Chapter 2
An Insight into Fungal Cellulases and Their Industrial Applications

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2.1 Introduction

Cellulases are not a single enzyme but are a family of three groups of enzymes, exoglucanase, endoglucanase, and glucosidase (Adhyaru et al. 2015). Exoglucanase or glucan cellobiohydrolase (CBH) or avicelase attacks the ends of the cellulose chain and produces the disaccharide, cellobiose, as the resultant product. Endoglucanase or glucan glucanohydrolase or carboxymethylcellulase (CMCase or EG) acts on the inner part of cellulosic molecules that produces oligosaccharides. Glucosidase or cellobiase specifically attacks cellobiose and produces glucose (Adsul et al. 2007). Figure 2.1 depicts the mechanism of cellulolytic action. Cellulases have a wide range of applications in agriculture, biotransformation and fermentation, detergents and laundry, the pulp and paper industry, textiles, and the food industry (Adsul et al. 2009). Figure 2.2 represents the industrial applications of cellulases. Structurally, fungal cellulases are simpler than bacterial cellulases. Fungal cellulases have two domains: the catalytic domain and the cellulose-binding molecule (Ahmed et al. 2009).

The factors that influence the production of cellulases are the type of organism (fungi or bacteria or actinomycetes), the fermentation method (submerged or solid), the constituents of the production medium (carbon source, nitrogen source, and trace elements), and the process parameters (substrate concentration, pH,

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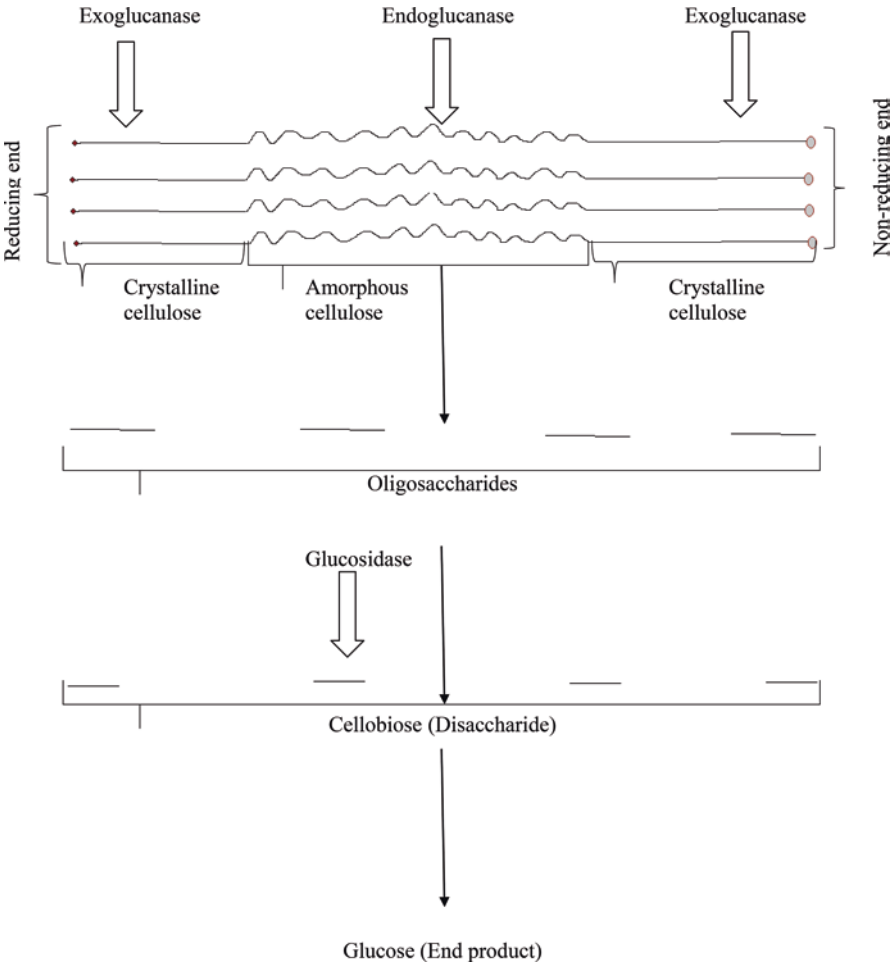

Fig. 2.1 Mechanism of cellulases action

temperature, time, inoculum size, and stirring rate) (Amir et al. 2011). Solid state fermentation is a process used in the production of fuels, food, pharmaceutical, and industrial products using microorganisms in a controlled environment. It is used as an alternative to submerged fermentation. Fermentation in the solid state takes place in the absence of free water. The advantages of solid state fermentation include a simpler process that requires less energy; produces higher volumetric productivity, similar to the natural environment of certain mushrooms; and makes purification easier than submerged fermentation (Anand et al. 2008).

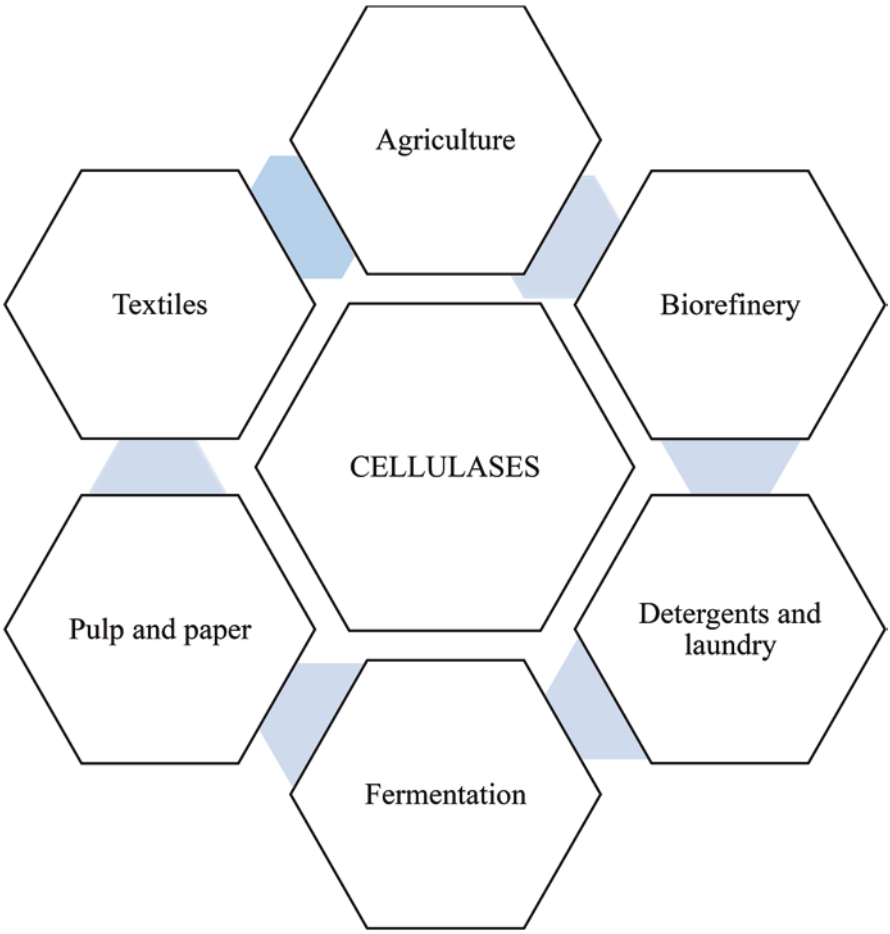

Fig. 2.2 Industrial applications of cellulases

2.2 Fungal Cellulases

Although it is known that bacteria, actinomycetes, and fungi produce cellulases, fungi play a major role. Of the fungi, the genera *Aspergillus*, *Trichoderma*, and *Penicillium* are predominant in the production of cellulases. *Aspergillus niger* and *Trichoderma reesei* were the most common microorganisms that produce cellulases (Anish et al. 2007). *Aspergillus* has more activity with respect to endoglucanase or CMCase (C_x) than exoglucanase or avicelase (C_1) and glucosidase or cellobiase, whereas *Trichoderma* has more significant activity of endoglucanase and exoglucanase than glucosidase. *Penicillium* produces more endoglucanase and glucosidase (Anita et al. 2009).

2.2.1 *Cellulases from* Aspergillus

Baba et al. have characterized *Aspergillus aculeatus* β-glucosidase 1 (AaBGL1), which promotes hydrolysis of cellulose by the *Trichoderma* cellulases system (Baba et al. 2015). Current research has also compared certain properties with a commercially available *A. niger* orthologue (AnBGL) to elucidate the benefits of recombinant AaBGL1 (rAaBGL1) for a synergistic effect on *Trichoderma* enzymes. Steady-state kinetic studies revealed that rAaBGL1 exhibited high catalytic efficiency for β protein-linked glucooligosaccharides. Milala et al. evaluated cellulases activity in *Aspergillus candidus* with rice husks, millet straw, guinea corn stalks, and sawdust as substrates (Milala et al. 2009). The substrates were pretreated with 5% NaOH and autoclaved. Fermentation studies showed that husks of rice, millet straw, and guinea corn stalks exhibited maximum cellulases activity of 7.50, 6.88, and 5.84 IU, respectively.

Schmidt et al. tested whether ochratoxin A (OTA) production of *Aspergillus niger* and *A. carbonarius* was related to a particular genotype and the identification of marker sequences with diagnostic value identifying *A. carbonarius* concerning the production of OTA in food and feed materials (Schmidt et al. 2004). The ability of isolates to produce OTA was tested by thin-layer chromatography (TLC). Strains were genetically characterized by AFLP fingerprints and compared with each other and with reference strains. Gomathi et al. explained the potential for CMCase production with the selective species *Aspergillus flavus* (Gomathi et al. 2012). The expression of CMCase in *A. flavus* was evaluated under different processing conditions using submerged fermentation (SmF) on various agricultural by-products. *A. flavus* produced high levels of CMCase under optimized culture conditions on the third day of incubation at optimal pH 6.0, at a temperature of 30 °C, and at a graft size of 4% in Czapek Dox using wheat bran as a substrate for SmF.

Immanuel et al. studied the production capacity of cellulases enzymes of *Aspergillus niger* and *A. fumigatus* against lignocellulose waste at pH 5–9 and at temperature of 20–50 °C (Immanuel et al. 2007). Enzyme production was analyzed separately with dinitrosalicylic acid (DNS) and filter paper (FPA). In the FPA method, *A. fumigatus* (0.292 IU/mL) and pH 6 of *A. niger* (0.262 IU/mL) resulted in a high level of enzyme production when coconut waste and sawdust were used as substrates, respectively. Similarly, with varying temperatures, both organisms achieved a high level of enzyme production at 40 °C with both substrates. Tao et al. purified endoglucanase (EG) from *Aspergillus glaucus* XC9 developed on 0.3% sugarcane bagasse as a carbon source from the culture filtrate using ammonium sulfate, a fast-flowing DEAE-Sepharose column and a Sephadex G-100 column, with a purge fold of 21.5% and a recovery of 22.3% (Tao et al. 2010).

Anita et al. studied the production of *Aspergillus heteromorphus* cellulases by submerged fermentation using wheat straw as a substrate (Anita et al. 2009). Process parameters such as pH, temperature, and time have been optimized for saccharification. The maximum reducing sugars were produced on the fifth day at pH 5 and 30 °C. Under optimal conditions, the activities of the filter paper and the CMCase

were, respectively, 3.2 IU/mL and 83 IU/mL. Herculano et al. studied the separation and purification of *Aspergillus japonicus* URM5620 cellulases in aqueous two-phase systems (ATPS) (Herculano et al. 2012). A factorial model (2^4) was used to determine the influence of the molarity of polyethylene glycol (PEG) (1000 to 8000 g/mol), its concentration (20.0–24.0% (w/w)), sodium citrate concentration (15–20% (w/w)), and pH (6.0–8.0) on the differential distribution and purification of the cellulolytic complex consisting of β-glucosidase (βG), endoglucanase (CMCase), and total cellulases (FPase). This process ensures an efficient and attractive increase in the purification factor.

Koseki et al. expressed the recombinant AkCel61, the wild-type enzyme (rAkCel61), and a truncated enzyme consisting of the catalytic domain (rAkCel61ACBM) in *Pichia pastoris* and analyzed their biochemical properties (Koseki et al. 2008). The purified rAkCel61 and rAkCel61ACBM migrated on sodium dodecyl sulfate polyacrylamide gel electrophoresis (SDS-PAGE), and their apparent molecular weights were 81 kDa and 34 kDa, respectively. The rAkCel61 protein bound to crystalline cellulose but not to arabinoxylan. The rAkCel61 and rAkCel61ACBM proteins produced small amounts of oligosaccharides from soluble carboxymethylcellulose. However, they showed no detectable activity against microcrystalline cellulose, arabinoxylan, and pectin. Lockington et al. characterized two genes encoding *A. nidulans* exo-cellulases and a gene encoding an endo-cellulases that is complementary to the endo-cellulases coding gene, for example, *eglA* (Lockington et al. 2002). The 5′ putative regulatory regions of all genes contain potential binding sites for the global carbon and nitrogen regulatory proteins, CreA and AreA. The 5′ *eglA* and *eglB* sequences contain potential consensus of XlnR-binding sites involved in induction in *A. niger*, but none of the 5′ sequence contains an exact copy of the AceII DNA binding consensus sequence involved in induction of *Trichoderma reesei*. Therefore, it is likely that they can be induced by different regulatory proteins specific to a pathway.

Coral et al. prepared a CMCase from a wild *Aspergillus niger* Z10 strain (Coral et al. 2002). Analyses of the enzyme preparation by SDS-PAGE revealed two protein bands with cellulolytic activity. The molecular weight of these bands has been estimated at about 83 kDa and 50 kDa. The optimum temperature of the enzyme was observed at about 40 °C. It was found that the activity of the enzyme had a broad pH range between 3 and 9 and that 41.2% of the initial activity was preserved after heat treatment at 90 °C for 15 minutes. Immanuel et al. also investigated the ability to produce cellulases enzymes from *Aspergillus niger* and *A. fumigatus* using lignocellulose wastes at pH 5–9 and at temperature of 20–50 °C (Immanuel et al. 2007).

Hui et al. studied the direct microbial conversion of wheat straw to lipid via a cellulolytic fungus of *Aspergillus oryzae* A-4 in solid state fermentation (SSF) (Hui et al. 2010). *A. oryzae* A-4 gave a lipid of 36.6 mg/g dry substrate (DS) and a cellulases activity of 1.82 FPU/g DS, with 25.25% of the holocellulose use in the substrates was detected. e Silva et al. studied the production of cellulolytic enzymes by the fungus *Aspergillus phoenicis* (e Silva et al. 2009). Grape waste from the wine industry has been selected as a growth substrate between various agro-industrial by-products. A centralized design was carried out with the quantity of grape and

peptone waste as independent variables. The fungus was cultured in a submerged fermentation at 120 °C and 120 rpm, and the activities of total cellulases, endoglucanases, and β-glucosidases were measured. The optimal production of the three cellulolytic activities was observed at values close to the central point. *A. phoenicis* has the potential to produce cellulases using grape waste as a growth substrate.

Gao et al. studied the production of extracellular cellulases by the thermoacidophilic fungus *Aspergillus terreus* M11 on lignocellulosic materials in solid state fermentation (SSF) (Gao et al. 2008). The results showed that the high-level cellulases activities of 581, 243, and 128 U/g of carbon source were obtained for endoglucanase, FPase, and β-glucosidase at 45 °C, pH 3, and 80% of moisture with corn straw and 0.8% yeast extract as sources of carbon and nitrogen. Adhyaru et al. investigated xylanase and cellulases activity using *A. tubingensis* FDHN1 and agricultural residues such as foundry waste, sugarcane bagasse, wood shavings, wheat straw, corn straw, peanut shell rice, and barley straw by solid state fermentation (Adhyaru et al. 2015). Wood chips showed maximum cellulases activity of 2.81 U/g with *A. tubingensis*.

In addition to the literature mentioned above, *A. ellipticus* (Hu et al. 2011), *A. flavus* (Obruca et al. 2012; Ojumu et al. 2003), *A. heteromorphus* (Singh et al. 2009a; b), *A. japonicas* (Herculano et al. 2011), *A. niger* (Mrudula and Murugammal 2011; Omojasola and Jilani 2008), *A. oryzae* (Kotaka et al. 2008), *A. terreus* (Narra et al. 2012), *A. tubingensis* (Decker et al. 2001), and other *Aspergillus* species were also found to produce cellulases.

2.2.2 *Cellulases from* Trichoderma

Kovacs et al. improved the cellulases production process and developed more efficient enzymes for lignocellulose degradation to reduce the costs of the enzymes required for the biomass to bioethanol process (Kovacs et al. 2009). Lignocellulolytic enzymatic complexes were produced by the mutant *Trichoderma atroviride* TUB F-1663 on three different pretreated lignocellulosic substrates, namely, fir, wheat straw, and sugarcane bagasse. The filter paper activities of the enzymes produced on the three materials were very similar, while β-glucosidase and hemicellulases activities were more dependent on the nature of the substrate. Ahmed et al. produced and partially purified cellulases complex using *T. harzianum* with carbon sources such as glucose, carboxymethylcellulose (CMC), corncobs, birch xylan, and wheat bran (Ahmed et al. 2009). Between cellulases complexes, exoglucanase showed more activity than endoglucanase and glucosidase. *T. harzianum* showed maximum cellulases activity with 1% CMC at 120 °C and pH 5.5 for 120 hours. Under optimal conditions, the enzymes were partially purified by ammonium sulfate precipitation and then by chromatography on Sephadex G-200 and Sephadex G-50 gel. Specific activities were found to be 49.22, 0.63, and 0.35 U/mg, respectively.

Omojasola et al. used sweet orange scrap as a substrate for cellulases production (Omojasola and Jilani 2008). The skin, the fruit wall, and the pulp were treated with

alkali and steam. Next, the pretreated materials were hydrolyzed by cellulolytic enzymes. The cellulases activities of *Trichoderma longi*, *Aspergillus niger*, and *Saccharomyces cerevisiae* were expressed in terms of reducing sugar concentrations and were found to be 3.86, 2.94, and 2.30 mg/mL, respectively. Leghlimi et al. isolated the native cellulolytic fungus *Trichoderma longibrachiatum* (GHL) from the soil near an Algerian hot spring and used it for the production of cellulases by submerged fermentation on Mandel's medium with Avicel cellulose (1%) as single source of carbon (Leghlimi et al. 2013). The endoglucanase and filter paper activities of the wild-type *Trichoderma* strain were compared to hypercellulolytically mutated *Trichoderma reesei* Rut C-30 in shake flask cultures at 35 °C. After 7 fermentation days, *T. longibrachiatum* has activities equivalent to *T. reesei* (10.61 IU/mL endoglucanase (CMCase) and 2.04 IU/mL filter paper activity (FPA)). On the other hand, the β-glucosidase activity of *Trichoderma* GHL was twice as great as that of *T. reesei*.

Boer et al. tested the heterologous expression of *T. reesei* cellobiohydrolase Cel7A in methylotrophic yeast *Pichia pastoris*, both under the *P. pastoris* alcohol oxidase (AOX1) promoter and glyceraldehyde-3-phosphate dehydrogenase (GAP) in a fermenter (Boer et al. 2000). The production of Cel7A with the AOX1 promoter gave a better yield. The k_{cat} and K_m values for the purified protein on soluble substrates are comparable to the values found for native *Trichoderma* Cel7A. The optimum pH measured also closely resembles that of purified *T. reesei* Cel7A. Circular dichroism (CD) measurements indicate that the formation of disulfide bridges is an important step in the correct folding of Cel7A. Van Wyk and Mohulatsi treated different waste materials with the enzyme *Trichoderma viride* cellulases, which convert their cellulosic component into fermentable sugars (Van Wyk and Mohulatsi 2003). All the materials exhibited different susceptibilities for cellulases as well as for the production of non-similar sugar release cartridges as increasing amounts of paper were treated with a solid enzyme concentration. A general decrease in hydrolytic efficiency was observed when sugar concentrations were increased during the biodegradation of all wastes.

In addition to the above scientific literature, *T. atroviride* (Kovács et al. 2008; Kovács et al. 2009), *T. harzianum* (da Silva Delabona et al. 2012; El-Katatny et al. 2001; Maeda et al. 2011), *T. reesei* (Kovács et al. 2009; Krishna et al. 2000; Lee and Koo 2001; Rocky-Salimi and Hamidi-Esfahani 2010; Singhania et al. 2006; Turner et al. 2003), and other *Trichoderma* species have also proved to produce cellulases.

2.2.3 *Cellulases from* Penicillium

Adsul et al. improved the strain of *Penicillium janthinellum* by mutation with ethyl methyl sulfonate for 24 hours and then by UV irradiation for 3 minutes (EMS-UV8) (Adsul et al. 2007). Subsequent mutation and selection led to the isolation of two promising mutants, one selected on the basis of Avicel hydrolysis (EU1) and the other based on the hydrolysis of Walseth cellulose in the presence of 2-deoxy-D-glucose (EU2D-21). All of these mutants produced twice as much FPase and

CMCase activity as the parental strain. Enzymatic preparation derived from Avicel hydrolyzed mutant EU1 to a greater extent. Adsul et al. produced high levels of CMCase and glucosidase from one of the *P. janthinellum* (EU2D-21) mutants on wheat bran (4 g) and wheat bran (3 g) with steam-exploded cane bagasse (2 g) as substrates by fermentation in the solid state (Adsul et al. 2009). The stability of the cellulases prepared from one of the mutants (EMS-UV8) was studied in one of the ionic liquids, 1-butyl-3-methylimidazolium chloride ([bmim] Cl), and revealed that all the enzymes exhibited significant activity at a concentration of 20% ionic liquid.

Belghith et al. studied the thermal stability of *Penicillium occitanis* cellulases (Po16) by spray drying and the effect of additives (Belghith et al. 2001a). The results showed that the CMCase activity assures a good stability at 50 °C, even after 60 hours of incubation. In addition, β-glucosidase activity was more sensitive and showed a 50% loss and reacted to total cellulases activity (FPU). The addition of hydrophilic agents such as ethylene glycol and polyethylene glycol (PEG6000) increased the enzyme activity. The effect of PEG and maltodextrin, another agent reducing the activity of water, was then tested during spray drying of Pol6 cellulases. The presence of 1% PEG provided the best recovery but had a negative effect on the stability of the enzyme, whereas 1% maltodextrin had a negative effect on the recovery of the enzyme but a positive effect on the recovery of the enzyme and its stability. Belghith et al. cultured the mutant *Penicillium occitanis* (Po16), which separated a large amount of cellulases into a fermenter using local paper pulp as an inducing substrate (Belghith et al. 2001b). High extracellular cellulases activity was obtained after batch treatment: 23 IU/mL filter paper, 21 IU/mL CMCase activity (endoglucanase units), and 25 mg/mL protein. This cellulases preparation was applied in a biodegradation process on an industrial scale. The abrasive effect of *P. occitanis* cellulases was very uniform and with comparable efficiency to that obtained commercially.

Camassola and Dillon treated bagasse with sugarcane containing the white rot fungus *Pleurotus sajor-caju* PS 2001 and were then used for the production of cellulases and xylanases by the fungus *Penicillium echinulatum* for saccharification (Camassola and Dillon 2009). Despite the environmental benefits offered by this type of pretreatment, the enzymatic activity obtained with the pretreated sugarcane bagasse (PSCB) was lower than that of the control treatments. Although the enzymatic activities of the culture with PSCB are inferior to those of cultures made with untreated sugarcane bagasse, it should be noted that the production of enzymes from the cellulases and hemicellulases complex after the production of mushrooms is another way to add value to this agricultural residue.

Camassola and Dillon studied the production of cellulases and xylanases from *Penicillium echinulatum* 9A02S1 by solid state fermentation (SSF) with different mass ratios of sugarcane bagasse (SCB) and wheat bran (WB) (Camassola and Dillon 2010). The largest FPase obtained was 45.82 ± 1.88 U/g DS in a culture containing 6 SCB/4 WB on the third day. The most important β-glucosidase activities were 40.13 ± 5.10 U/g DS obtained on the third day for culture at 0 SCB/10 WB. For endoglucanase, the highest activity was 290.47 ± 43.57 U/g DSF for culture 6 SCB/4 WB on the fourth day of culture.

Camassola and Dillon evaluated the production of cellulases and hemicellulases by *Penicillium echinulatum* 9A02S1 of cellulases and hemicellulases with different concentrations of pretreated cane bagasse (PSCB) and wheat bran (WB) (Camassola and Dillon 2007). The highest activities of FPase, β-glucosidase, and endoglucanases were measured at 32.89 ± 1.90, 58.95 ± 2.58, and 282.36 ± 1.23 U/g DS. The inclusion of inexpensive sources in lignocellulosic enzyme production media would help reduce the cost of producing enzyme complexes capable of hydrolyzing lignocellulose residues for the formation of fermented syrups, thereby contributing to the economic production of bioethanol. Camassola et al. characterized *Penicillium echinulatum* cellulases for their FPase and β-glucosidase activities (Camassola et al. 2004). Both activities showed maximum values between pH 4 and 5. The activities were slightly higher in citrate buffer than in acetate buffer with the same pH. The thermal stability of both activities was good at 55 °C. FPase was significantly reduced at higher temperature.

Penicillium brasilianum (Jørgensen and Olsson 2006; Jørgensen et al. 2003; Jung et al. 2015; Krogh et al. 2010; Panagiotou et al. 2006), *P. citrinum* (Dutta et al. 2008; Ng et al. 2010), *P. echinulatum* (Dillon et al. 2011; Martins et al. 2008; Sehnem et al. 2006), *P. funiculosum* (de Castro et al. 2010), *P. janthinellum* (Singhania et al. 2014), *P. purpurogenum* (Davies et al. 2000; Lee and Koo 2001), and other *Penicillium* species also produce cellulases.

2.2.4 Cellulases from Other Genera

In addition to *Aspergillus*, *Trichoderma*, and *Penicillium*, the following organisms have also been considered to produce cellulases:

Amir et al. optimized the pH (3–9), the time (1–7 days), and the temperature (25–40 °C) for maximal enzymatic activity with *Alternaria alternata* with the corncob as a source of carbon by fermentation in the solid state (Amir et al. 2011). *A. alternata* exhibited a maximum cellulases activity of 31.24 μg/mL with 5 g corn at 35 °C and a pH of 6 for 96 hours. Anand et al. produced more cellulolytic enzymes, namely, C_1 and C_x in vitro, virulent isolates of *Colletotrichum capsici*, and *Alternaria alternata* and that the activity of these enzymes increased with increasing age of culture (Anand et al. 2008). Anish et al. used an alkali-stable endoglucanase from the alkalothermophilic society *Thermomonospora* sp. (T-EC) for denim biofinishing (Anish et al. 2007). The current study has shown that the use of acidic and neutral cellulases causes staining back of the indigo dye on the tissue. T-EG is effective at removing hair with negligible weight loss and soft tissue. Higher abrasion activity with lower background staining was a preferred feature for denim biofinishing presented by T-EG. The enzyme was also effective under non-swab conditions, which is an added advantage for use in the textile industry. An enzymatic finishing mechanism of the cotton fabric is presented based on the unique properties of T-EG.

Baba et al. cloned two cDNAs homologous to the rce1 gene of *Rhizopus oryzae*, called mce1 and mce2 cDNAs, from *Mucor circinelloides*, a member of the *Zygomycota* subdivision (Baba et al. 2005). The mcel cDNA encoded an endoglucanase (family 45 glycoside hydrolase) with a carbohydrate-binding module (CBM), called mce1, and the mce2 cDNA encoded the same endoglucanase with two replicate tandem CBMs, called mce2. The specific activity of CMCase of mce2 was almost identical to that of mce1, whereas the specific activity of avicelase of mce2 was twice as high as that of mce1. In addition, mce2, of which two tandem CBMs would be more effective for the degradation of crystalline cellulose than CBM, was excreted only in an early culture phase in which crystalline cellulose was abundant.

Baldrian and Gabriel studied the activities of cellulolytic (endo-1,4-L-glucanase, exo-1,4-L-glucanase, 1,4-L-glucosidase), hemicellulolytic (endo-1,4-L-xylanase, 1,4-L-xylosidase, and 1,4-L-mannosidase), and ligninolytic (Mn-peroxidase and laccase) during growth of *Pleurotus ostreatus* on wheat straw in the presence and absence of cadmium (Baldrian and Gabriel 2003). The activities of endo-1,4-L-glucanase, 1,4-L-glucosidase, and laccase were increased in the presence of cadmium. Boisset et al. examined the digestion of bacterial cellulosic tapes with mixtures of ternary enzymes consisting of recombinant cellulases (two cellobiohydrolases, Cel6A and Cel7A, and the endoglucanase Cel45A) from *Humicola insolens* over a wide range of mixture compositions (Boisset et al. 2001). The degree of digestion was followed by saccharification analysis and transmission electron microscopy (TEM) observations. It has been found that the addition of very small amounts of Cel45A induces a dramatic increase in the saccharification of the substrate with Cel7A or the mixture of Cel6A and Cel7A. But only moderate saccharification resulted from mixing Cel45A and Cel6A.

Bhatti et al. produced β-glucosidase from *Fusarium solani* with agricultural waste using solid state fermentation (SSF) (Bhatti et al. 2013). The optimal β-glucosidase activity of 3206 U/g DS was obtained with a rice husk at pH 5, a 60% moisture content, 65 °C, and a 72-hour fermentation period with the supplemented medium in lactose. Then, the enzyme was partially purified with ammonium sulfate precipitation to give a specific activity of 97.5 U/mg. It was observed that β-glucosidase was thermally stable at 65 °C. β-Glucosidase was subjected to kinetic studies. The K_m and V_{max} values were 1 mM and 55.6 μmol/min, respectively. Mg^{2+} ions increased enzymatic activity. These characteristics suggest that β-glucosidase isolated from *F. solani* can be used in various applications such as textile, paper, biofuel, starch, animal feed, and fruit industries.

Agaricus arvensis (Jeya et al. 2010b), *Alternaria alternate* (Eshel et al. 2002), *Brassica napus* (Mølhøj et al. 2001), *Chaetomium thermophilum* (Li et al. 2003), *Clostridium cellulolyticum* (Desvaux 2005; Guedon et al. 2002; Higashide et al. 2011), *Colletotrichum capsici* (Anand et al. 2008), *Coniophora puteana* (Kajisa et al. 2009; Kajisa et al. 2004), *Coriolopsis caperata* (Deswal et al. 2014), *Fomitopsis palustris* (Deswal et al. 2011; Shimokawa et al. 2008), *Fusarium solani* (Obruca et al. 2012), *Fusarium oxysporum* (Panagiotou et al. 2005; Panagiotou et al. 2003; Ramanathan et al. 2010), *Fusarium chlamydosporum* (Qin et al. 2010), *Gloeophyllum trabeum* (Cohen et al. 2005; Deswal et al. 2014; Niemenmaa et al. 2008), *Humicola*

insolens (Davies et al. 2000; Mariyam 2011), *Humicola grisea* (Nascimento et al. 2010; Takashima et al. 2007), *Kluyveromyces marxianus* (Ballesteros et al. 2004; Pessani et al. 2011; Suryawati et al. 2009; Tomás-Pejó et al. 2009), *Melanocarpus albomyces* (Haakana et al. 2004; Hirvonen and Papageorgiou 2003; Miettinen-Oinonen et al. 2004; Parkkinen et al. 2008; Szijártó et al. 2008), *Mucor circinelloides* (Saha 2004), *Mucor indicus* (Karimi et al. 2006), *Neurospora crassa* (Dogaris et al. 2009; Phillips et al. 2011; Tian et al. 2009), *Paecilomyces inflatus* (Kluczek-Turpeinen et al. 2005), *Phanerochaete chrysosporium* (Martinez et al. 2004; Shi et al. 2008), *Phlebia gigantea* (Niranjane et al. 2007), *Piptoporus betulinus* (Valášková and Baldrian 2006), *Pleurotus ostreatus* (Obodai et al. 2003; Reddy et al. 2003; Taniguchi et al. 2005; Valášková and Baldrian 2006), *Pleurotus florida* (Deswal et al. 2014), *Pleurotus sajor-caju* (Reddy et al. 2003), *Poria placenta* (Highley et al. 2007; Niemenmaa et al. 2008), *Rhizopus oryzae* (Karimi et al. 2006; Murashima et al. 2002; Park et al. 2004), *Saccharomyces cerevisiae* (Den Haan et al. 2007; Karimi et al. 2006; Omojasola and Jilani 2008), *Sporotrichum thermophile* (Dimarogona et al. 2012; Kaur and Satyanarayana 2004), *Thermoascus aurantiacus* (Kalogeris et al. 2003), *Trametes hirsuta* (Jeya et al. 2009), *Trametes versicolor* (Valášková and Baldrian 2006), and other fungi are also reported to produce cellulases.

2.3 Conclusion

Cellulases and cellulolytic microorganisms constitute one of the most important groups of enzymes for industrial applications, as emphasized in this review. They exhibit good catalytic properties which make them versatile. Based on the progress in recent research on fungal cellulases, their applications have been broadened to reduce the costs. There are still many limitations to overcome. One of the problems is the practical feasibility of commercial cellulases. Their complex nature and the downstream processing stages result in the low yield of cellulases. The utilization of residues from agro-industrial residues as substrates can improve their applications. Also, various microorganisms used to produce fungal cellulases, mechanism of cellulolytic action, cheap substrates used for enzyme production, and the industrial applications were emphasized.

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