

Microbial Xylanases: A Review

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ABSTRACT

Enzymes play a key role in producing important and useful products in our daily life. They act as biocatalysts that increase the rate of chemical reactions. A category of enzymes known as xylanases are hydrolyzing enzymes that hydrolyze the β -1,4-xylan, the principal constituent of hemicelluloses, into xylose sugar. Xylanases are categorized as endoxylanase, xylosidases, arabinofuranosidase, glucuronidase and esterases. The substrate xylan is highly expensive for enzyme production, so for reducing its cost, agricultural residues like wheat bran, rice bran, corn cobs, sugarcane bagasse, sawdust and oat bran *etc.* are used as substrate. Enzyme production can be carried out by using fermentation techniques through microorganisms such as fungi, yeasts, bacteria, actinomycetes *etc.* Xylanases are considered an important tool in industrial sectors like pulp and paper industry, textile industry, food and feed industry, bio-ethanol production and fruit juices and wine clarification.

Figure : 01

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KEY WORDS : Catalyst, Enzymes, Xylanases, Xylan.

Introduction

Enzymes are distinct biocatalysts that catalyze chemical reactions and also help to accelerate the reactions. They can convert substrate molecules into various product molecules and remain unchanged at the end of a chemical reaction. Enzymes are extensively used in different industries like paper making industry, food & feed industry, textile industry, pharmaceutical industry *etc.* Among various microbial enzymes, xylanases are the group of enzymes that have the capability to hydrolyze the complex and branched xylan into a simple structure.

Xylan is the major component of hemicelluloses and the second most abundant heteropolysaccharide of lignocellulosic materials mainly in plants. Lignocellulosics have the potential to support increasing energy demands worldwide. The chemical makeup of lignocellulosic materials make them biotechnologically valuable substrates⁴⁵. It consists of mainly three polymer types: cellulose (40-60%), hemicelluloses (20-30%) and lignin (15-30%) – that are connected with covalent as well as non - covalent linkages and maintain the structural integrity of plant cell wall³⁵.

Xylan, a main carbohydrate of hemicelluloses, contributes 7-12% of total dry weight in gymnosperm and 15-30% in angiosperm^{26,62}. It's a branching polysaccharide with a 1, 4-linked- β -D-xylopyranose backbone. Because of its complexity, complete xylan

hydrolysis necessitates the cooperation of many hydrolytic enzymes known as xylanases, which can hydrolyze both the main chain and the side chains of xylan. Multiple xylanases have been reported in various microbial systems such as protozoans, molluscs, actinomycetes, bacteria, fungi, marine algae, crustaceans and also found in the rumen of higher animals^{8,53}. Among these microorganisms, fungi and bacteria have most powerful types of machinery to produce xylanase enzyme. Advances from biology to biotechnology have to lead a path for conversion of lignocellulosic biomass into useful products through fermentation process by using microorganisms. Thus, xylanases have a wide range of applications in paper making industry, textile industry, bioethanol industry, food industry, animal feed industry, agricultural and environmental industry *etc.*

This review is focused on structure, sources, production and applications of industrially potent enzyme xylanase.

Xylan Structure

Structurally, xylan is a homopolymer of D-xylopyranose units linked by β -1,4-linkages with high degree of polymerization of 150-200 units¹². Based on the nature of substituent xylan are mainly classified into four categories *viz.*, arabinoxylans, glucuronoxylans, glucuronoarabinoxylans and galacto-glucurono arabinoxylans.

TABLE-1: Showing bacteria produced xylanase at optimized parameters

Microorganisms	Substrate	Incubation period	Temperature	pH
Bacteria				
<i>Bacillus badius</i> ⁸⁰	Corn cobs	48 hrs	50°C	9.0
<i>Bacillus pumilus</i> MTCC 8964 ³⁷	Maltose	48 hrs	40°C	6.0
<i>Bacillus arseniciselenatis</i> DSM-15340 ³¹	Wheat bran	72 hrs	45°C	8.0
<i>Bacillus subtilis</i> ⁴⁷	Xylose	48 hrs	40°C	9.0
<i>Bacillus subtilis</i> (BS7) ³³	Wheat bran	48 hrs	50°C	8.0
<i>Bacillus subtilis</i> BS04 ²⁹	Corn cobs	48 hrs	35°C	8.0
<i>Bacillus megaterium</i> BM07 ²⁹	Corn cobs	72 hrs	40°C	8.0
<i>Chromohalobacter</i> sps. ⁵⁴	Sugarcane bagasse	140 hrs	40°C	9.0
<i>Bacillus mojavensis</i> AG137 ⁵⁸	Oat bran	48 hrs	37°C	8.0
<i>Thermomyces lanuginosus</i> ⁶³	Sorghum straw	144 hrs	50°C	6.0
<i>Promicromonospora</i> sp. MARS ³⁸	Rice straw	48 hrs	65°C	8.0

Arabinoxylan comprises 1,4- β xylan as a main chain but is substituted with α -L-arabinofuranosyl residues⁷⁵. Glucuronoxylans is based on α -(1-2) linked 4-O-methyl- D- glucuronic acid side chain of xylans. In case of glucuronoarabinoxylans both arabinofuranose and uronic acid are linked with backbone of xylan. Galactoglucurono arabinoxylans consist of terminal β -D-galactopyranosyl residues on complex oligosaccharide side chains of xylan^{23,9}. Besides this, there is another category of xylan named as homoxylans categorized to have only xylosyl residues present either in linear or branched manner⁷⁰.

The complexity from linear to highly branched structure of xylan is determined by side chains. The side chains control the solubility, physical conformation, and reactivity of xylan with other hemicellulosic components, and so have a significant impact on the mechanism and amount of enzymatic cleavage¹². Xylan is distributed among all terrestrial plants and account for 30 % of the

cell wall material of annual plants, 15-30% in hard woods and 7-10% in soft woods⁵⁹.

Xylan Hydrolyzing Enzymes

The enzymatic role in breakdown of xylan was observed by Hopper – Seyler over 100 years ago⁵. Due to heterogeneity and complexity of xylan structure, its depolymerization requires the action of several hydrolytic enzymes with multiple modes of action and specific nature. Xylanases play a key role in degradation of xylans (Fig. 1).

Hydrolysis of O-acetylglucuronoxylan requires five types of enzymes –

a) Endoxylanases (EC 3.2.1.8)

Different enzymes with their respective functions participate in the hydrolysis of xylan which convert it into monomeric units, out of which the principal enzyme is the endo- β -1, 4- xylanases⁷¹. They can cleave the

glycosidic bonds of xylan, as a result short chains xylo-oligosaccharide of varying lengths are liberated. Endoxylanases are grouped into two categories as debranching or arabinose liberating and non – debranching or arabinose non-liberating¹⁷. These enzymes can be differentiated according to their end products that they release after depolymerization of xylan e.g. xylose, arabinose, xylobiose and xylotriose. They can be grouped into two families G10 and G11. Bacteria, fungi and plant enzymes come under G10 family while G11 family comprises only fungal and bacterial enzymes⁴¹. G10 family is composed of β -1,4-endoxylanase in majority with few β -1,3-endoxylanase. Endoxylanases from fungi and bacteria are exclusively single subunit proteins which vary widely in molecular weight from 8.5 to 85 kDa with isoelectric point (pI) ranging from 4.0 to 10.3, most of them are glycosylated^{16, 53}.

b) β - Xylosidases (EC 3.2.1.37)

Another xylan debranching enzyme which belong to the hydrolase family include exo -1,4-D- β -xylosidases that hydrolyze 1,4-D- β -xylooligosaccharides and xylobiose from the non- reducing end. Endoxylanases release xylose during xylan degradation but they have no activity against xylobiose which can be easily hydrolyzed by β -xylosidases. As degree of polymerization increases the enzyme affinity towards xylo-oligosaccharides decreases. These are bulkier enzymes having molecular weight ranging from 60 to 360 kDa and may be monomeric, dimeric or tetrameric proteins⁵¹.

c) α - Glucuronidases (EC 3.2.1.1)

Glucuronidases are required for breaking the α – 1,2- glycosidic bond between xylose and D- glucuronic acid or its 4-O-methyl ether¹⁵. Their molecular weight is less than 100 kDa.

d) α – L-Arabinofuranosidases (EC 3.2.1.55)

Arabinofuranosidases cleaves the terminal non – reducing α -L-arabinosyl groups of arabinans, arabinogalactans and arabinoxylans. These enzymes are categorized into two groups with their specific mode of action: exo- α -L-arabinofuranoside (EC 3.2.1.55) which is active against p- nitrophenyl- α - L-arabinofuranosidases and on branched arabinans where as linear arabinans are degraded by endo-1,5- α -L- arabinase (EC 3.2.1.99)⁷⁶. The size of this enzyme may reach upto 495 kDa and is also found in monomeric, dimeric, tetrameric, hexameric and octameric forms¹⁵.

e) Esterases (EC 3.1.1.6)

Acetylxylan esterases break the ester link between xylose in xylan and acetic acid. They can also get rid of phenolic acids like ferulic acid (feruloyl esterase) and p-coumaric acid (p-coumaryl esterase). Breakdown

of acetyl xylan, elimination of feruloyl and p-coumaryl groups from the xylan are supportive in lignin removal⁵¹. They may contribute to lignin solubilization by hydrolyzing the ester linkages between lignin and hemicelluloses.

Xylanases Producing Microorganisms

Several studies have reported that xylanases are produced by variety of microorganisms such as bacteria, fungi, yeast, marine algae, crustaceans, seeds, snails and protozoan etc.⁵³ but fungi and bacteria have been reported as the main sources of xylanase production.

Xylanolytic Bacteria

Xylanases of bacterial origin are less studied because fungi are known to be better producers of these enzymes. The major bacteria are of genera *Bacillus*, *Cellulomonas*, *Micrococcus*, *Staphylococcus*, *Arthrobacter*, *Microbacterium*, *Pseudoxanthomonas*, *Paenibacillus*, *Thermotog* and *Rhodothermus* have been reported for producing xylanases^{66,24,13}. Among bacteria *Bacillus* was found to be potential source of xylanase and a number of Bacilli like *Bacillus circularis*, *B. pumilus*, *B. halodurans*, *B. subtilis*, *B. stearothermophilus*, *B. amyloliquefaciens*, *B. cereus*, *B. megatorium* and *B. licheniformis* have been found to have considerable xylanase activity at higher temperature and at alkaline pH^{25,44,46,67}. Therefore, due to their thermostability and alkaline tolerance property, bacterial xylanases are industrially important (Table 01).

Xylanolytic Fungi

Xylanases of fungal origin are well characterized and have been studied in detail (Table 02). Fungi are the key producer of xylanases because of higher yield and extracellular release of enzyme⁵⁰. Fungal strains that produced xylanases are – *Aspergillus* spp. (*A. niger*, *A. foetidus*, *A. brasiliensis*, *A. nidulans*, *A. flavus*, *A. terreus*, *A. japonicus*, *A. tamarii*), *Trichoderma* spp. (*T. viride*, *T. aureoviride*, *T. reesei*, *T. longibrachiatum*, *T. harzianum*), *Fusarium oxysporum*, *Talaromyces emersonii*, *Alternaria alternata*, *Schizophyllum commune* and *Penicillium* spp.^{30,72}. As compared to bacteria or yeasts, fungi have greater activity for xylanases. Alternatively, Xylanases generated from fungal sources have a number of properties that make them unsuitable for several industrial uses⁴⁶. Most of the fungal xylanases can tolerate temperature below than 50°C and have pH range of 4-6^{7,26}. For example-xylanases produced by fungi cannot be used in pulp and paper industry that needs an alkaline pH and high temperature as 60 - 70°C⁴⁶. Another problem with fungal xylanases is the cellulase enzyme. Fungal xylanases are produced simultaneously with cellulases that increase length of down streaming processing. However, this is not in the case of bacteria. Low pH and low temperature

for fungal growth and cellulase synthesis need additional downstream processing steps, making fungal xylanase less interesting⁶⁷.

Production of xylanases

Xylanases are industrially important enzymes mainly used in the bioconversion of hemicellulose, which is the significant constituent of lignocellulosic wastes. Agricultural residues which are often considered as waste contain appreciable amount of hemicelluloses. Xylanases production is carried out by a different fermentation processes using various microorganisms. The most prevalent methods for producing xylanases are

submerged fermentation (SmF) and solid-state fermentation (SSF). The fermentation procedure chosen is usually determined by the microorganisms utilized. For bacterial growth, high amount of water is required therefore SmF is used for xylanase production by bacteria. Because fungus contain mycelia, their growth needed less moisture and can be grown in an SSF environment⁷⁸. It has been found that xylanase production is relatively high in SSF in comparison to SmF^{43,69}. As a result of the commercial and engineering benefits, SSF has gained greater attention in recent years from researchers⁶⁵. It has a number of advantages including low cultivation costs, low operating costs, low contamination rates,

TABLE-2: Showing fungi produced xylanase at optimized parameters

Microorganisms	Substrate	Incubation period	Temperature	pH
Fungi				
<i>Penicillium sclerotiorum</i> ³⁴	Wheat bran	120 hrs	30°C	6.5
<i>Penicillium</i> sp. ZH30 ⁴³	Wheat bran	72 hrs	30°C	5.3
<i>Aspergillus niger</i> ³²	Wheat straw	120 hrs	30°C	6.0
<i>Aspergillus niger</i> ⁵⁷	Rice bran	144 hrs	35°C	6.5
<i>Aspergillus niger</i> ⁶⁸	Wheat bran	96 hrs	35°C	5.6
<i>Aspergillus niger</i> (AN100) ⁶⁴	Xylose	168 hrs	30°C	5.0
<i>Aspergillus niger</i> ⁶¹	Wheat bran, corn cobs	168 hrs 216 hrs	30°C	5.5
<i>Aspergillus flavus</i> ⁵²	Wheat bran	144 hrs	32°C	8.0
<i>Aspergillus flavus</i> ⁵⁶	Wheat bran, corn cobs	144 hrs 192 hrs	30° for both substrates	6.0 7.0
<i>Chaetomium globosum</i> ²	Pomegranate peel	168 hrs	40°C	6.6
<i>Fusarium solani</i> SYRN7 ¹	Wheat bran	96 hrs	50°C	5.0
<i>Humicola lanuginose</i> ³	Wheat bran	72 hrs	45°C	6.5
<i>Trichoderma viride</i> -IR05 ⁴⁹	Sugarcane bagasse	168 hrs	30°C	4.5

quicker enzyme recovery and high productivity⁷⁸.

There are few factors which play a critical role in enzyme production such as nutritional factor and environmental factors. Carbon source is the main nutritional factor which plays a major role in the economics of xylanase production. In order to replace the expensive xylan, lignocellulosic waste such as wheat bran, wheat straw, rice straw, rice bran, sugarcane bagasse, corn cobs, rice husk, sorghum straw, soy meal have been found to be most effective and cheaper substrates for xylanase production^{48,55,82}.

Several researchers worked on the xylanase production and optimized its production to enhance the yield of the enzyme. This is presented in Tables-1 and 2.

Industrial Uses of Xylanases

Xylanases are considered as important tool in many industrial sectors such as in pulp and paper making, processing of animal feed, clarification of beverages and production of bio-fuels from agro-residues. Major applications of xylanases are discussed below –

a) Pulp and Paper Industry

Pulp and paper industry has been scanning for novel biotechnological ways used for the replacement of chemicals utilized in paper making process. In paper industry, whitening of paper needs the removal of lignin from pulps. To obtain brightened and completely finished white paper, the most important process is the removal of lignin. Bleaching is the treatment of cellulosic fibers with chemicals by removing the low amount of residual lignin present after cooking without declining the molecular weight of the cellulose. Bleaching is of two types – Chemical and Biological. Chemical bleaching involves the use of chlorinated agents Cl_2 , ClO_2 and hypochlorite at higher temperature (170°C) with alkali conditions which causes environmental problems as well as release carcinogenic and strong mutants⁸¹. The effluents of this bleaching method are the primary contributors to waste water pollution from paper industries⁶⁶. Another is biological method, which utilizes microbial enzymes like xylanases for bleaching process. Biobleaching or biopulping are other names for this bleaching process. Ligninases and xylanases were reported as the most efficient biobleaching agents. It has been demonstrated from several studies that xylanase treatment of pulp is an environment friendly and economically cheap innovation¹⁴. The role of xylanase was first observed in 1986⁷⁷ in biobleaching of pulp. The use of xylanase from *B. pumilus* ASH5 in biobleaching of Eucalyptus kraft pulp reduced chlorine and chlorine dioxide use by 20% and 10%, respectively, while also improving the brightness and whiteness of the pulp⁶. Overall, the major profits of

biobleaching are – reduced utilization of bleaching chemicals, reduction in absorbable organic halogen compounds, improved paper quality and its brightness, reduced effluent toxicity and pollution load⁶⁰.

b) Food industry

Because of their potential usefulness in the production of bread, the use of xylanases has expanded in recent decades¹⁰. Xylanolytic enzymes are used in food industries like in dairy products, juices, soy milk, beer production, papad and bread are well documented⁴⁰. Hemicellulases or xylanases hydrolyse the hemicelluloses present in wheat, helping in the redistribution of water content and leaving the dough fluffy and make it easier to knead⁵³. Xylanase can delay the crumb formation and let the dough to ferment⁴⁶. Xylanases improve the quality of bread, increase the bread volume, increase water absorption quantity and also improve resistance to fermentation^{11,27}. Greater amount of arabioxylo-oligosaccharides in bread would be beneficial to health⁴⁶. Another application for xylanases is dough strength, as these enzymes create dough with good tolerance to changes in processing conditions and flour quality⁶⁷. Xylanases are enzymes that transform water-insoluble hemicelluloses into a soluble form that binds water in dough. As a result, the dough stiffness is reduced while the volume is increased, resulting in finer and more uniform crumbs¹⁰.

In biscuit making, xylanases are recommended for making cream crackers lighter and improving the texture, palatability and uniformity of wafers⁵³.

Other important part of enzyme marketing is juice industry. The juice product from vegetables and fruits requires a method of its extraction, clarification and stabilization. Xylanases along with pectinases, cellulases, amylases has been used in juice processing which helps in the liquefaction of vegetables and fruits, stabilization of fruit pulp, increases recovery of aromas, essential oil, edible dyes and pigments, vitamins and also reduces viscosity, hydrolyzes those substances that interfere in clearing of juices or those which cause cloudiness in the concentrate⁵³.

Xylanases are also applied for the preparation of coffee-bean mucilage⁷⁹. During beer manufacturing, xylanases hydrolyzes long chain of arabinoxylans into lower oligosaccharides which decreases viscosity of beer and consequently eliminates its muddy texture¹⁹. The chief desirable properties of xylanases for use in the food industry are high stabilization and showing optimum activity at acidic pH.

c) Animal feeds

Xylanases are applied to improve digestibility and

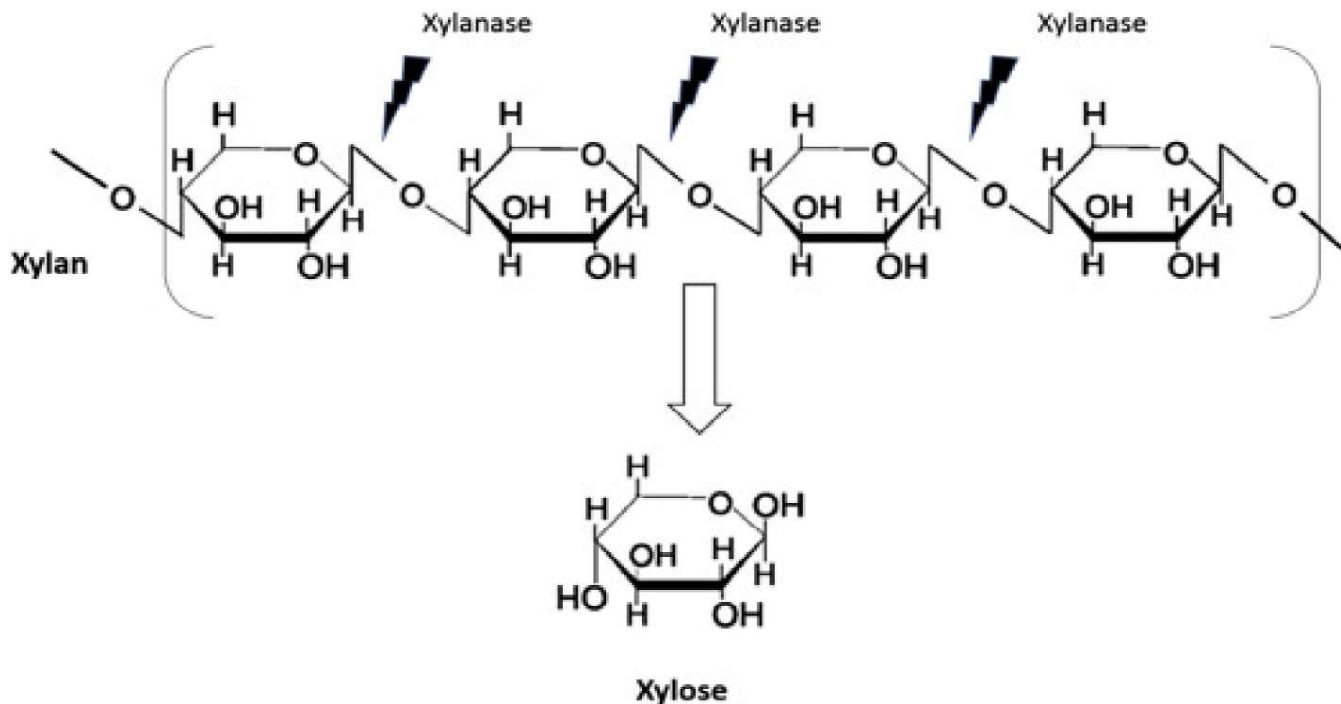


Fig.1: Showing hydrolysis of complex xylan into xylose through xylanases

nutritional value of animal feed²⁸. Low-grade viscosity in few crops like maize, rye, sorghum, wheat and many other grains are attributed to their arabinoxylan (hemicelluloses) content which renders them unsuitable as feed¹². To improve the digestibility of ruminant feeds and make composting easier, xylanases are used in the pre-treatment of forage crops²². Xylanases along with other enzymes such as cellulases, pectinases, proteases, amylases, phytases, lipases, glucanases and galactosidases are used to improve animal feed digestibility. They can hydrolyze arabinoxylans in animal feed ingredients, lowering the raw materials viscosity⁷⁴. However, total xylan removal is not desirable because hemicelluloses are key components of dietary fibre, and their removal could lead to an increase in bowel disorders^{18,46}.

d) Bio-fuel production

Xylanases together with other hydrolyzing enzymes ligninases, xylosidases, glucosidases, mannanases, glucanases are used in the production of biofuels like ethanol and xylitol from lignocellulosics using microbes and their enzymes^{4,21}. Production of ethanol from renewable resources has been of great interest in recent years as an alternate fuel⁶⁰. The biological method of ethanol generation requires firstly, delignification *i.e.* removal of lignin and liberation of celluloses and hemicelluloses. The next steps include the depolymerization of carbohydrate polymer (Celluloses and hemicelluloses) into free sugars and finally formation

of mixed pentoses and hexoses that produce ethanol or bio-ethanol^{39,42}.

e) Other applications

Few xylanase enzymes are utilized to improve cell wall maceration in generation of plant protoplasts⁸. Purified alkalophilic xylanase can be used to boost the cleaning power of detergents, making them more effective at cleaning fruits, vegetables, soils, and grass stains^{20,36}. Xylanase treatment can remarkably remove hemicellulosic impurities and enhance the water absorption property. These enzymes together with the cellulases and pectinases can be used for preparing dextrans used as food thickeners⁷³. A combination of xylanases and pectinases is used in debarking, first step of processing of wood, xylanases increases the retting process. This combination is also utilized in degumming of bast fibers like hemp, flax, jute fiber *etc.*⁸.

Conclusion

Xylanases are well known for their use in various industries such as food, animal feed, pharmaceutical, pulp and paper industry. To meet the growing demand for xylanases in industries, it is necessary to develop ways that make its production easier and less expensive. Using lignocelluloses or agro-waste materials for the generation of xylanase enzymes through submerged and solid state fermentation process is the best alternative. For producing maximum xylanases on large scale, all cultural parameters must be optimized.

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