei* are known to produce alkaline xylanase (Mewada et al. 2017). The cultivation of the crude extracellular extract of the strain *Trichoderma inhamatum*, Xyl I and Xyl II were stable at a temperature of 40 °C and at pH 4.5–6.5 for Xyl I and 4.0–8.0 for Xyl II. These xylanases were stable at a temperature of 40 °C and at pH 4.5–6.5 for Xyl I and 4.0–8.0 for Xyl II. The activity of enzyme was strongly reduced by ion Hg^{2+} and the detergent SDS, whereas 1,4-dithiothreitol was found to stimulate both Xyl I and Xyl II enzymes (Silva et al. 2015). *Trichoderma viride* VKF-3 produces xylanase using coconut oil cake as substrate with an activity of 3.045 IU/mL (Nathan et al. 2017). Rifai, a strain of *Trichoderma harzianum,* isolated from decaying *Aspidosperma sp.* (peroba) wood was used to produce xylanase using sugarcane bagasse as substrate. The high-

est xylanase activity was observed to be 288 U/mL on the seventh day using this method (Rezende et al. 2002).

8.3 *Fusarium Species*

Xylanase can be purified from *Fusarium heterosporum,* using barley remnants by SSF. The molecular mass of xylanase obtained by this method was found to be 19.5 kDa. The optimum pH for the xylanase was 5.0. Xylanase activity can be enhanced by Ba^{2+}, Ca^{2+}, Mg^{2+}, dithiothreitol (DTT) and β-mercaptoethanol, whereas Hg^{2+}, Pb^{2+} and Zn^{2+} strongly inhibited the enzyme activity (Heinen et al. 2014). High amounts of xylanase can be produced on birchwood xylan and agricultural residues like wheat bran and peptone by using a mutant strain of *Fusarium oxysporum* (NTG-19) (Kuhad et al. 1998). *Fusarium sp*. BVKT R2 are known producers of xylanase. For maximum production, a temperature of 32.5 °C and a pH of 5 are required along with 1.5% of yeast and sorbitol extract. This should also be kept under agitation at 175 rpm (Ramanjaneyulu and Reddy 2016).

8.4 *Penicillium Species*

Using cheap substances like wood, rice, wheat bran and sesame oil, the production of xylanase from *Penicillium oxalicum* under SSF was optimized. Xylanase can also be produced by the fungus *Penicillium sclerotiorum* under submerse cultivation. The best inducers of xylanase activity were oat spelts xylan and wheat bran. The conditions for optimum production of xylanase were found to be at a temperature of 30 °C and a pH of 6.5 and under stationary condition for 5 days using liquid Vogel medium. The optimum activity was found at a temperature of 50 °C and at pH 4.5 (Knob and Carmona 2008). Xylanase can also be produced from submerged cultures of *Penicillium echinulatum* 9A02S1. The highest activity of xylanases was observed in the medium containing 0.25% (w/v) cellulose and 0.75% (w/v) sorbitol added after 36 h of cultivation (Todero Ritter et al. 2013). Xylanase can be characterized and purified by the usage of agro-industrial waste which was proved when *Penicillium glabrum* was found to produce xylanase enzyme by the use of brewer's spent grain as a substrate. For optimum production of Xylanase by *P. glabrum*, it was grown at a pH of 5.5 and a temperature of 25 °C in a liquid medium kept under stationary condition for straight 6 days. Xylanase was purified by *P. glabrum* by using inexpensive procedures like molecular exclusion chromatography and also ammonium sulfate fraction at ion. The optimum activity of xylanase was found at a pH of 3.0 and temperature of 60 °C. The xylanase activity can be enhanced by the use of Mn^{2+} ion and by DTT and *β*-mercaptoethanol, both of which are reducing agents, whereas detergent SDS, the ions Hg^{2+}, Zn^{2+} and Cu^{2+}, were found to be strongly inhibiting the enzymes (Knob et al. 2013). *Penicillium janthinellum* FS22A are known to produce cellulolytic-xylanolytic enzymes (Okeke et al. 2015) (Table 4.4).

Table 4.4 Table showing characteristics of some xylanases produced by different microorganisms (Polizeli et al. 2005)

Microbial species	Optimal temperature (°C)	Optimal pH
Aspergillus aculeatus	50, 50, 70	4.0, 4.0, 5.0
Aspergillus oryzae	60	5.0
Aspergillus sydowii	50	4.0
Aspergillus kawachii	60, 55, 50	5.5, 4.5, 2.0
Aspergillus fischeri	60	6.0
Aspergillus sojae	60, 50	5.0, 5.5
Acrophialophora nainiana	22 55	7.0
Myceliophthora sp.	75	6.0
Cryptococcus sp.	40	2.0
Chaetomium cellulolyticum	50	2.0
Thermomyces lanuginosus	50	5.0–7.0
Penicillium capsulatum	48	3.8
Penicillium sp.	70	6.0–6.5

9 Applications of Xylanases

Xylanases have great potential application in many industrial processes. About 20% of the world enzyme market is occupied by xylanase, cellulase and pectinase. Due to the potential effectiveness of xylanolytic enzymes in bread making, they are used in baking and brewing industries. Xylanases are used as animal feed, where arabinoxylans which are present in feed ingredients are broken down by them reducing the viscosity of the raw material (Harris and Ramalingam 2010). Xylan and xylanases are also used in pharmaceutical industries. Xylanases along with enzymes like proteases and hemicellulase are used for treating indigestion. The hydrolytic products of xylan can be used to make artificial sweeteners, solvents, ethanol etc. Xylanolytic complex also finds varied application in textile industries and is also used for making plant fibres like linen or hessian. Xylanases are also used in bleaching of cellulose pulp. Xylanases are also used to enhance sugar recovery from agricultural residues (Chakdar et al. 2016) (Table 4.5).

10 Comparison of Xylanase Production from Bacterial and Fungal Sources

Xylanases are known to be produced by organisms like bacteria, snails, fungi, yeast, protozoans, fruit and vegetable seeds and insect. Bacterial genera like *Bacillus, Pseudoxanthomonas, Rhodothermus, Paenibacillus, Cellulomonas, Staphylococcus* and *Microbacterium* are known to produce xylanase enzyme. Also, thermostable

Table 4.5 Table showing commercial xylanases produced by microorganisms

Microorganisms	Optimal pH	Optimal temperature (°C)	Application
Aspergillus niger	5.3	5.3	Used in the improvement of animal feed
Humicola	n.c.	n.c.	
A. niger	n.c.	n.c.	Used in the preparation of feed for pigs and birds
Bacillus sp	9.5	50	Used in paper-making industry
Trichoderma reesei	5.0–6.0	5.0–6.0	Cellulose pulp bleaching
T. longibrachiatum	5.0–5.5	5.0–5.5	Used in food industry
Trichoderma koningii	5	5	Used in the production manufacture of mushrooms and vegetable extracts, peeling of cereals through enzymatic methods, making of bread, preparation of animal feed
Trichoderma sp	n.c.	n.c.	Utilized for structural studies of carbohydrates

SbmF submerged fermentation, *SSF* solid-substrate fermentation, *n.c.* not cited

xylanases that are active at 60–70 °C are produced by *Thermotoga* sp., *Streptomyces* sp., *Clostridium thermocellum, Bacillus* spp., *Rhodothermus marinus* and *Stenotrophomonas maltophilia*. *Flavobacterium frigidarium, Penicillium Strain* and *Clostridium* sp. produce cold-adaptive xylanases (Chakdar et al. 2016).

Different organisms produce xylanase in different conditions. For example, bacterial species produce xylanase neutral/alkaline pH and xylanase are produced in acidic range by fungal species. Fungal xylanases are less attractive as the low pH requirement for growth of fungi and production of fungal xylanases necessitates additional steps in the subsequent stages. The secondary structures especially at the loop areas are different in bacterial and fungal xylanases. The nucleophile and proton donor in bacterial and fungal xylanases are always the glutamic acid, though their position may change. Fungal xylanases are produced with cellulose and hence there is increase in the length of downstream processing. In bacteria, xylanases are mostly produced alone and hence reduces the downstream process time (Chakdar et al. 2016).

11 Conclusion

Xylanases are hydrolases which are capable depolymerizing xylan polysaccharide. Xylan being a cell component is also known to be the second most widely available polysaccharide. Xylanases are known to be produced by insect, snails, bacteria, fungi, algae (marine), crustaceans, hulls and husks, seeds, protozoans, etc., but the filamentous fungi are the principal commercial sources of xylanase. These enzymes

are synthesized by extremophiles, mesophiles and thermophiles microorganisms as the enzyme produced by them is found to be more stable. In order to consolidate the entire economics of the pre-treatment of lignocellulosic material, strategies are being carried out to convert xylan into useful products, and to this end xylanases have been identified as key enzymes with diverse industrial applications. The bulk production of xylanases at an economically viable rate is the major bottleneck in commercial applications of xylanase-based enzymatic processes. The study conducted by authors of this chapter is focussed on the sources, production and applications of fungal xylanolytic enzymes in the context of their biotechnological potential.

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