Chapter 10
Biotechnological Applications of β-Glucosidases in Biomass Degradation

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10.1 Introduction

Cellulose, the chief chemical constituent of primary cell walls, forms the most abundant group of carbohydrates produced by plants. For example, the cellulose content forms ~90% in cotton fibres, 40–50% in wood and approximately 57% in dried hemp. In contrast to starch, cellulose is an unbranched linear polymer of D-glucose units linked by β(1→4) glycosidic linkages between C#1 of one glucose and C#4 of the next glucose (Shahzadi et al. 2014). In fact, it is these beta linkages present between the monomer units that enable the formation of long, rigid chains of cellulose microfibrils that bear numerous intra- and intermolecular hydrogen bonds. The chains are oriented in parallel and form highly ordered, crystalline domains that are responsible for high tensile strength of plant cell walls (Beguin and Aubert 1994; Shahzadi et al. 2014). In nature, cellulose is degraded mainly by fungi and bacteria. The degradation of cellulose to glucose molecules is catalysed by the synergistic activity of three individual enzymes (Fig. 10.1): *endoglucanase* (1,4-β-D-glucan hydrolase, EC 3.2.1.4), *exoglucanase* (1,4-β-D-glucan glucohydrolase EC 3.2.1.74) and *β-glucosidase* (β-D-glucoside glucohydrolase EC3.2.1.21) (Dashtban et al. 2010; Tiwari et al. 2013; Seo et al. 2013; Lambertz et al. 2014). Exoglucanases, also known as *cellobiohydrolase*, hydrolyse cellulose polymers from the ends releasing mainly cellobiose, a disaccharide consisting of two β-glucose molecules. Endoglucanases hydrolyse glucosidic bonds at random positions in cellulose chains to generate oligosaccharide chains of different length, also

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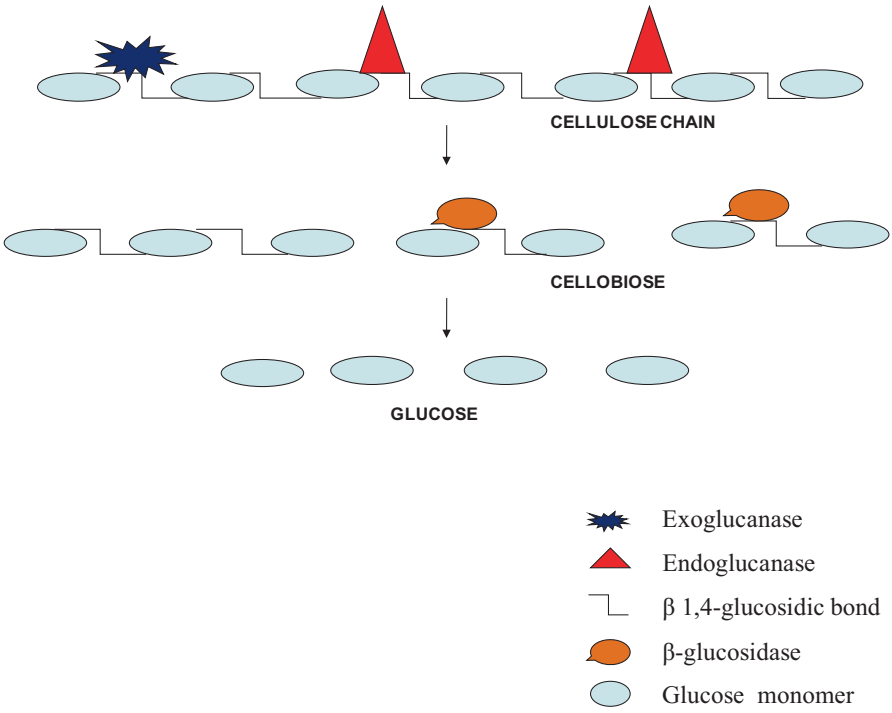

Fig. 10.1 Cellulose degradation by the synergistic action of endoglucanase, exoglucanase and β-glucosidase

producing new sites to be attacked by exoglucanases. Finally, β-glucosidase breaks down cellobiose and short oligosaccharides into glucose units (Kumar et al. 2008; Sukumaran et al. 2005). In other words, in the enzymatic hydrolysis of cellulose, endoglucanases and exoglucanases are responsible for degrading cellulose to cellobiose, after which β-glucosidases hydrolyse cellobiose to free glucose molecules. In this process, the step catalysed by β-glucosidases is generally the rate-limiting step and hence is responsible for the regulation of the entire cellulose degradation process. This inhibition is mainly caused due to the inhibitory effects by cellobiose on both endoglucanase and exoglucanase activities (Bok et al. 1998; Kruus et al. 1995).

The most widely accepted system of classification of β-glucosidases is based on their nucleotide sequence identity (NCI) and hydrophobic cluster analysis (HCA). In this system, enzymes with overall amino acid sequence similarity and well-conserved sequence motifs are placed in a family (Henrissat 1991; Cairns and Esen 2010). According to the data collected in June 2018, 153 glycoside hydrolase (GH) families are listed in Carbohydrate Active enZYme website (http://www.cazy.org). This is the most widely accepted classification, and β-glucosidases are placed in glycoside hydrolase (GH). Most of the β-glucosidases are reported in GH1, GH3, GH5, GH9, GH30 and GH116 families. HCA system of classification is believed to reflect structure, evolutionary relationship and catalytic mechanisms of this

enzyme (Cairns and Esen 2010). β-Glucosidases belonging to GH family 1 are mainly reported from archaebacteria, plants and animals, whereas β-glucosidases belonging to GH family 3 are from bacteria, fungi and yeast.

β-Glucosidases could also be classified on the basis of substrate specificity into three classes: aryl-β-glucosidases that hydrolyse only aryl-β-glucoside linkage, cellobiases that hydrolyse only disaccharides and broad substrate specificity β-glucosidases that hydrolyse wide range of substrates with different bonds such as β(1→4), β(1→3), β(1→6), α(1→4), α(1→3) and α(1→6) (Singh et al. 2016).

Cellulose recycling forms an important part of the carbon cycle in biosphere, as it is the major carbohydrate synthesised by plants. As mentioned above, this degradation process is brought about by the synergistic activity of a series of enzymes, where the terminal steps catalysed by β-glucosidases form the rate-limiting step. Consequently, the entire cellulolytic process is limited by the activity of this enzyme. Hence, an increased understanding of the factors affecting β-glucosidase activity would promote efficient conversion of the otherwise abundant cellulose into the much needed biofuels and other economically important products. With this objective in mind, the authors have tried to present an overview of β-glucosidase enzyme and its biotechnological applications, followed by major rate-limiting components and possible solutions for large-scale conversion of lignocelluloses into ethanol.

10.2 Sources of β-Glucosidases

β-Glucosidases are a class of hydrolytic enzymes produced by various organisms, ranging from microorganisms to higher plants and animals. Wood-degrading organisms like termites and wood-decomposing fungi have been generally targeted by the researchers for isolating cellulolytic enzymes (Sanderson 2011). Among plants, β-glucosidases have been well characterised from *Arabidopsis thaliana*, rice, cherry, wheat, sorghum and maize (Tiwari and Verma 2017; Sue et al. 2006; Dharmawardhana et al. 1995; Seshadri et al. 2009; Kittur et al. 2007). Some of the in-planta functions of β-glucosidases include chemical defence, plant–microbe interactions, cell wall remodelling, alkaloid metabolism and phytohormone regulation (Seshadri et al. 2009; Singh et al. 2016).

However, for industrial production of β-glucosidases, fungi are the best source due to several advantages like high yield, fast growth, cost-effectiveness, etc. (Kour et al. 2019b; Yadav et al. 2015, 2016a, b, 2017b, 2019a, b). Many fungi such as *Trichoderma reesei* (Chen et al. 1992), the filamentous fungus *Acremonium persicinum* (Pitson et al. 1997), *Aspergillus oryzae* (Riou et al. 1998), *Thermoascus aurantiacus* (Parry et al. 2001), *Chaetomium thermophilum* (Venturi et al. 2002), *Penicillium purpurogenum* (Karnchanatat et al. 2007), *Daldinia eschscholzii* (Kaur et al. 2007), *Melanocarpus* sp. MTCC 3922 (Chen et al. 2012), *Neocallimastix patriciarum* W5 (Daroit et al. 2008), *Monascus purpureus* and brown-rot basidiomycete *Fomitopsis palustris* (Yoon et al. 2008) produce β-glucosidase (Tables 10.1 and 10.2). In addition, this enzyme has recently been produced from *Penicillium*

Table 10.1 Large-scale production methods of β-glucosidases from fungi

Fungal species	Fermentation method	References
Tolypocladium cylindrosporum Syzx4	Submerged fermentation (SMF)	Bai et al. (2013)
Penicillium simplicissimum H-11	Submerged fermentation	Elyas et al. (2010)
Aspergillus strain SA 58	Solid-state fermentation (SSF)	Ng et al. (2010)
Penicillium citrinum YS40-5	Solid-state fermentation	Bhatti et al. (2013)
Fusarium proliferatum	Submerged fermentation	Gao et al. (2012)
Fusarium solani	Solid-state fermentation	Raza et al. (2011)
Aspergillus niger + *A. oryzae*	Solid-state fermentation	Vaithanomsat et al. (2011)
Fomitopsis palustris	Submerged fermentation	Yoon et al. (2008)
Aspergillus niger SOI017	Submerged fermentation	Qian et al. (2012)
Flammulina velutipes	Submerged fermentation	Mallerman et al. (2015)
Monascus sanguineus	Solid-state fermentation	Dikshit and Tallapragada (2015)
Phoma sp. KCTC11825BP	Submerged fermentation	Choi et al. (2011)
Thermomucorindicae-seudaticae N31	Solid-state fermentation	Ling et al. (2011)
Aspergillus niger HDF05	Solid-state fermentation	Cassia et al. (2015)
Gongronella butleri	Solid-state fermentation	Ling et al. (2011)
Penicillium miczynskii	Submerged fermentation	Beitel and Knob (2013)
Fusarium oxysporum	Submerged fermentation	Santos et al. (2016)
Aureobasidium pullulans	Submerged fermentation	Saha et al. (1994)
Candida peltata	Submerged fermentation	Olajuyigbe et al. (2016)
Kluyveromyces marxianus	Submerged fermentation	Rajoka et al. (2004)
Aureobasidium sp.	Solid-state fermentation + submerged fermentation	Saha and Bothast (1996)
Saccharomyces cerevisiae	Submerged fermentation	Iembo et al. (2002)

purpurogenum KJS506, *Phoma* sp. KCTC11825BP (Choi et al. 2011), *Aspergillus fumigatus* Z5 (Liu et al. 2012), *Penicillium italicum* (Park et al. 2012), *Fusarium proliferatum* NBRC109045 (Gao et al. 2012), *Aspergillus saccharolyticus* (Sorenson et al. 2014), *Aspergillus niger* A20 (Abdel-Naby et al. 1999), *Fusarium solani* (Bhatti et al. 2013), *Flammulina velutipes* (Mallerman et al. 2015), *Monascus sanguineus*, *Sporothrix schenckii* (Hernández et al. 2016), *Gongronella butleri* (Santos et al. 2016) and *Fusarium oxysporum* (Olajuyigbe et al. 2016). The fungal species, *Aspergillus niger*, is the major source of commercial β-glucosidase under the name of Novazym188 (Sorenson et al. 2013).

β-Glucosidase has been identified, purified and characterised from several bacterial species as well, such as *Clostridium thermocellum* (Ait et al. 1982), *Pyrococcus furiosus* (Kengen et al. 1993), *Bacillus circulans* subsp. *Alkalophilus* (Paavilainen et al. 1993), *Flavobacterium johnsoniae* (Okamoto et al. 2000), actinomycete *Thermobifida fusca* (Spiridonov and Wilson 2001), *Lactobacillus brevis* (Michlmayr et al. 2010), *Caldicellulosiruptor saccharolyticus* (Hong et al. 2009)

Table 10.2 Optimum physical parameters for industrial production of β-glucosidases from microbial sources

Microorganisms	Preferred carbon source	Preferred nitrogen source	Preferred temp.	Preferred pH	References
Aspergillus niger	Wheat bran	Ammonium sulphate	30 °C	5.5	Raza et al. (2011), Vaithanomsat et al. (2011)
Penicillium purpurogenum	Sucrose	Sodium nitrate	28 °C	4.0	Jeya et al. (2010), Jeya and Lee (2013)
Candida peltate	Glucose and xylose	–	50 °C	5.0	Saha and Bothast (1996), Rajoka et al. (2004)
Fusarium proliferatum	Corn stover and wheat bran	Urea	25 °C	5.0	Gao et al. (2012)
Chaetomium thermophilum	Cellulose	Peptone, yeast extract	45 °C	5.5	Venturi et al. (2002)
Aspergillus protuberus	Glucose	Ammonium sulphate	30 °C	3.0	Yadav et al. (2016a, b)
Penicillium citrinum	Maltose	Ammonium sulphate	70 °C	5.0	Ng et al. (2010)

and *Terrabacter ginsenosidimutans* (An et al. 2010). *Thermoanaerobacterium thermosaccharolyticum* is known to produce a glucose-tolerant β-glucosidase (Pei et al. 2012).

10.3 Biotechnological Applications of β-Glucosidases

The use of cellulases in biotechnology began in the early 1980s in animal feed and food industry (Chesson 1987; Thomke et al. 1980). Subsequently, these enzymes were used in textile, laundry as well as in pulp and paper industries (Godfrey et al. 1996; Wong and Saddler 1992). Today, β-glucosidases are also used for production of biofuels, detoxification of cassava cyanogenic glucosides and in the treatment of Gaucher's disease (Cairns and Esen 2010; Prasad et al. 2012). The catalytic activity of β-glucosidases include hydrolysis of β(1–4), β(1–3), β(1–6) and β(1–2) glucosidic linkages in aryl-, amino-, or alkyl-β-D-glucosides, cyanogenic glucosides, and disaccharides, polysaccharides and glucose-substituted molecules. Apart from hydrolysis of sugars, some mutant β-glucosidases have been reported to catalyse synthetic reactions of sugars by reverse hydrolysis and transglycosylation (Mackenzie et al. 1998). Due to the diverse types of reactions and substrates of β-glucosidases, they have several industrial applications, some of which have been described below.

10.3.1 Conversion of Lignocellulose into Biofuels

Lignocellulose refers to the woody parts of plants, mainly agricultural residues like wheat stems, corn stalks and leaves, and forestry wastes like wood shavings from logging. The lignocellulose, which is generally considered to be 'plant waste' and discarded, could be converted into energy sources. These so-called second-generation biofuels have many advantages in comparison to first-generation biofuels that were derived mainly from food crops (Sanderson 2011; Guo et al. 2015; Prasad et al. 2014; Rastegari et al. 2019; Prasad et al. 2019; Yadav et al. 2017a, 2018). Apart from being a renewable and sustainable way of energy production, the bioconversion of lignocellulose into ethanol has an additional advantage of solving the problem of waste disposal of agricultural residues and other biomass (Khan et al. 2018, 2019). Lignocelluloses, chemically made up of cellulose, hemicellulose and lignin, which when converted into fermentable sugars, could be used to produce liquid fuels like ethanol or oil and gaseous fuels like biogas and electricity (Menon and Rao 2012; Prasad et al. 2009, 2013; Kour et al. 2019a; Rana et al. 2019a, b). Briefly, the lignocellulose is first subjected to heat and acid or ammonia to separate lignin, thereby exposing cellulose and hemicelluloses. Thereafter, the combined action of exoglucanase, endoglucanase and β-glucosidases converts this polymer into glucose sugar, which could then be fermented to give rise to ethanol or the longer chain alcohol butanol. The pentose and hexose obtained after cellulose degradation could be fermented to ethanol by the action of yeast and certain enzymes. The preferred physical conditions required by some of the commonly used microbial sources of β-glucosidases for lignocelluloses degradation are mentioned in Table 10.2.

The bioconversion of lignocellulose involves two steps: hydrolysis of cellulose in lignocellulosic biomass to produce reducing (fermentable) sugars, and fermentation of the sugars to ethanol (Sun and Cheng 2002). An outline of steps involved in biomass degradation is presented in Fig. 10.2. Briefly, plant parts are first cut into small size by either milling or chipping, followed by a *pre-treatment* step using either physical or chemical agents. The pre-treatment step mainly disrupts the close inter-component association between main constituents (cellulose, hemicellulose, lignin) of the plant cell wall (Jönsson and Martín 2016). Some of the most commonly used pre-treatment methods include acid hydrolysis with mineral acids/organic acids, steam heating followed by sudden decompression, hydrothermal processing and oxidative methods (Jonsson and Martin 2016). These methods basically aim to remove hemicelluloses and/or lignin from the lignocellulosic matrix, thereby facilitating the subsequent enzymatic degradation of cellulose to D-glucose.

Together, endoglucanases, exoglucanases and β-glucosidases make a potent system for cellulose degradation. These three enzymes could be present either as multienzymatic complex called cellulosome or exist as individual enzymes (Bae et al. 2013). Being the terminal enzyme in cellulose degradation pathway, β-glucosidases play a critical role in this process (Bhatia et al. 2002). If β-glucosidases are not present in sufficient amounts, not enough glucose will be produced, and cellobiose will

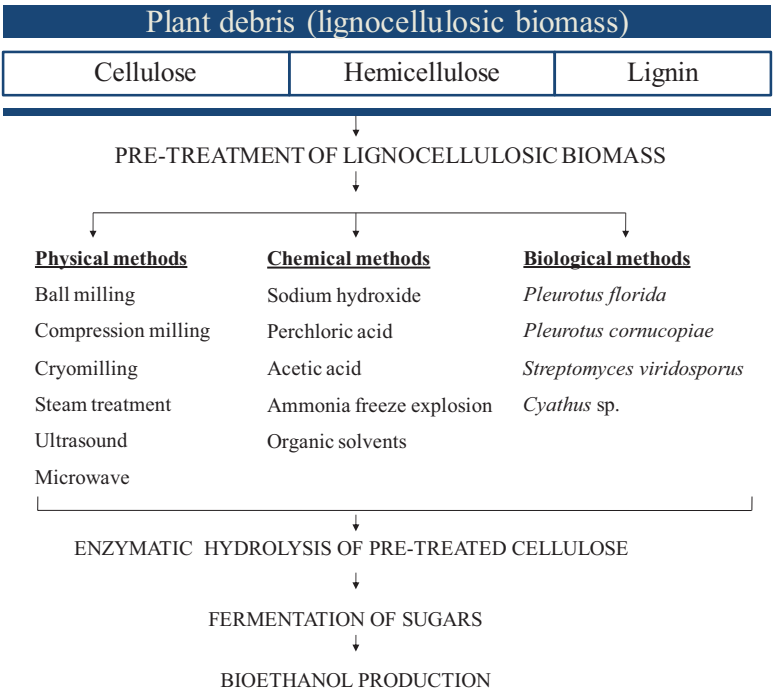

Fig. 10.2 Various steps involved in degradation of plant biomass. The pre-treatment of lignocellulosic biomass could be done either by physical, chemical or biological methods. Subsequently, the plant biomass is subjected to cellulase degradation to convert cellulose to sugars, which could be fermented to yield ethanol

accumulate. Since cellobiose is an inhibitor of endo- and exoglucanases, this would negatively affect glucose formation, making it the rate-limiting step of the pathway (Dekker 1986). Therefore, the activity of β-glucosidase could be regulated to increase the efficiency of conversion of cellulose to glucose (Dashtban et al. 2010; Lambertz et al. 2014). This aspect has been dealt with in detail in the next section on 'Challenges in Lignocellulose Bioconversion'.

10.3.2 Production of High-Value Bioproducts

Apart from ethanol, which forms the primary product of lignocellulose degradation, the by-products could be used to generate a number of organic chemicals. For example, the fermentation of hexoses and pentoses obtained after cellulose degradation could be used to produce lactic acid by using the bacteria, *Bacillus coagulans* (Patel et al. 2006). Likewise, the lignocelluloses conversion of palm waste produces

xylose, which could be further processed to form xylitol, a sweetening agent (Rahman et al. 2007). Another by-product, furfural, obtained from hydrolysis of hemicelluloses, is reported to be used in plastic, varnishes and herbicide preparation (Montane et al. 2002).

10.3.3 Hydrolysis of Isoflavone Glycosides

Phenolic compounds like flavonoids, flavonones, flavones and isoflavones form a class of secondary metabolites in plants that have antioxidant, anticancerous, antiallergic, anti-inflammatory and antihypertensive properties (Kabera et al. 2014; Karimi et al. 2012; Servili et al. 2013). Majority of these metabolites are present in the form of glycosides, which increase their water solubility and stability, but limit their absorption. The release of non-carbohydrate part requires the action of specific enzymes such as arabinosidases and β-glucosidases. For example, daizdin, genistin and glycitin are some of the glucosidic isoflavones in soybean and soy (a soybean-based food), which are generally found in an inactive state. Aglycone forms of these isoflavones, produced by β-glucosidases, exhibit phytoestrogenic properties and hence are useful in the treatment of various diseases like prostate cancer, breast cancer, cardiovascular disease and menopause treatment (Izumi et al. 2000; Hati et al. 2015). The different microbial sources of β-glucosidases for the hydrolysis of isoflavone or flavonoid compounds are represented in Table 10.3.

10.3.4 Flavour and Nutrition Enhancement

In plants, flavour compounds generally occur in the form of glycoconjugates, in order to suppress the flavour and make them non-volatile. The β-glucosidase enzyme releases the glycoconjugate form of flavour compounds, thereby imparting the unique flavour to plants. For example, β-glucosidase isolated from *Sporidiobolus pararoseus* and *Aureobasidium pullulans* have been found to hydrolyse terpenyl glycosides and improve aroma of wines (Baffi et al. 2013). Likewise, it has also been reported to improve the organoleptic properties and reduce the bitterness of citrus fruit, which is caused by the glucosidic compound, naringin (Roitner et al. 1984). β-Glucosidase isolated from *Bacillus subitilis* is used for improving sugarcane juice quality (Singh et al. 2016) by immobilising it on alginate beads for industrial production. β-Glucosidases could also be used in the release of some nutritionally important components, such as vitamins and antioxidants from their glycoside-conjugated form. For example, vitamin B_6 of rice could be released from pyridoxine glucoside form by the application of β-glucosidase (Opassiri et al. 2004).

Table 10.3 β-Glucosidases with the ability to hydrolyse flavonoid compounds

Source of β-glucosidase	Flavonoid glycoside	Product	Biological activity	References
L. acidophilus LA-5	Delphinidin-3-glucoside, malvidin-3-glucoside	Gallic, Syringe homogentisic acid	Antioxidant	Ávila et al. (2009)
Paecilomyces thermophila J18	Daidzin, genistin, glycitin	Genistein, Daidzein, Glycitein	Anticancer, osteoporosis, antihypercholesterolaemia	Yang et al. (2009)
Thermoanaerobacter ethanolicus JW200	Daidzin, genistin	Genistein, Daidzein	Anticancer, antipostmenopausal syndrome	Song et al. (2011)
Pseudomonas ZD-8	Genitin and daidzin	Genistein, Daidzein	Anticancer, osteoporosis, etc.	Yang et al. (2004)
Bacillus subtilis 18	Genistin and daidzin	Genistein, Daidzein	Anticancer, osteoporosis, etc.	Kuo et al. (2006), Kuo and Lee (2007)
Gongronella sp.	Daidzin and genistin	Daidzein, Genistein,	Anticancer, osteoporosis	Fang et al. (2014)
Saccharomyces cerevisiae HJ014	Ginseng	Ginsenoside Rd, F2 Compound K (CK)	Anti-inflammatory, anti-cancer, anti-aging, antioxidant activities	Choi et al. (2014)
Paecilomyces bainier sp. 229	Ginsenoside Rb1	Compound K	Tonic, adaptogenic, immunomodulatory, anti-aging effects	Yan et al. (2008)
*Mucilaginibacter*s	Protopanaxatriol-type ginsenoside mixture (PPTGM)	(S)-Rh1 (S)-Rg2	Antineoplastic, antistress, antioxidant activities	Cui et al. (2013)
Paenibacillus sp. KB0549	2,6-O-di(β-D-glucopyranosyl)-β-D-glucopyranosylsesaminol (STG)	Sesaminol	Antioxidants	Nair et al. (2013)
Pyrococcus furiosus	Hesperidin, neohesperidin, naringin, poncirin, diosmin, neoponcirin, rutin	Hesperetin, Hesperetin, Haringenin, Naringenin, Quercetin, Rutinose	Antiallergic, antioxidant, anti-inflammatory, antihypertensive	Shin et al. (2013)
Bifidobacterium bifidum	Daidzin, genistin	Daidzein, Genistein	Anticancer, osteoporosis, antihypercholesterolaemia	You et al. (2015)
Bacteroides thetaiotaomicron VPI-5482	Daidzin, genistin, glycitin	Daidzein, Genistein, Glycitein	Anticancer, osteoporosis, antihypercholesterolaemia	Byun et al. (2015)
Aspergillus terreus	Daidzin, genistin, glycitin	Daidzein, Genistein, Glycitein	Anticancer, osteoporosis, antihypercholesterolaemia	Yan et al. (2016)

10.3.5 Detoxification of Cyanogenic Glycosides in Cassava

Cassava is a carbohydrate-rich food and a source of food for ~500 million people in the world. Cassava fruit contains cyanogenic glycosides like linamarin and lotaustralin, which have been reported to cause Konzo syndrome, a human central nervous system disorder (Vasconcelos et al. 1990). Although certain glucosidases are naturally present in cassava roots, their insufficient expression leaves a significant part of the cyanogenic glycosides in the processed food. Therefore, an additional treatment of cassava with β-glucosidases has the potential of detoxifying and liberating these cyanogenic glycosides, thereby improving its nutritional quality (Gueguen et al. 1997; Maduagwu 1983).

10.3.6 Deinking of Waste Paper

Waste paper causes environmental pollution; its recycling can solve the two-dimensional problem of forest wood consumption and waste management. Removal of ink from paper is the most challenging obstacle, which could be overcome by using enzymes. The enzymatic method for waste paper recycling has been reported to be efficient in solving this problem. The enzyme preparations for waste paper recycling contain cellulase, β-glucosidase and hemicellulase (Prasad et al. 1992; Pathak et al. 2011; Lee et al. 2013).

10.3.7 Applications Based on Synthetic Activity

Apart from the hydrolytic activity, β-glucosidases also exhibit synthetic activity (through reverse hydrolysis and transglycosylation), leading to the production of oligosaccharides and alkyl and aryl β-glucosides (Ahmed et al. 2017). Alkyl glucosides like hexyl, heptyl and octyl glucosides are biodegradable and, therefore, find wide applications as emulsifier and antimicrobial agents (Bankova et al. 2006). Synthetic glucosides are also used in the preparation of therapeutic drugs like heparin and acarbose. They act as probiotic agents and increase the number of useful microorganisms in human gut. Some of the in-planta functions of these oligosaccharides include fertilisation, embryogenesis and cell proliferation (Singh et al. 2016; Krisch et al. 2010). Galacto-oligosaccharides and isobutyl-galactosides are synthesised from lactose in water-organic media by the action of β-glucosidase produced by *Aspergillus oryzae* (Bankova et al. 2006). Arbutin-β-glycoside was found to be synthesised via the transglycosylation reaction of β-glucosidase produced by *Thermotoga neapolitana* to manufacture a skin whitening agent, and these products were checked for their melanogenesis inhibitory activities (Jun et al. 2008).

10.4 Challenges in Lignocellulose Bioconversion

10.4.1 Complex Structure of Plant Biomass

The primary challenge in lignocellulose conversion to fermentable sugars is its complex structure: constituting approximately 33–40% of cellulose, 20–25% of hemicellulose and 15–20% of lignin (Hess et al. 2011). Although cellulose is a simple homopolysaccharide composed of D-glucose residues, the linear cellulose microfibrils are associated with several hydrogen bonds that make the macromolecule highly crystalline and difficult to hydrolyse (Jørgensen et al. 2007). In addition, cellulose exists in complex with hemicelluloses, the heterogenous polysaccharides composed of variety of sugars, making it difficult to be converted into a single product, ethanol. In addition, the cellulose and hemicellulose are complexed with lignins, which form extensive cross-linking, making it resistant against microbial degradation.

10.4.2 Inhibition of Enzyme Activity Due to Pre-treatment Methods

The pre-treatment of lignocellulosic biomass is often required to promote the subsequent step of enzymatic conversion of cellulose to sugars (Jørgensen et al. 2007). This step is basically aimed at removal of hemicelluloses and/or lignin from the lignocellulosic matrix A drawback of the pre-treatment step is formation of by-products like carboxylic acids, gluconic acid and glucaric acid, phenolic compounds, furfurals, benzoquinones, etc. that inhibit downstream processes by interfering with microbial activity (Jönsson and Martín 2016). For example, acid hydrolysis of lignocellulose results in corrosion of pre-treatment equipment and release of heavy metal ions like copper, nickel, chromium and iron, which can be inhibitory to fermenting microorganisms (Watson et al. 1984; Garrote et al. 2008).

10.4.3 End-Product Inhibition

End-product inhibition is a method of negative feedback regulation, where the final product in a series of reactions inhibits an enzyme from an earlier step in the sequence. The product binds to an allosteric site of the enzyme and temporarily inactivates the enzyme via non-competitive inhibition. This mode of regulation is also seen in enzyme-mediated lignocellulose degradation. The enzymes, cellobiohydrolase and β-glucosidase, are subjected to end-product inhibition by cellobiose and glucose, respectively (Qing et al. 2010; Teugjas and Väljamäe 2013; Kumar and Wyman 2014). This limits the turnover number of these enzymes, leading to

decline in product formation. This problem gets adverse when lignocellulosic degradation is performed at high solid concentrations in order to reduce the consumption of water and running cost of the process (Kristensen et al. 2009).

10.4.4 Other Challenges

In addition to the above limitations, the activity of cellulases could also be inhibited by non-productive binding to lignins and residual hemicelluloses (Rahikainen et al. 2013; Pareek et al. 2013). Other factors limiting plant biomass degradation include relatively low activity of currently available hydrolytic enzymes, high cost of enzyme production and thermal inactivation of enzyme (Sun and Cheng 2002). The optimum fermentation conditions vary with species and other controlling parameters like source of carbon and nitrogen used in media. The carbon source may contain some contaminants in the form of secondary metabolites and chemicals that can interfere with the rate of β-glucosidase enzyme production. Therefore, a thorough screening of these secondary metabolites/inhibitors and their subsequent degradation or inactivation is crucial for the optimum enzyme production. Research should also be focused on the possibility of temperature stress on the yield and activity of β-glucosidase. Thermal inactivation of β-glucosidase is a major roadblock towards achieving high enzyme efficiency. The thermal stability of β-glucosidases could be enhanced by recombinant DNA technology and genetic modification of microbial strains. Precise genome editing using site-specific nucleases like CRISPR/Cas9 is a suitable option to achieve this goal. The other major hurdles in the commercial β-glucosidase production are product inhibition, low product yields and high cost of enzyme production. The search for better alternatives to the currently available enzyme preparations should be highly promoted. Isolation of novel fungal species having higher β-glucosidase activity would contribute towards revolutionising the field of lignocellulose-mediated production of biofuels.

10.5 Approaches for Enhancing β-Glucosidase Activity

Researchers are trying to engineer cellulases with high specific activity, high thermal stability, high adsorption capacities, high catalytic efficiency and lower end-product inhibition. Some of the major limitations in cellulase- or β-glucosidase-mediated biomass degradation have been addressed by using approaches like increasing the production of β-glucosidase through strain improvement by *mutagenesis*, *co-cultivation* of microbes in fermentation to increase the quantity of desirable components of cellulase complex, improving the performance of existing lignocellulose-degrading enzymes by *genetic engineering*, and finally, *metagenomics approach* that involves identification of novel β-glucosidases by DNA analysis of environmental samples. These approaches have been described below.

10.5.1 Co-culturing

As mentioned above, cellulose degradation requires synergistic action of three enzymes: exoglucanase, endoglucanase and β-glucosidase; however, no native microbial strain produces optimum amounts of all three enzymes under the same condition. For instance, while *T. reesei* produces exoglucanase and endoglucanase in abundant amounts, it produces β-glucosidase in very low amounts (Peterson and Nevalainen 2012). Likewise, *Aspergillus niger* produces large quantity of β-glucosidase, but limited amount of exoglucanase and endoglucanase (Stockton et al. 1991; Kumar et al. 2008). Therefore, co-cultivation of *T. reesei* and *A. niger* using paper mill sludge as a cellulosic substrate has proven to be a solution for efficient hydrolysis of cellulosic residues (Maheshwari et al. 1994). Other successful cases include co-culturing *Aspergillus ellipticus* with *A. fumigatus* (Gupte and Madamwar 1997) and *T. reesei* with *A. phoenicis* using bagasse and corncobs as cellulose substrate in solid-state fermentation (Duenas et al. 1995). Different strains of *Trichoderma* fungus are used for production of beta glucosidase and are represented in Table 10.4.

Table 10.4 Studies done on β-glucosidase isolated from different strains of *Trichoderma*

Trichoderma strain	β-Glucosidase	Isolation strategies	References
T. citrinoviride	Extracellular β-glucosidase	Protein purification, biochemical and proteomic characterisation	Chandra et al. (2013)
T. reesei	TrBgl2	Mutational studies involving active site residues of the enzyme	Lee et al. (2012)
T. reesei QM9414	bgl1	Overexpression of bgl1 from *Periconia* sp. in *T. reesei* QM9414 under *T. reesei* tef1 promoter	Dashtban and Qin (2012)
Recombinant *T. reesei* strain, X3AB1	bgl1	Construction of *T. reesei* strain expressing *Aspergillus aculeatus* bg1 under control of xyn3 promoter	Nakazawa et al. (2012)
T. reesei	bgl I	Molecular cloning and expression in *Pichia pastoris*	Chen et al. (2011)
T. reesei CL847	BGL1	Protein purification and kinetic characterisation	Chauve et al. (2010)
T. reesei	β-Glucosidase (cel3a)	Molecular cloning and expression in *T. reesei*	Murray et al. (2004)
T. ressei	β-Glucosidase BGLII (Cel1A)	Molecular cloning, expression in *E. coli* and characterisation	Saloheimo et al. (2002)
T. harzianum C-4		Protein purification and biochemical characterisation	Yun et al. (2001)
T. reesei	BGL2	Molecular cloning and expression in *Aspergillus oryzae*	Takashima et al. (1999)
T. harzianum strain P1	1,3-β-Glucosidase	Protein purification and characterisation	Lorito et al. (1994)
T. reesei QM9414	Aryl-β-D-glucosidase	Protein purification and characterisation	Chirico and Brown (1987)
T. viride	β-Gluc I	Protein purification and biochemical characterisation	Beldman et al. (1985)

10.5.2 Genetic Manipulation

Genetic engineering approach involves introduction of specific desirable genes from one species to another species using recombinant DNA technology (Sticklen 2008). This strategy could be used to generate novel β-glucosidases with desirable properties like high efficiency, thermotolerance and high specificity for plant biomass degradation (Blumer-Schuette et al. 2014). *T. reesei*, the most commonly used source of cellulases, being mesophilic loses its enzyme activity at higher temperatures. Transformation of thermotolerant β-glucosidase genes into *T. ressei* from thermophilic fungus like *T. emersonii* was found to confer higher specific activity and temperature tolerance of up to 71.5 °C (Dashtban and Qin 2012; Druzhinina and Kubicek 2017). Similar results were obtained in *Paenibacillus polymyxa* where single amino acid substitution contributed increased thermal resistance (Garvey et al. 2013). Apart from targeting β-glucosidase, chimeric proteins have been constructed by the fusion of endoglucanase from *Acidothermus cellulolyticus* and exoglucanase from *T. reesei*, which resulted in improved saccharification (Chandel et al. 2012).

Another attractive option of increasing cellulase production is to express cellulase from heterologous systems (Garvey et al. 2013). This involves codon optimisation, use of strong and inducible promoters and elimination of inhibitory sequences to enable efficient protein expression from heterologous systems. Cellulases were originally produced from anaerobic bacteria isolated from animal digestive systems (Chandel et al. 2012). In addition, recombinant systems like *E. coli* and *Bacillus subtilis* are being increasingly used for protein production because of the increased enzyme yields from these systems. Apart from bacterial expression hosts, yeasts like *Saccharomyces cerevisiae*, *Pichia pastoris* and *Kluyveromyces marxianus* have been employed due to its superior post-translational modification of secreted proteins (Tanaka et al. 2012).

10.5.3 Mutagenesis

The inherently low β-glucosidase activity of *T. reesei* has been improved by mutagenesis through the use of chemical mutagens and UV radiations. The *T. reesei* RUT-C30 mutant was reported to produce 4–5 times higher β-glucosidase than wild *T. reesei* (Montenecourt and Eveleigh 1979). In another study, *T. atroviride* were modified through mutagenesis by the use of N-methyl-N′-nitro-N-nitrosoguanidine and UV light, and these mutants were found to have high cellulolytic activity than wild types (Kovacs et al. 2008). Apart from random mutagenesis through the use of physical and chemical mutagens, site-directed mutagenesis has also been used to enhance cellulase activity. In one of the study, Mahadevan et al. (2008) altered the amino acids around the active site of endoglucanase of *Thermotoga maritima* creating a mutant which displayed 10% higher activity than the wild-type enzyme. Similarly, mutation of the conserved residue F476 to Y476 from Cel9A of

Thermobifida fusca displayed 40% improved cellulase activity. This was achieved through the integration of computer modelling with site-directed mutagenesis (Escovar-Kousen et al. 2004).

10.5.4 Metagenomics Approach

A relatively recent approach involves analysis of DNA collected from environmental samples, enabling identification and quantification of microbial species that inhabit the natural environment. Metagenomics of microbial communities from cow rumen (Hess et al. 2011), termite hindgut (Warnecke et al. 2007) and mangroves (Simões et al. 2015) have provided detailed insights into the diversity of lignocellulose-degrading enzymes through the identification of uncultivable bacteria. Bergmann et al. (2014) have isolated two novel β-glucosidases from soil of Amazon forest. In addition, new genes could be discovered that encode novel lignocellulolytic enzymes.

10.5.5 Other Strategies for Enhancing Lignocellulose Degradation

One of the simple ways to prevent end-product inhibition of lignocellulose degradation is continuous elimination of end-products through sophisticated reactor designs (Andric et al. 2010). Another method to relieve end-product inhibition is simultaneous saccharification and fermentation, a process in which fermenting microorganism is added along with hydrolytic enzymes (Teugjas and Väljamäe 2013). This prevents accumulation of cellobiose and glucose in the reaction mixture that may interfere or inhibit cellulase activity. This method, however, has a major drawback that different conditions are required for optimal hydrolysis and fermentation. While the optimum temperature for yeast fermentation is approximately 35 °C, the optimum temperature of ~50 °C is optimal for cellulase activity. This issue could be addressed by the use of thermostable enzymes involved in fermentation of sugars, produced after cellulose hydrolysis, into ethanol.

10.6 Conclusion and Future Perspectives

The first-generation biofuels, obtained primarily from food crops such as grains, sugar beet and oil seeds, have raised a number of concerns in terms of food security, climate change mitigation, economic growth and sustainability. Most of these concerns could be addressed through the use of second-generation biofuels that involve

the use of non-food biomass like cereal straw, bagasse, forest residues and other lignocellulosic materials. This would also serve as an attractive alternative for disposal of non-edible portions of plants. However, compared with the production of ethanol from food crops, the use of lignocellulosic biomass is more complicated because the polysaccharides are more stable and the pentose sugars are not readily fermentable by *Saccharomyces cerevisiae*. Several biotechnology-based approaches are being used to overcome such problems, including the development of microbial strains, use of alternative yeast species that naturally ferment pentose sugars and the engineering of enzymes that are able to break down cellulose and hemicellulose into simple sugars. Many fungal species are reported to produce various isoforms of β-glucosidases. Thus, it is of utmost importance to screen the best yielding isoform for a particular species. In addition, the thermal stability of β-glucosidases could be enhanced by recombinant DNA technology and genetic modification of microbial strains. Precise genome editing using site-specific nucleases like CRISPR/Cas9 is a suitable option to achieve this goal. The other major hurdles in the commercial β-glucosidase production are product inhibition, low product yields and high cost of enzyme production. The search for better alternatives to the currently available enzyme preparations should be highly promoted. Isolation of novel fungal species having higher β-glucosidase activity would contribute towards revolutionising the field of lignocellulose-mediated production of biofuels. To conclude, the lignocellulosic biomass holds a large potential to meet the energy needs of the world without compromising food security.

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