

Agro-residues as Alternative for Xylanase Production by Filamentous Fungi

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Agro-industrial wastes are the most abundant renewable resource on earth and are available in large quantities. However, the disposal of these wastes presents an increasing environmental problem. Recently, there has been a great interest in the exploitation of these wastes as low-cost raw materials for the production of value-added compounds as microbial enzymes by submerged or solid-state fermentation systems. This review focuses on alternatives for xylanase production using agro-residues as substrates. In recent years, the interest in xylanase, which plays an important role in the breakdown of xylan, has markedly increased due to its wide variety of biotechnological applications. Among several agro-industrial residues that have been intensively investigated, many, such as wheat bran, wheat straw, and sugarcane bagasse, are suitable and result in high yields of xylanase, leading to low production costs. In addition, many relatively unexplored residues, such as oil palm wastes, sorghum straw, and coffee by-products, are some of the most promising substrates for xylanase production, requiring further assessment.

Keywords: Xylanolytic enzymes; Lignocellulosic materials; Solid-state fermentation; Submerged fermentation

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INTRODUCTION

Environmental issues and concerns aimed at reducing ambient pollution have prompted an increase in the search for environmentally friendly technologies to be used in the production of many commodities (Martins *et al.* 2011). White biotechnology, which can be defined as the use of biotechnology for industrial production, remains a challenge because new biocatalytic processes have to compete economically with well-established chemical processes that have been optimized for years (Otten and Quax 2005). In this context, agricultural waste utilization for industrial development has emerged as an important area in industrial biotechnology. These residues are abundant sources of lignocellulose, are treated as waste in many countries, and are available worldwide (Dashtban *et al.* 2009).

The conversion of lignocellulosic biomass into valuable enzymes is of strategic importance for the sustainability and advancement of several industries. These materials may be used by microorganisms as a carbon source, which results in the production of cellular proteins, enzymes, organic acids, biologically important secondary metabolites, and prebiotic oligosaccharides. In addition, agro-industrial wastes can be used as source of fermentable sugars in second generation ethanol production (Anwar *et al.* 2014; Chandel *et al.* 2012; Mussato and Teixeira 2010; Sánchez 2009). Regardless of a worldwide and enormous utilization of natural cellulosic sources, there are still abundant quantities of cellulose-containing raw materials and waste products that are not exploited or which could be used more efficiently (Sethi *et al.* 2013).

Successful biotechnological applications require low cost enzymes. Thus, the use of purified xylan as an inducer for enhanced xylanase production is unviable. One recent trend in this area is to use lignocellulosic residues, which not only serve as cost-effective substrates but also offer environmental advantages. Because of their biotechnological importance, significant progress has been made in the use of agro-residues for microbial enzyme production. In the present review, the main efforts for xylanase production by filamentous fungus, as have been described to date, are presented.

AGRO-INDUSTRIAL WASTES

As the most abundant and renewable source on earth, lignocellulosic biomass includes various agro-industrial wastes (straws, hulls, stems, and stalks), deciduous and coniferous woods, waste from pulp and paper industry, municipal biodegradable wastes, and herbaceous energy crops (Limayema and Rickea 2012). With the increasing expansion of agro-industrial activities, large quantities of lignocellulosic residues are generated annually worldwide (Sánchez 2009). Disposal of these wastes causes serious environmental problems. In addition, the non-use of agro-industrial residues constitutes a loss of potentially valuable resources (Mussato and Teixeira 2010). These potentially valuable materials were treated as waste in many countries in the past (and still are today in some developing countries) and disposed of in the environment, many times without an adequate counteractive measure, increasing environmental damage (Palacios-Oureta 2005; Dashtban *et al.* 2009). In other countries, they are also used to generate thermal energy by traditional means, such as fire for cooking and heat, or in modern ways, including the production of electricity, steam, and liquid biofuels (Dawson and Boopathy 2007; Kim and Dale 2004).

Agro-residues serve as low-cost raw material for other processes and can be purchased in regions that are located close to the local processing of the material. Because these wastes are rich in sugars, which are easily assimilated by microorganisms, they are very appropriate for use as raw materials in the production of industrially relevant compounds by fermentation (Mussato and Teixeira 2010).

Average values of the main components in some lignocellulose wastes are shown in Table 1. Like other lignocellulosic materials, agro-residues are composed primarily of structural, cellular-wall polysaccharides. In such residues, cellulose is usually the dominant polysaccharide (35 to 50%), followed by hemicellulose (20 to 35%), and lignin (10 to 25%).

Table 1. Composition of Some Lignocellulosic Materials

| Composition (% dry weight basis) | | | | |
|----------------------------------|-----------|---------------|--------|------------------------------|
| Type of biomass | Cellulose | Hemicellulose | Lignin | References |
| Banana straw | 53 | 29 | 15 | Silveira <i>et al.</i> 2008 |
| Barley straw | 23 | 21 | 21 | Adapa <i>et al.</i> 2011 |
| Canola straw | 22 | 17 | 20 | Adapa <i>et al.</i> 2011 |
| Coconut fiber | 36-43 | 15-25 | 41-45 | Graminha <i>et al.</i> 2008 |
| Coffee husk | 18 | 13 | - | Mussato <i>et al.</i> 2011b |
| Coffee spent grains | 9 | 37 | - | Mussato <i>et al.</i> 2011a |
| Corn bran | 34 | 39 | 49 | Graminha <i>et al.</i> 2008 |
| Corn cob | 45 | 35 | 15 | Limayema and Ricke 2012 |
| Corn fiber | 15 | 35 | 8 | Saha <i>et al.</i> 2003 |
| Corn stalks | 34 | 24 | 9 | Graminha <i>et al.</i> 2008 |
| Corn straw | 33 | 25 | 8 | Graminha <i>et al.</i> 2008 |
| Corn silage | 38-40 | 28 | 7-21 | Graminha <i>et al.</i> 2008 |
| Corn Stover | 40 | 25 | 17 | Saha <i>et al.</i> 2003 |
| Cotton stalks | 58 | 14 | 22 | Nigam <i>et al.</i> 2009 |
| Grape seed | 7 | 31 | 44 | Graminha <i>et al.</i> 2008 |
| Grape vine | 30 | 35 | 23 | Graminha <i>et al.</i> 2008 |
| Grasses | 25-40 | 25-50 | 10-30 | Sun and Cheng 2002 |
| Hardwoods | 40-55 | 24-40 | 18-25 | Sun and Cheng 2002 |
| Nut shells | 25-30 | 25-30 | 30-40 | Howard <i>et al.</i> 2003 |
| Oat bran | 49 | 25 | 18 | Graminha <i>et al.</i> 2008 |
| Oat straw | 40 | 27 | 18 | Nigam <i>et al.</i> 2009 |
| Rice bran | 35 | 25 | 17 | Graminha <i>et al.</i> 2008 |
| Rice husk | 22 | 23 | 15 | Megawati <i>et al.</i> 2011 |
| Rice straw | 32 | 24 | 18 | Limayema and Ricke. 2012 |
| Rye straw | 38 | 31 | 19 | Nigam <i>et al.</i> 2009 |
| Sawdust | 45 | 28 | 24 | El-Tayeb <i>et al.</i> 2012 |
| Softwoods | 45-50 | 25-35 | 25-35 | Sun and Cheng 2002 |
| Sorghum bagasse | 40 | 36 | 4 | Dogaris <i>et al.</i> 2009 |
| Sorghum stalks | 27 | 25 | 11 | Graminha <i>et al.</i> 2008 |
| Sorghum straws | 35 | 24 | - | Télléz-Luis 2002 |
| Soya stalks | 35 | 25 | 20 | Nigam <i>et al.</i> 2009 |
| Sugar beet waste | 26 | 19 | 3 | El-Tayeb <i>et al.</i> 2012 |
| Sugarcane bagasse | 35-45 | 26-36 | 11-25 | Zhao <i>et al.</i> 2009 |
| Sugarcane straw | 36 | 21 | 16 | Saad <i>et al.</i> 2008 |
| Sunflower stalks | 34 | 20 | 17 | Ruiz <i>et al.</i> 2008 |
| Water hyacinth | 21 | 34 | 7 | Deshpande <i>et al.</i> 2008 |
| Wheat bran | 30 | 50 | 15 | Graminha <i>et al.</i> 2008 |
| Wheat straw | 27 | 21 | 23 | Adapa <i>et al.</i> 2011 |

Proteins, oils, and ash make up the remaining fraction of lignocellulosic biomass. Nevertheless, amounts of cellulose, hemicellulose, and lignin vary from one plant species to another. In addition, many factors influence the ratio between various constituents in a single plant, such as age, stage of growth, and other conditions (Saha 2003; Zhu *et al.* 2009).

XYLAN-DEGRADING ENZYMES

Xylan is a major structural polysaccharide of plant-cell walls and is the second most prevalent in nature after cellulose, representing up to 30 to 35% of a plant's total dry weight. It is a heterogeneous polymer composed primarily of a linear β -(1,4)-D-xylose backbone that is partially acetylated and substituted at different degrees by a variety of side chains, mostly α -D-glucuronosyl and α -L-arabinosyl units (Collins *et al.* 2005; Knob *et al.* 2010). The frequency and composition of the branches are dependent on the xylan source (Saha 2003). In addition, the side chains determine the solubility, physical conformation, and reactivity of the xylan molecule with the other hemicellulosic components. This greatly influences the mode and extent of enzymatic cleavage (Shallom and Shoham 2003).

Because of its heterogeneity and structural complexity, complete degradation of xylan involves the synergistic action of several hemicellulases, including endo- β -1,4-xylanases (EC 3.2.1.8), which attack the main chain of xylan, and β -D-xylosidases (EC 3.2.1.37), which hydrolyze xylooligosaccharides into D-xylose. Moreover, several accessory enzymes, such as α -L-arabinofuranosidases (EC 3.2.1.55), β -glucuronidases (EC 3.2.1.139), acetylxylan esterases (EC 3.1.1.72), ferulic acid esterases (EC 3.1.1.73), and p-coumaric acid esterases (EC 3.1.1.-), are required to achieve the complete degradation of complex, substituted xylans (Collins *et al.* 2005; Knob *et al.* 2010; Shallom and Shoham 2003).

BIOTECHNOLOGICAL APPLICATIONS OF XYLANASES

Xylanase is a key enzyme in the xylanolytic system with a great potential in many biotechnological applications. The use of xylanases as bleaching agents of wood kraft pulps has been considered the main industrial application of these enzymes. Currently, some of the bleaching processes commonly employed for the brightening and further delignification of kraft pulp call for large amounts of chlorine-based chemicals, which are toxic, mutagenic, and persistent; they also cause numerous harmful disturbances in biological systems (Yeasmin *et al.* 2011). Many studies have demonstrated that the pulp treatment with xylanases contributes to reduce the chlorine required in this process (Khandeparker and Numan 2008; Gupta and Kar 2009; Albert *et al.* 2011). Xylanases cleave the glycosidic bonds in the macromolecular chains of the xylan present in the wood pulp, facilitating the release of lignin, which is then readily available for further bleaching and thereby increasing the efficiency of this process (Birijlall *et al.* 2011; Dehia *et al.* 2013; Yeasmin *et al.* 2011). However, for application in biobleaching process, an ideal xylanase should be cellulase-free, alkali and thermo-

stable enzyme, which requires minimum downstream processing for its production (Chapla *et al.* 2012; Saleem *et al.* 2012; Yeasmin *et al.* 2011).

Enzymes are widely added to feeds, and these have contributed to the substantial gains in feed conversion efficiency that have been achieved. Several studies have demonstrated that the use of xylanases can result in improvement of nutritive values of feed and performance of animals such as poultry, piggery, and fishery (Alpine *et al.* 2012; Bobeck *et al.* 2014; Guo *et al.* 2014; Lin *et al.* 2007; Omogbenigun *et al.* 2004). The mode of action of xylanases has been described as being predominately associated with hydrolysis of high molecular weight non-starch polysaccharides in cereals and, to a lesser extent, in vegetable protein meals, with a reduction in luminal viscosity and an improved access for endogenous enzymes to cell contents (Bedford and Cowieson 2012). Since only a partial hydrolysis of xylan is needed for viscosity reduction, the xylanase addition to feed is already highly effective. Many current studies are focusing on the development of enzymes that are resistant to natural inhibitors, as well as high temperatures, while at the same time being well suited for the conditions in the digestive tract of the target animal.

Another biotechnological application of xylanases is the bioconversion of lignocellulosic residues in the constituent sugars of xylan, which can be converted into bioethanol and xylitol (Dhiman *et al.* 2008; Polizeli *et al.* 2005; Sharma and Kumar 2013). The ethanol production from pentoses, such as xylose, has received renewed interest from researchers in recent years. As some of the most promising native strains for pentose fermentation, *Scheffersomyces stipitis* (formerly known as *Pichia stipitis*) and *Scheffersomyces shehatae* have been widely studied for their xylose fermentation capabilities, which provide high ethanol productivities (Liang *et al.* 2013; Martiniano *et al.* 2014). Great progress has also been achieved in the last decade by genetic engineering to make *S. cerevisiae* able to ferment xylose (Diao *et al.* 2013; Kuyper *et al.* 2005; Zhou *et al.* 2012). Moreover xylose has also been used by microorganisms for production of xylitol, a polyalcohol which finds wide application as a natural food sweetener, a dental caries reducer, and a sugar substitute for diabetics (Chandel *et al.* 2012; Ghosh and Sudha 2012; Sarrouh *et al.* 2009). Furthermore, as mentioned above, the lignocellulosic residues can be converted into other high value-added chemicals, with extensive applications in food, feed, pharmaceutical, and cosmetics industries, such as 2,3-butanediol, lactic, itaconic and ferulic acids (Mazzaferro *et al.* 2011; Sanchéz 2009).

Xylooligosaccharides are sugar oligomers consisting of xylose units, with different polymerization degrees, usually showing 2 to 5 residues, naturally occurring in fruits, vegetable, milk, and honey (Kumar *et al.* 2012). The industrial production of xylooligosaccharides is obtained through xylan-rich lignocellulosic raw materials that are partially hydrolyzed either by acids or specific enzymes (Yang *et al.* 2007). The latter process is preferred in the industry because of the lack of undesirable side reactions and products. Xylooligosaccharides have a sweet taste and are used as an alternative sweetener (Lachke 2006; Kumar *et al.* 2012). They also function as a prebiotic by stimulating the growth of healthy microflora, such as bifidobacteria (Aachary and Prapulla 2012; Childs *et al.* 2014). Xylooligosaccharides are also widely employed in fields of medicine and in health products, foods, beverages, and feed (Aachary and Prapulla 2012; Kumar *et al.* 2012; Moure *et al.* 2006).

In the baking industry, xylanases are used for their ability to improve textural properties of bread (Santala *et al.* 2011). The beneficial role of xylanases is generally attributed to their ability to hydrolyze the cell wall polysaccharides. These enzymes

degrade the insoluble xylans in such a way that they become more soluble, which results in a higher viscosity of the dough (Polizeli *et al.* 2005; Sharma and Kumar 2013). The monomers and oligomers resulting from enzyme activity affect the water balance and modify the protein-starch interaction during bread storage. The effects on the arabinoxylan structure and functionality result in better crumb structure, improvement of texture profile, crumb porosity, firmness, higher moisture retention, and extended shelf-life of the bread (Collins *et al.* 2005; Butt *et al.* 2008; Harris and Ramalingam 2010). Xylanases that are only able to degrade water-soluble xylans to smaller parts are less suitable for use in baking industries, since small xylan molecules result in slackening and softening of the dough. Moreover, for use in biobleaching processes, xylanases should preferably be insensitive to inhibition by proteinaceous xylanase inhibitors present in wheat to display good efficiency (Courtin *et al.* 2001; Butt *et al.* 2008). In these cases, the use of xylanase in combination with other enzymes is a good strategy, because the synergistic effects of these enzymes provide better results as compared to the sole use of an isolated enzyme (Butt *et al.* 2008).

Other industrial applications include the clarification of wines, juices and beers, bio-processing of fabrics, and plant product processing (Harris and Ramalingam 2010; Goswami *et al.* 2013; Sharma and Kumar 2013). Because of the immense application possibilities, xylanase is regarded as industrially important and research has been conducted for its production using different strategies.

XYLANASE-PRODUCING FUNGI

Microorganisms are primarily responsible for xylan degradation in nature. Thus, xylanases have been isolated from a variety of fungi and bacteria such as *Aspergillus*, *Trichoderma*, *Streptomyces*, *Phanerochaete*, *Chytridiomyces*, *Fibrobacter*, *Clostridium*, *Bacillus*, and *Pichia* (Collins *et al.* 2005). Microorganisms differ considerably in their ability to produce these enzymes in terms of their activities, as well as the spectrum of different xylanases (Hinz *et al.* 2009). However, the majority of industrially applicable sources of xylanase are limited to fungi. Currently, most commercial xylanolytic preparations are produced by genetically modified *Trichoderma* or *Aspergillus* strains (Mussatto and Teixeira 2010).

Filamentous fungi are the most distinguished producers of enzymes involved in the decomposition of lignocellulosic material. In recent decades, the use of fungi in bioprocesses has grown in importance because of the production of numerous enzymes with different biochemical properties and excellent potential for biotechnological application. According to Polizeli *et al.* (2005), filamentous fungi are widely utilized as enzyme producers and are generally considered more potent xylanase producers than bacteria or yeast. Xylanases in bacteria are not only produced at lower activity levels than in fungi, but they are also restricted to the intracellular or periplasmic fractions (Knob *et al.* 2010). Furthermore, enzymes produced by bacteria are not subjected to post-translational modifications such as glycosylation, which is an important process that affects the stability of protein conformation, protects proteins from proteolysis, and improves protein solubility (Polizeli *et al.* 2005).

One must also consider the fact that fungal xylanases are highly advantageous for their elevated activity levels and specificity (Knob *et al.* 2010). Nevertheless, the major problem associated with fungi is their reduced enzyme yield in bioreactor studies. With

agitation, the shearing forces in the fermenter can disrupt the fragile fungal biomass, resulting in low productivity (Motta *et al.* 2013; Subramaniyan and Prema 2002).

Several mesophilic fungal species have been evaluated in relation to xylanase production, including members of *Aspergillus*, *Trichoderma*, and *Penicillium*. *Aspergillus niger* has been one of the most investigated microorganisms as a xylanase producer, regardless of carbon source or system used (submerged or solid state fermentations). On the other hand, thermophilic microorganisms such as *Thermomyces lanuginosus*, *Thermoascus aurantiacus*, *Talaromyces thermophiles*, and *Myceliophthora thermophila* have been widely investigated, due to the increased biotechnological importance of thermostable xylanases (Maalej *et al.* 2009; Milagres *et al.* 2004; Moretti *et al.* 2012; Yang *et al.* 2006).

Many of the xylanase-producing fungi express multiple isoforms. These enzymes exhibit a diversity of physicochemical properties, structures, specific activities, yields, and particular specificity, leading to an increment in xylan degradation. Various mechanisms have been suggested to account for the multiplicity of function and specificity of xylan degrading enzymes, such as heterogeneity and complexity of the xylan structure, genetic redundancy, and post-translational modifications (Ghotori *et al.* 2006).

New Xylanase-Producing Fungal Strains

The search for new strains that display high enzyme production potential is of great biotechnological importance. Thus, the selection of the new fungal strains with high enzyme synthesis ability as well as the need to be germ-free, stable, easily preserved, and produced are of strategic importance. According to Narasimha *et al.* (2006), the use of modern techniques to improve the production of metabolites does not invalidate the search for wild organisms producing useful metabolites. In fact, the screening of naturally occurring microorganisms may be the best way to obtain new strains and/or enzymes for industrial purposes.

Nevertheless, the enzymes produced by wild microorganisms are not always sufficient to meet the demand, due to low yields and incompatibility of the standard industrial fermentation processes (Ahmed *et al.* 2009). Therefore, several attempts have been made to increase fungal xylanase production by fungal strains, through mutagenesis and recombinant DNA technology. According to Otten and Quax (2005), large-scale production of xylan-degrading enzymes has been facilitated with genetic engineering. Additionally, recent advances in genomics have helped to overcome problems such as limited enzyme availability, substrate scope, and operational stability.

Some fungal xylanase encoding genes have been cloned in homologous and heterologous hosts, in order to overproduce the xylanolytic enzymes and modify its properties to suit commercial needs (Ahmed *et al.* 2009). As industrial applications require cheaper enzymes, high-level expression of enzymes in recombinant hosts is essential for ensuring the viability of the process (Juturu *et al.* 2011). Usually, higher production levels have been obtained when the expressed genes were from organisms taxonomically related to the host (Ahmed *et al.* 2009). Nevertheless, *Escherichia coli* (Le and Wang 2014; Yi *et al.* 2010; Xie *et al.* 2012), *Pichia pastoris* (Damaso *et al.* 2003; Driss *et al.* 2012; Fan *et al.* 2012; He *et al.* 2009) and, to a lesser extent, *Saccharomyces cerevisiae* (La Grange *et al.* 2001; Tian *et al.* 2013) have been used as hosts for expression of filamentous fungal xylanase genes.

Filamentous fungi are attractive hosts for recombinant DNA technology because of their natural ability to secrete large amounts of proteins in the medium with post-translational processing such as glycosylation (Demain and Vaishnav 2009). Regardless of the considerable amount of work dedicated to the topic and rapid development of new techniques, only a few articles concerned with the cloning of fungal xylanases genes into filamentous fungal host have been published in recent decades.

A. niger is one of the fungi that dominate the scene as a xylanase recombinant production host. Three *Phanerochaete chrysosporium* endo-1,4-beta-xylanase genes are cloned and expressed in *A. niger*. The levels of xylanase activity presented by the XynA, XynB, and XynC transformants in medium containing saccharose correspond to 0.47, 3.17, and 1.22 U/mL, respectively (Decelle *et al.* 2004). The xylanase II (*xyn2*)-encoding region of *Trichoderma reesei* QM6a was also successfully expressed in *A. niger* D15 under the transcriptional control of the glyceraldehyde-6-phosphate dehydrogenase promoter from *A. niger* and the *glaA* terminator of *Aspergillus awamori*. A stable Xyn2 transformant produced xylanase activity of 8,000 nkat/ml in shake-flask cultures containing molasses medium (Rose and van Zyl 2002).

A homologous expression system in *A. niger* was used by Levasseur *et al.* (2005). The authors cloned the gene *xynB* of *A. niger* under the control of the strong and constitutive glyceraldehyde-3-phosphate dehydrogenase (*gpdA*) gene promoter from *Aspergillus nidulans*. Overproduction of XynB was achieved in shake flask cultures with minimal medium containing glucose, and the secretion yield was estimated to be 625 U/mL.

The fungus *T. reesei* is an attractive host for expression of homologous or heterologous genes, and the inducible CBHI promoter is generally used. A *xyn2* gene (cDNA) from *Humicola grisea* was cloned under the CBHI promoter and secretion signal and overexpressed in *T. reesei* (de Faria *et al.* 2002). The highest xylanase activity was exhibited by the transformant T2-8 (12,700 nkat mL⁻¹) cultivated on avicel-celulose that might have activated the CBHI promoter. Salles *et al.* (2007) describe the heterologous expression of the *Acrophialophora nainiana xyn6* gene in *T. reesei* Rut C-30 also under CBHI promoter. Conversely, Li *et al.* (2012) utilized constitutive promoters for high level homologous expression of xylanase II in *T. reesei*. The recombinant *T. reesei* strains were able to produce 9,266 U/mL and 8,866 U/mL of xylanase activities when grown in a medium with high glucose concentration.

A. nidulans and *Aspergillus oryzae* are also common choices as hosts to express recombinant xylanases. The xylanase activity was enhanced up to 40-fold by the introduction of multiple copies of xylanase gene *exlA* from *A. awamori* in *A. nidulans* (Hessing *et al.* 1994). The *xynF1* gene was overexpressed under a strong *A. oryzae TEF1* gene promoter that gives high expression levels even in the glucose-containing medium (Kitamoto *et al.* 1999), while the gene encoding xylanase F3 (*xynF3*) was successfully expressed in *A. oryzae* when grown in the medium containing wheat bran as a carbon source (Kimura *et al.* 2002).

Furthermore, Osipov *et al.* (2011) obtained an increased heterologous expression of Xyl-31 xylanase gene from *Penicillium canescens* in *Penicillium verruculosum* strains. The authors achieved enzymatic preparations that are biocatalysts for the hydrolysis of wastes from wood processing industries. Despite the good prospects on enzyme development provided by developments of mutations and genetic engineering studies, suitable fermentation strategies need to be developed for xylan-degrading enzyme production by cloning hosts at the industrial level.

PRODUCTION OF FUNGAL XYLANASES WITH AGRO-RESIDUES

Submerged and Solid-state Fermentations

Submerged fermentation (SmF) and solid state fermentation (SSF) systems are currently employed to produce compounds of industrial interest from lignocellulose, as an alternative for valorization of these wastes and also to solve environmental problems caused by their disposal (Kumar *et al.* 2012). Both systems have been used at the research level, but some techniques yielded better results than others. Because the metabolism exhibited by microorganisms is different in both systems and the influx of nutrients and efflux of waste materials needs to be carried out based on these metabolic parameters, any slight deviation from the specified parameters will result in an undesirable product (Subramaniyam and Vimala 2012).

Submerged fermentation is also known as submerged culture, and its main characteristic is the use of a liquid fermentation media with soluble nutrients. In this type of fermentation, the substrate is dissolved or suspended in a water source that is not a limiting factor. Submerged fermentation is generally used in industrial processes, as modern methods of control are more easily adapted to fermentation, the yields are higher, and the costs and risks of contamination are lower (Krishna 2005). Nevertheless, it has some drawbacks, such as physical space and requirements for energy and water (Jain *et al.* 2013). For this reason, interest in solid state fermentation (SSF) has increased in the last years, as it provides various advantages from both practical and economic perspectives.

Solid state fermentation has been defined as any fermentation process that involves a solid matrix acting as both a physical support and source of nutrition that allows the development of microorganisms in the absence of free flowing liquid (Pandey *et al.* 2000; Singhanian *et al.* 2009). This system provides many advantages, such as mimicking the natural habitat in which the microorganism grows and reducing water activity, which can reduce microbial contaminations, and limit water consumption and equipment size. Also, it has been reported that solid-state cultures present higher volumetric yield, greater end-product stability, and less energy requirements than submerged cultures (Ayyachamy and Vatsala 2007; Jain *et al.* 2013; Singhanian *et al.* 2009).

However, scaling up represents another obstacle to be overcome in SSF processes once different gradients (moisture, temperature, substrate concentration, and others) form along the bioreactor, especially the static bed ones, which may negatively influence the process. Heat dissipation, mass transfer, and control of fermentative parameters are the main challenges to be overcome in this process (Hölker and Lenz 2005; Khanahmadia *et al.* 2006; Singhanian *et al.* 2009). In this respect, more research on design, modeling, operation, and scaling up are necessary to allow the employment of SSF processes involving bioreactors.

Fungi and yeast are the most suitable microorganisms for SSF, while bacteria have been considered unsuitable, according to the theoretical concept of water activity (Chinn *et al.* 2007). According to Orozco *et al.* (2008), some bacterial strains may be adapted to this type of process, although many advantages can be obtained with SSF systems when fungi are used. Unlike other microorganisms, fungi are normally found in nature growing on solid substrates such as seeds, roots, pieces of wood, stems, and dried parts of animals, such as skin and bones, and on fecal matter (Bhargav *et al.* 2008). Since SSF provides an environment closer to the natural habitat of fungi, these microorganisms

can be stimulated to produce more xylanolytic enzymes. The highest xylanase yields have been obtained under solid-state conditions, rather than liquid state conditions (Assamoi *et al.* 2008; Nair *et al.* 2008; Kulkarni and Gupta 2013; Roy *et al.* 2013; Singh *et al.* 2013). The findings of Jin *et al.* (2012) also support the use of SSF bioreactors and suggest that they are good not only for the control of microbial fermentation that affect the growth of some important parameters, but also for substantially increasing xylanase production as well.

Despite the potential advantages presented by SSF, more than 75% of industrial enzymes are produced using SmF. This can be explained by the fact that SmF supports the utilization of genetically modified organisms to a greater extent than SSF. Moreover, SmF is widely used due to the lack of equipment required for the production of various enzymes under SSF (Subramaniyam and Vimala 2012). However, current trends emphasize that solid-state fermentation systems have potential for increased xylanase production.

Induction of Xylanases by lignocellulosic materials

The capacity of a particular microorganism to grow in lignocellulosic substrates is directly related to the production of a broad spectrum of enzymes that act synergistically to deconstruct the plant cell wall by substrate depolymerization of varying complexity (Siqueira *et al.* 2010; Moreira *et al.* 2012). It has been proposed that substrates containing xylan are necessary for xylanase production because its hydrolysis products serve both as inducers as well as a carbon source for the organism (Haltrich *et al.* 1996). In most of the fungi studied, xylanolytic enzymes expression regulation is mediated by the transcriptional activator XlnR, which regulates the expression of a number of genes involved in xylan degradation (Hasper *et al.* 2002; Stricker *et al.* 2008). The *xlnR* gene transcription is modulated by carbon sources, such as xylan and xylose (de Vries *et al.* 1999; Tamayo *et al.* 2008; Mandal *et al.* 2012). Xylan was found to be the best inducer of most microbial xylanases (Khucharoenphaisan *et al.* 2010; Joshi and Khare 2012) followed by the monosaccharides xylose and arabinose (Mandal *et al.* 2012), medium- to large-sized xylooligosaccharides (Miyazaki *et al.* 2005), xylitol, and arabinol (Mach-Aigner *et al.* 2011). In many cases, basal constitutive synthesis was detected in absence of an inducer added, leading to the formation of easily metabolizable compounds (Mandal *et al.* 2012).

Several studies have demonstrated that xylanase-encoding genes are subject to catabolic repression. This mechanism alters transcription and it is regulated by CreA protein, a transcriptional repressor of glucose-repressible genes (de Vries *et al.* 1999; Sun *et al.* 2011). The repression of xylan-degrading enzymes by preferred carbon sources such as glucose is an efficient energy-conserving mechanism, once when glucose is abundant in the environment; the xylan degrading enzymes are unnecessary (Amore *et al.* 2013; Sun and Glass 2011). In spite of being an inducer of xylanolytic gene expression, xylose also represses the expression of xylanolytic genes. In *T. reesei* and *Neurospora crassa*, it has been reported that xylose can function as both a repressor and an inducer of xylanase expression, depending on concentration (Mach-Aigner *et al.* 2010; Sun *et al.* 2012). In *A. niger*, CreA mediates carbon repression of xylanolytic enzymes by xylose, beginning at 1 mM and increases in strength up to in the area between 30-70 mM (de Vries *et al.* 1999).

According to Glass *et al.* (2013), despite recent progress, knowledge on the order of events, the timing, and the regulatory mechanism behind the induction of genes

encoding plant polysaccharide-degrading enzymes during the exposure of fungi to complex lignocellulosic substrates remains poorly understood. However, recent studies have been able to elucidate part of this intricate process.

When saprophytic fungus such as *A. niger* and *N. crassa* are exposed to complex lignocellulosic materials, their response is complex and leads to the up-regulated transcription of several carbohydrate active enzymes and accessory proteins (Coradetti *et al.* 2012; Znameroski and Glass 2013; Benz *et al.* 2014; van Munster *et al.* 2014). It has been shown that carbon starvation plays a major role in the induction or initial fungal response. The relief of carbon catabolite repression, by glucose depletion or deletion of *creA*, activate the expression of genes of the early degradative response, including genes that encode enzymes that are active on arabinan or arabinogalactan side chains of pectin, as well as (arabino)xylan and galacto(gluco)mannan. On the other hand, expression levels of genes of the major, later, degradative response were not affected (Nakari-Setälä *et al.* 2009; Delmas *et al.* 2012). The enzymes encoded by the genes that have increased transcription levels under early lignocellulose degradation can be responsible for release of small inducers from substrates in the environment of the fungus, acting either alone or together with enzymes encoded by constitutively expressed genes (Martens-Uzunova and Schaap 2009; Glass *et al.* 2013; van Munster *et al.* 2014).

Thus, this model of induction suggests that both types of enzymes (constitutively expressed and up-regulated by carbon starvation) contribute to the release of inducing molecules. The early up-regulation of the xylanolytic genes that are transcriptionally activated by the xylanolytic regulator XlnR could be related to the early release of xylose, arabinose, and (arabino)xylan oligosaccharides from the substrate by these enzymes. Alternatively, it could be related to the presence of low amounts of xylose in the cultivation medium containing the lignocellulosic substrate (Delmas *et al.* 2012).

Agro-Residues Used for Fungal Xylanase Production

The market demand for xylanases has significantly increased during the past few decades. The practical application of these enzymes cannot be achieved unless they are available in sufficient amounts. Because biotechnological applications require large quantities of low-cost enzymes, several approaches for xylanase production have been applied. The use of agro-residues as substrates for the microbial production of xylanase has shown promise as an alternative that could substantially reduce enzyme costs and increase productivity.

The nature of particles and moisture content of the agro-industrial waste utilized in fermentation systems are critical factors (Singhania *et al.* 2009). The choices of suitable agro-industrial waste for the fermentation process have indicated the types of a lignocellulosic material that favor both fungal growth and product formation (Kumar and Kanwar 2012). The evaluation of this parameter and other process conditions, such as temperature, pH, and aeration, has encouraged the screening of several agricultural-residues for the production of xylanase (Singhania *et al.* 2009). However, because the growth of microorganisms in different carbon sources is associated with a differential expression of functionally distinct xylanases (Badhan *et al.* 2007), much exploration still needs to be carried out to identify sustainable substrates that allow production of xylanases with desirable characteristics.

Since compounds derived from xylan are required for xylanase induction, several reports evaluated the xylanase production using isolated xylans as substrate. Higher xylanases titers obtained with oat spelt xylan (a highly substituted xylan) were produced

by *T. aurantiacus*, corresponding to 575.9 U/mL (Yu *et al.* 1987), whereas Ghatora *et al.* (2007) achieved notable xylanase levels using birchwood xylan (a less-branched xylan) with *Melanocarpus* sp. (264.2 U/mL). However, the high cost of xylans has limited their applications for large-scale production processes. In this context, some lignocellulolytic substrates, such as sawdust, sugarcane bagasse, soy flour, maize straw, or wheat bran, have been compared in relation to purified xylans (Okafor *et al.* 2007; Goyal *et al.* 2008; Jhosi and Khare 2012; Guimaraes *et al.* 2013). Many of these have performed significantly better than isolated xylans with respect to the yields of xylanase in large-scale production processes. However, the successful application of enzymes depends not only on the substrate choice but on the optimization of production, which may directly result in cost reduction.

A comparison of the production levels of fungal xylanase reported in the literature of recent years was performed. The greatest xylanase yields for several agro-residues that were evaluated in SSF and SmF are shown in Tables 2 and 3, respectively.

Table 2. Comparisons of Xylanase Production Levels from Different Filamentous Fungi Grown on Agro-residues in SSF

| Substrate | Microorganism | Production (U.g ⁻¹) | References |
|----------------------|---------------------------------|---------------------------------|---------------------------------|
| Apple pomace | <i>A. niger</i> | 5662 | Liu <i>et al.</i> 2008 |
| Barley bran | <i>A. niger</i> | 42 | Soliman <i>et al.</i> 2012 |
| Brewer's spent grain | <i>Neurospora crassa</i> | 1073 | Xiros <i>et al.</i> 2008 |
| Canola meal | <i>Humicola lanuginosa</i> | 610 | Rajoka <i>et al.</i> 2005 |
| Citrus peel | <i>A. niger</i> | 106.42 | Tao <i>et al.</i> 2011 |
| Citrus pulp | <i>Eupenicillium javanicum</i> | 397 | Neves <i>et al.</i> 2011 |
| Coba husk | <i>Aspergillus carneus</i> | 1721 | Fang <i>et al.</i> 2010 |
| Coffee husk | <i>Penicillium sp.</i> | 23494 | Murthy and Naidu 2012 |
| Corn cobs | <i>Aspergillus foetidus</i> | 3065 | Shah and Madamwar 2005 |
| Corn stover | <i>Fusarium oxysporum</i> | 1840 | Panagiotou <i>et al.</i> 2003 |
| Grape pomace | <i>A. awamori</i> | 38 | Botella <i>et al.</i> 2007 |
| Jatropha seed cake | <i>A. niger</i> | 6087 | Ncube <i>et al.</i> 2012 |
| Oil Palm fiber | <i>Aspergillus terreus</i> | 115000 | Lakshmi <i>et al.</i> 2009 |
| Orange bagasse | <i>E. javanicum</i> | 106.42 | Tao <i>et al.</i> 2011 |
| Orange peel | <i>A. niger</i> | 917.7 | Dai <i>et al.</i> 2011 |
| Paddy straw | <i>Penicillium frequentans</i> | 735 | Palaniswamy <i>et al.</i> 2012 |
| Pearl millet bran | <i>Aspergillus flavus</i> | 1530 | Bhatt <i>et al.</i> 2012 |
| Rice bran | <i>H. lanuginosa</i> | 842 | Rajoka <i>et al.</i> 2005 |
| Rice husk | <i>A. niger</i> | 6500 | Venegas <i>et al.</i> 2013 |
| Rice straw | <i>A. niger</i> | 5070 | Kang <i>et al.</i> 2004 |
| Spent tea leaves | <i>Talaromyces emersonii</i> | 1065.4 | Gilleran <i>et al.</i> 2010 |
| Sorghum straw | <i>T. lanuginosus</i> | 48000 | Sonia <i>et al.</i> 2005 |
| Soya oil cake | <i>P. canescens</i> | 18895 | Antoine <i>et al.</i> 2010 |
| Soybean fiber | <i>T. reesei</i> | 757.4 | Lio and Wang 2012 |
| Soybean meal | <i>A. niger</i> | 47.7 | Vitcosque <i>et al.</i> 2012 |
| Sugarcane bagasse | <i>T. lanuginosus</i> | 19320 | Maninaran <i>et al.</i> 2009 |
| Sugarcane straw | <i>T. aurantiacus</i> | 1679.8 | Monte <i>et al.</i> 2010 |
| Sunflower sludge | <i>Trichoderma harzianum</i> | 8.75 | Sakthiselvan <i>et al.</i> 2012 |
| Sunflower meal | <i>H. lanuginosa</i> | 608 | Rajoka <i>et al.</i> 2005 |
| Tomato pomace | <i>A. awamori</i> | 100 | Umsza-Guez <i>et al.</i> 2011 |
| Watermelon rinds | <i>Trichoderma virens</i> | 70 | Mohamed <i>et al.</i> 2013 |
| Wheat straw | <i>Paecilomyces thermophila</i> | 18580 | Yan <i>et al.</i> 2006 |
| Wheat bran | <i>A. niger</i> | 14637 | Xu <i>et al.</i> 2008 |

In general, the values in Table 2 were obtained after optimizing the xylanase production process. It is emphasized that this comparison may not reflect the real differences between the levels produced, as no standard enzyme substrate has yet been adopted. Historically, xylanase activity has been measured by the DNS-method using purified xylan from several sources, such as oat spelt, larch wood, birch wood, or beech wood, as a substrate. In addition, other variables such as inoculum size, experimental design, and operational conditions directly affect the levels of xylanase produced. However, it still is possible to infer from the data which of the raw materials may be the most promising.

Table 3. Comparisons of Xylanase Production Levels from Different Filamentous Fungi Grown on Agro-residues in SmF

| Substrate | Microorganism | Production (U.ml ⁻¹) | References |
|------------------------|-----------------------------------|-------------------------------------|--------------------------------|
| Bocaiuva fruit residue | <i>Lichtheimia ramosa</i> | 1802 | Silva <i>et al.</i> 2013 |
| Brewer's spent grain | <i>Penicillium glabrum</i> | 51.43 | Knob <i>et al.</i> 2013 |
| Canola meal | <i>T. reesei</i> | 210 | Gattinger <i>et al.</i> 1990 |
| Coconut coir pith | <i>Phanerochate chrysosporium</i> | 16.4 | Kanmani <i>et al.</i> 2009 |
| Corn cob | <i>T. lanuginosus</i> | 3575 | Singh <i>et al.</i> 2000 |
| Mandarin peel | <i>Pseudotremella gibbosa</i> | 195 | Elisashvili <i>et al.</i> 2009 |
| Maize straw | <i>T. viride</i> | 4.62 | Goyal <i>et al.</i> 2008 |
| Melon peel | <i>T. harzianum</i> | 26.5 | Isil and Nulifer 2005 |
| Oat straw | <i>A. awamori</i> | 820 | Smith and Wood 1991 |
| Palm leaf | <i>A. niger</i> | 1906.5 | Norazlina <i>et al.</i> 2013 |
| Pineapple peel | <i>T. viride</i> | 73.09 | Fortkamp and Knob 2014 |
| Rice husk | <i>A. niger</i> | 89.71 | Abbas <i>et al.</i> 2011 |
| Rice straw | <i>A. fumigatus</i> | 1040 | Sarkar and Aikat 2012 |
| Sandusk | <i>Penicillium sp.</i> | 10.7 | Bajaj <i>et al.</i> 2011 |
| Soy flour | <i>Scytalidium thermophilum</i> | 14.44 | Jhosi and Khare, 2012 |
| Sugarcane bagasse | <i>T. lanuginosus</i> | 946 | Ali <i>et al.</i> 2013 |
| Tequila industry waste | <i>A. niger</i> | 1.52 | Huitron <i>et al.</i> 2008 |
| Wheat bran | <i>A. niger</i> | 74.5 | Gawande and Kamat 1999 |
| Wheat straw | <i>Melanocarpus albomyces</i> | 550 | Biswas <i>et al.</i> 2010 |

A greater number of agro-residues are currently being exploited by both systems. The different production levels observed among the lignocellulosic materials that have been evaluated are likely related to the differences in composition and the accessibility of the substrates to the fungi. Additionally, each fungal species shows an intrinsic ability to produce xylanases in the presence of specific substrates. Interestingly, high titers of xylanase have been obtained with some substrates not commonly explored for xylanase production, such as soya oil cake, coffee husk, and sorghum straw. In addition,

lignocellulosic materials such as maize straw, sawdust, grape pomace, citrus peel, soybean meal, and barley bran provided low levels of xylanases when compared to other materials. These substrates have not been extensively exploited, possibly due to lower observed yields in comparison with other substrates.

In most cases, agro-residues used to produce enzymes by SSF or SmF either do not contain all the necessary nutrients for this purpose or they may be available but in sub-optimal concentrations. In these circumstances, the substrate must be supplemented to stimulate or improve enzyme production by the addition of extra carbon or nitrogen sources (Galiotou-Panayotou and Kapantai 1993; Patil and Dayanand 2006; Ritter *et al.* 2013). Supplementation can also be carried out by using a mineral salt solution to adjust the initial moisture content of the residue (Khandeparkar and Bhosle 2006; Papinutti and Forchiassin 2007). Moreover, for each organism or strain to have its own special conditions, including specific carbon sources for maximum yields, other fungal strains must be evaluated to verify the real potential of these substrates as xylan-degrading enzyme inductors. The representative studies on agro-residues that have been concerned with fungal xylanase productivity are described below.

Wheat bran

Wheat bran, produced worldwide in large quantities as a by-product of the wheat milling industry, constitutes a significant underutilized source of sugars. Annually, over 650 million tons of wheat is produced in the world. The accumulated biomass of wheat bran can be estimated at 150 million tons, which is predominantly used in the feed industry (Prückler *et al.* 2014).

Recently, there has been an increase in attempts to produce xylanases, especially through SSF, using wheat bran. It is interesting to note that, although a number of substrates have been employed for cultivating different fungi, wheat bran has been the preferred choice in most of these studies. This substrate shows a natural ability to induce xylanase synthesis. This quality is attributed to its cell-wall polysaccharides that contain 40% xylan, favorable degradability, and the presence of some nutrients in the carbon source. Additionally, wheat bran is able to remain loose in moist conditions, thereby providing a large surface area (Betini *et al.* 2009; Dhillon *et al.* 2011; Singh *et al.* 2008). On the other hand, it can be an expensive carbon source for large scale usage, which can represent problems for its industrial application (Virupakshi *et al.* 2005; Yang *et al.* 2006).

The biochemical composition of wheat bran indicates that when this material is hydrolyzed, it contains a considerable amount of soluble sugars, such as glucose (42.5% dry wt), xylose (15.4% dry wt), arabinose (3.1% dry wt), and galactose (2.7% dry wt), which are required to initiate micro-organism growth and replication (Archana and Sathyanarayana 1997). In the literature, many works have reported the use of wheat bran to produce xylanase by several fungal species. These fungi, such as those belonging to the genera *Aspergillus* (Li *et al.* 2006; Betini *et al.* 2009; Dhillon *et al.* 2011; Sorgatto *et al.* 2012; Guimaraes *et al.* 2013), *Penicillium chrysogenum* (Okafor *et al.* 2007), *Sclerotinia sclerotiorum* (Ellouze *et al.* 2008), *Fusarium solani* (Bakri *et al.* 2013), and *Simplicillium obclavatum* (Roy *et al.* 2013), have exhibited different levels of enzyme production.

Remarkable xylanase levels were produced by *A. niger* XY-1, when grown under SSF in the presence of wheat bran. After 48 h of fermentation, xylanase activity reached 14,637 U/g dry substrate (Xu *et al.* 2008). With a shortened fermentation time, higher

xylanase production, and no need for the addition of expensive mediums, this process shows the potential ability to be utilized for industrial purposes. Among the lignocellulosic substrates tested by Kamra and Satyanarayana (2004), wheat bran supported a high xylanase secretion (7,832 U/g of dry carbon source) by *H. lanuginosa* in SSF after parametric optimization. It is also important to highlight the xylanase production titers of *A. foetidus* MTCC 4898, which corresponded to 8,450 U/g dry substrate after optimizing the xylanase production process (Chapla *et al.* 2010).

In relation to SmF, significant levels of xylanase were produced by *A. niger* (74.5 U/mL) and *A. terreus* (68.9 U/mL) using wheat bran after optimization of process parameters, such as moistening agent, level of initial moisture content, temperature of incubation, inoculum size, and incubation time (Gawande and Kamat 1999). Gottschalk *et al.* (2013) evaluated xylanase production by *A. awamori* 2B.361 U2/1 in the presence of wheat bran. An improved yield was achieved with the use of poor nitrogen sources, such as sodium nitrate, corresponding to 44.88 U/mL. Efficient production was also obtained with *Penicillium* sp. WX-Z1, using Plackett-Burman and Box-Behnken designs (46.5 U/mL) (Cui and Zao 2012).

Wheat straw

Wheat straw is one of the most abundant crop residues in the world. It is estimated that 354 million of tons of wheat straw may be available globally (Bhatia *et al.* 2012). The huge amount of this residue may constitute a promising raw material that could potentially be transformed into a more edible feed for ruminants (Rodrigues *et al.* 2008) or, alternatively, it could also be used for microbial enzyme production. Wheat straw is also one of the substrates that has been extensively investigated as a carbon source for xylanase production (Narang *et al.* 2001; Gupta *et al.* 2009; Sanghvi *et al.* 2010; Liao *et al.* 2012; Pandya and Gupte 2012). The high xylan content in wheat straw makes it an accessible and cheap inducer source that can be applied in large volumes for fermentation, such as in industrial bioreactors (Michelin *et al.* 2012).

P. thermophila J18, a thermophilic fungus, was able to produce substantial quantities of xylanase under SSF in the presence of wheat straw. The production was enhanced by optimizing the particle size of wheat straw, nitrogen source, initial moisture level, growth temperature, and initial pH level. Under optimized conditions, yields as high as 18,580 U/g dry substrate were achieved (Yang *et al.* 2006). *M. albomyces* IIS-68, *Aspergillus tubingensis* JP-1, and *T. aurantiacus* also showed promising xylanase activity in the presence of wheat straw, with yields of 7,760 U/g, 6,887 U/g, and 6,193 U/g dry substrate, respectively (Kalogeris *et al.* 1998; Narang *et al.* 2001; Pandya and Gupte 2012).

Under SmF, high amounts of xylanase were produced by *M. albomyces* IITD3A when cultivation was performed with wheat straw (550 U/mL). The statistical optimization of the process parameters by response surface methodology revealed that xylanase production was most affected by fungus morphology and changes in the pH medium (Biswas *et al.* 2010). A similar level of production by *M. albomyces* was verified by Gupta *et al.* (2013). The authors found that xylanase production is influenced by the synergic effect of nitrogen sources in the fermentation medium, reaching a production of 520 U/mL.

Sugarcane bagasse

Sugarcane plays a vital economic role as one of the main crops cultivated in countries such as Brazil, India, and China (Chandel *et al.* 2012). The remnants left over after the juice extraction from the sugarcane stem are called sugarcane bagasse (Pandey *et al.* 2000). Sugarcane bagasse represents a sizeable portion of annually collected agro-residues. Approximately 1.6 billion tons of sugarcane is collected annually from around the world. This production yields approximately 279 million metric tons of sugarcane waste (Krishnan *et al.* 2010; Chandel *et al.* 2012). This waste is typically used as a source of fuel for heat and electricity in sugar mills.

The use of SSF for enzymes production is an interesting alternative for the valorization of sugarcane bagasse. Consequently, various reports on the production of xylanases using this lignocellulosic material have been published. High xylanase yields under SSF using sugarcane bagasse as a substrate were described by Manimaran *et al.* (2009) with *T. lanuginosus* SSBP (19,320 U/g dry substrate). Expressive xylanase titers (2,600 U/g dry substrate) were also obtained when *T. reesei* and *A. niger* were co-cultured (Gutierrez-Correa and Tengerdy 1998). In addition, Milagres *et al.* (2004) used sugarcane bagasse in xylanase production with a *T. aurantiacus* strain and obtained levels of 1,597 U/g dry substrate. Similar xylanase production was recorded by Ghoshal *et al.* (2012). The SSF of sugarcane bagasse by *Penicillium citrinum* MTCC 2553 was optimized, resulting in 1,645 U/g dry substrate.

Many investigations have also been carried out to evaluate xylanase production when employing sugarcane bagasse under SmF. Optimization of growth conditions for xylanase production by *T. lanuginosus* resulted in substantial xylanase activity of 946 U/mL (Ali *et al.* 2013). Rezende *et al.* (2002) showed that *T. harzianum* produced high levels of xylanase with sugarcane bagasse, reaching 288 U/mL.

Rice straw

Rice straw, a renewable lignocellulosic biomass, is an attractive feedstock because it is one of the most abundant lignocellulosic waste materials in the world (Binod *et al.* 2010). About 60% of the mass produced by rice crops is rice straw, which has high cellulose and hemicellulose contents that can be hydrolyzed into fermentable sugars. The annual global generated amount of this residue is 685 million tons (Lim *et al.* 2012).

Usually, rice straw is removed from the field at harvest time and is subjected to open field burning. However, this practice creates serious environmental, safety, and health issues (Sarkar and Aikat 2012; Shafie *et al.* 2012). For this reason, there is a strong desire to find alternative ways to remove the rice straw after each harvest season. Recent research findings have provided new options for the reutilization of rice straw as a feedstock for enzyme and monosaccharide production (Sarkar and Aikat 2012).

Rice straw is ostensibly a feasible medium for xylanase production under SFF, as has been demonstrated in recent research. Kang *et al.* (2004) reported a total xylanase production of 5,070 U/g dry substrate by *A. niger* KK2 in a basal medium that was supplemented with rice straw as a carbon source. Soroor *et al.* (2013) described xylanase production by *T. reesei* F418 when cultivated on a medium containing rice straw, corresponding to 2,232 U/g dry carbon source.

Under SmF, substantial amounts of xylanase have also been obtained with rice straw. The xylanase production by *A. fumigatus* NITDGPKA3 was statistically optimized by response surface methodology based on a central composite design. A

significant titer of xylanase was obtained, corresponding to 1,040 U/mL (Sarkar and Aikat 2012). Among several fungal strains that were isolated from paper mill effluent, *A. fumigatus* produced high levels of xylanase in the presence of rice straw (135 U/mL) and negligible levels of endocellulase (Anthony *et al.* 2003).

Corn cob

Agricultural residues such as corn cob represent large, renewable sources of lignocellulosic biomass. Corn cob is an important by-product of the sweet corn processing industry (Kumar *et al.* 2008). For every 100 kg of corn grain that is processed, approximately 18 kg of corn cobs is generated. The large quantities of corn cob produced have negligible value and are mostly discarded, with small quantities sold at very low prices for supplementary animal feed or used as fertilizer (Topakas *et al.* 2004; Ashour *et al.* 2013).

Because of its nutritional content, corn cob can be used as a medium to cultivate microorganisms, or it may be converted into added-value chemicals, such as lactic acid, citric acid, sugars, and ethanol (Ashour *et al.* 2013). In addition, the elevated xylan content in corn cob (40%), the highest among all agricultural waste, makes it a potential substrate for xylanase production. Remarkable xylanase production by *A. foetidus*, 3065 U/g dry substrate, was achieved by Shah and Madamwar (2005) using corn cob under optimized growth conditions, taking into account the parameters of temperature, pH, moistening agents, moisture level, and nitrogen sources. The xylanase production process by *A. niger* CECT 2700 was successfully established in a laboratory-scale horizontal tube bioreactor, achieving the highest xylanase activity of 2.926 U/g of corn cob (Pérez-Rodríguez *et al.* 2014).

Moreover, corn cob has potential as a substrate for SmF xylanase production. *T. lanuginosus* has been reported to be one of the best producers of xylanase when grown on corn cob (3,575 U/mL) (Singh *et al.* 2000). Similar quantities of xylanase were produced by *T. lanuginosus* MC 134 (3,399 U/mL), according to a report by Kumar *et al.* (2009), showing the xylanase production potential of these strains using corn cobs.

Other potential substrates

Among the substrates evaluated for fungal xylanase production, oil palm wastes are one of the least explored, but one of the most promising. Remarkably, an *A. terreus* strain showed xylanase activity corresponding to 115,000 U/g after optimization, using palm fiber as a carbon source. Expressive production was also obtained with oil palm waste by *A. terreus* (41,000 U/g dry substrate) and *A. fumigatus* (35,380 U/g dry substrate) (Lakshmi *et al.* 2011). In addition, oil palm leaf has also been shown to be a promising raw material for xylanase production by *A. niger* under SmF, reaching 1,906 U/mL (Norazlina *et al.* 2013). These substrates are a by-product from extracting the oil of palm fruits that are normally burned as fuel to provide energy for the palm oil mills (Neoh *et al.* 2011) and have only recently been explored as a viable alternative for xylanase production.

Sorghum straw is a renewable and cheap resource, commonly used as livestock feed. However, it has scarcely been studied as a raw material for biological processes (Sene *et al.* 2011). Nevertheless, because of the high xylose content of sorghum straw (19.16 % dry weight) (Téllez-Luis *et al.* 2002), it may be explored as a xylanase inducer. Sonia *et al.* (2005) have reached notable xylanase levels using sorghum straw with *T.*

lanuginosus D2 W3 via SSF (48,000 U/g dry substrate), after optimizing conditions using Box-Behnken methodology.

Oil cakes are by-products obtained after oil is extracted from seeds. These materials have been explored by several researchers for their employability as substrates in SSF or as supplements for production media (Ramachandran *et al.* 2007). Soya oil cakes, however, have occasionally been used for enzyme production (Assamoi *et al.* 2010), the potential for which was demonstrated by Antoine *et al.* (2010). Various fermentation parameters were optimized for enhanced xylanase production by *P. canescens* under SSF, with production amount of 18,895 U/g dry substrate. Assamoi *et al.* (2008) also reported high xylanase production by *P. canescens* 10-10c when cultivation was performed with soya oil cake, which corresponded to 14,000 U/g dry substrate.

Coffee, after petroleum, is the second largest traded commodity in the world. Therefore, the coffee industry is responsible for the generation of large amounts of residue (Nabais *et al.* 2008). Despite the large quantities of coffee wastes that are generated, there are few studies focusing on their use in other, profitable applications (Mussatto *et al.* 2011b). However, the chemical composition data (Table 1) suggest that coffee husk and spent coffee grounds can be of value as raw material for biotechnological processes, including xylanase production.

The feasibility of using coffee by-products for xylanase production under SFF by *Penicillium* sp. has recently been studied. The process parameters, such as fermentation time, carbon source, nitrogen source, moisture, particle size, and inoculum size were optimized, resulting in an expressive production of 20,388 U/g dry substrate when coffee husk was employed as carbon source. Xylanase titers were further improved to 23,494 U/g dry substrate with a steam pre-treatment (Murthy and Naidu 2012). The high enzyme titers obtained with coffee husk proved it to be a promising substrate for xylanase production.

Combinations of agro-industrial residues as carbon sources for xylanase production

In recent research, agro-industrial residues combinations being used as carbon sources for xylanase production have been reported for several types of fungi. However, there have been very few reports concerning the production of xylanases on mixed agro-industrial wastes in SmF. Mostly, mixed agro-industrial wastes are employed in SSF processes. In general, good levels of productivity have been obtained through these combinations, many times exceeding the titers obtained with the use of substrates alone (Pang *et al.* 2006; Betini *et al.* 2009; Su *et al.* 2011). Despite the limited attention devoted to the development of enzyme production processes employing mixed agro-residues, this is an important and emerging area for waste management.

Among several lignocellulosic substrates that have been evaluated, a mixture of corn cob and wheat bran supported a high xylanase secretion by *H. lanuginosa* in SSF, corresponding to 8,237 U/g dry substrate (Yang *et al.* 2011). The xylanase production by the thermotolerant fungus *A. fumigatus* was substantially enhanced through media optimization process. The combination of corn straw and wheat bran yielded enzyme levels of 7,232 U/g dry substrate (Moretti *et al.* 2012).

A. niger DFR-5 exhibited its highest xylanase production (2,596 U/g dry substrate) in media containing a mixture of wheat bran and soybean powder in a ratio 7:3 (Pal and Khanum 2010), while a combination of rice straw and wheat bran (3:2) was found to be the best substrate for xylanase production by *A. niger* mixed with *T. reesei*.

(Dhillon *et al.* 2011). Among a few easily available lignocellulosic substrates that were tested, a combination of soybean meal and crushed corn cob increased xylanase activity by *Aspergillus japonicus* C03 (Facchini *et al.* 2011), while a mixture of wheat bran and rice straw improved the xylanase production by *A. fumigatus* ABK9, reaching 1,130 U/g dry substrate (Das *et al.* 2013).

Xylanase production by *A. awamori* in both SSF and SmF was stimulated by mixing grape pumice with orange peels. The enzyme synthesis was similar to or higher than those produced by other agro-industrial residues (Díaz *et al.* 2012). In addition, high quantities of xylanase were obtained by *T. lanuginosus* SDYKY-1 under SmF. The adjustment of corn cob and soybean meal concentrations resulted in maximum enzyme production of 3,078 U/mL (Su *et al.* 2011).

CONCLUDING REMARKS

Recently, many efforts have been made to convert lignocellulosic residues into valuable products. For this reason, a number of such substrates have been evaluated for their potential as a carbon source for xylanase production, and many benefits have been obtained by these processes, such as high productivity and low production cost. So far, lignocellulosic biomass has been the most promising source to be employed as feedstock for microbial xylanase production. However, taking into account the variability of waste composition as well the optimization of the production process, larger studies are needed to determine if these wastes are suitable for pilot-scale production of the same or at even an industrial scale.

Molecular techniques developed during the past few decades have improved characteristics of the xylan degrading enzymes and increased its expression rates. However, the search for new microbial strains with improved enzyme expression profiles or higher protein secretion levels should be intensified in order to develop viable enzymatic production technologies that employ agro-industrial wastes as substrates.

Finally, in relation to environmental questions, it is necessary to emphasize the importance of removing wastes from the environment and adding value to them, allowing various industrial sectors to benefit from the use of xylanases that are obtained from lignocellulosic materials.

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