Chapter 4
The Current Biotechnological Status and Potential of Plant and Algal Biomass Degrading/Modifying Enzymes from Ascomycete Fungi

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1 Introduction

Plant and algal biomass are main substrates for various industries and have become even more in the spotlight, with the global push toward a sustainable biobased society and economy. The main fraction of both types of biomass are their cell walls that mainly consist of various polysaccharides. Depending on the desired end product, processing the biomass requires modification of these polysaccharides or partial or complete degradation of them to their monomeric building blocks. Fungal enzymes play a critical role in these processes (Bischof et al. 2016; de Vries et al. 2016; Kruger et al. 2018; Mäkelä et al. 2014b). Fungi produce a high diversity of enzymes targeting these polysaccharides (de Vries et al. 2017; de Vries and Visser 2001; Rytioja et al. 2014; Vesth et al. 2018), making them highly suitable sources of industrial enzymes. In fact, fungal enzymes make up more than half of the enzymes currently used in industrial applications (Fig. 4.1), demonstrating that they are the enzyme source of choice for many applications.

In this chapter, we will discuss the use of plant and algal biomass active enzymes from ascomycete fungi in relation to their current and potential applications. The plant biomass section is structured based on the type of application. However, due to the less well-established applications of algal biomass, this section is not structured based on application but rather by type of algae.

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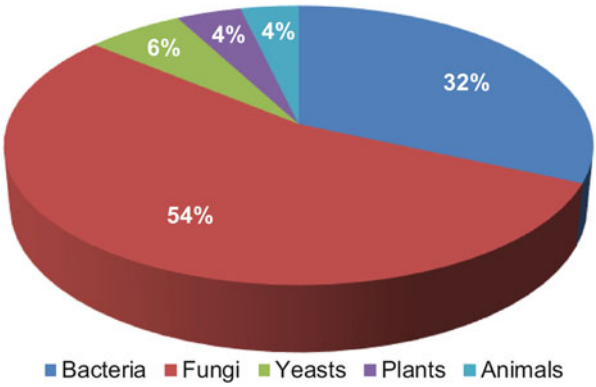

Fig. 4.1 Division of commercial enzymes used in biotechnological applications according to the organism they originate from. Based on AMFEP (2015) List of commercial enzymes. Association of manufacturers and formulators of enzyme products. http://www.amfep.org/list.html

2 Applications of Fungal Plant Biomass Degrading and Modifying Enzymes

2.1 Applications in Food and Feed Production

Fungi and fungal enzymes have been used in production of food for centuries, such as in fermentation, baking, and food modification (Table 4.1; Fig. 4.2) (Beppu 2000; Buchholz and Collins 2013). Enzymes produced by ascomycete fungi, specifically *Aspergillus* spp. and *Trichoderma reesei*, are used as food ingredients, additives, or processing aids (Table 4.2). Enzymatic processing of food has distinct advantages over traditional chemical-based technology, in that there is less waste and by-products, less energy consumption, and decreased environmental impact (James and Simpson 1996; Meyer 2010; Sharma et al. 2017). The food industry utilizes fungal enzymes for modification of products, rather than their full degradation. To this end, researchers have been able to engineer and produce very specific recombinant proteins/enzymes that cleanly carry out the required modifications, in large enough quantities to be used in industry.

2.1.1 Bread and Baking

Bread baking using baker's yeast is one of the oldest biotechnological processes in the world. In modern times, the bread industry faces several challenges: how to decrease preparation time, increase the staling time of the product, and reduce flour variability, to ensure a product that is consistent in size, texture, and taste (Dahiya and Singh 2019). To this end, various combinations of enzymes from fungi are often employed and more importantly have replaced chemical additives. The effectiveness of these enzyme combinations is significant (Martinez Anaya and Jimenez 1997). The strains producing these enzymes have been genetically modified to improve the production yield and decrease costs.

Table 4.1 Overview of the roles of fungal enzymes in industrial applications

Enzyme	Function	Industry	Applications	Reference
Xylanases	Degradation of water-insoluble (arabino)xylan to its soluble form by cleaving the main chain of the polysaccharide	Baking	Improvement of rheological properties of dough and bread Manufacture of lighter cream crackers, with an improved texture, palatability, and uniformity	Delcour et al. (1991), Michniewicz et al. (1991), de Queiroz Brito Cunha et al. (2018), Camacho and Aguilar (2003), Maat et al. (1992), Polizeli et al. (2005)
		Wine production	Improvement of wine aroma	Ganga et al. (1999)
		Beer production	Used in release of fermentable sugars from starch, the carbohydrate storage in grain before fermentation Hydrolysis of arabinoxylans in barley cell wall, which results in decreased beer viscosity and muddiness	Polizeli et al. (2005)
		Animal feed	Treatment of fiber in grains to release nutrients trapped inside macromolecules, producing a high energy, easily digestible food mixture for animals	Polizeli et al. (2005), Cafe et al. (2002)
		Prebiotics	Production of xylo-oligosaccharides and arabinoxylooligosaccharides, by-products of xylan metabolism, for improvement of gut microbiota	Aachary and Prapulla (2011), Kumar et al. (2018), Gullon et al. (2014), Courtin et al. (2008)
		Paper and pulp production	Improvement of pulp brightness and thickness, by improving chemical extraction of lignin from pulp without compromising cellulose	Ferreira et al. (2016), Walia et al. (2017), de Vries and Visser (2001)
Lipases	Degradation of lipids, releasing fatty acids	Baking	Production of free fatty acids that increase strength of gluten protein network	Monfort et al. (1999)
			Stabilization of gas cell structure in bread, resulting in better loaf volume and crumb structure	Gerits et al. (2014)
		Paper and pulp production	Control of pitch	Singh and Mukhopadhyay (2012), Gutiérrez et al. (2009), Farrell et al. (1997)
		Biodiesel production	High production yields and easier downstream purification steps	Gog et al. (2012), Mohamed and Bornscheuer (2003), Adachi et al. (2011)

(continued)

Table 4.1 (continued)

Enzyme	Function	Industry	Applications	Reference
α-Amylase	Degradation of starch by hydrolyzing α-1,4 glycosidic bonds, resulting in short-chain dextrins	Baking	Increase in dough mobility, enhancing taste, crust color and toasting qualities of bread	Vandam and Hilde (1992), van der Maarel et al. (2002)
			Release of fermentable sugars that increase yeast activity, resulting in a bigger bread loaf	Martinez Anaya and Jimenez (1997)
		Juice clarification	Removal of starch, thus preventing accumulation with pectins and proteins, removing haze	Dey and Banerjee (2014)
		Animal feed	Increase in energy derivation from feed for chickens and pigs, by degradation of starch in grain and grain by-products	Gracia et al. (2003)
		Pulp and paper production	Production of starch with improved properties (e.g., lower viscosity, higher molecular weight) for paper coating and improvement of the writing quality of paper	de Souza and de Oliveira Magalhães (2010)
		Detergent industry	Used along with lipases, proteases, cellulases, and cutinases, to increase the efficiency of detergents	Belhaj et al. (2010), Kirk et al. (2002), Singh et al. (2016b)
Proteases	Weakening of gluten structure by breaking down its peptide bonds	Baking	Regulation of gluten structure in dough that improves dough viscoelastic properties, resulting in decreased mixing times, easier use with machinery, and better bread crumb quality	Deng et al. (2016)
		Beer production	Modification of proteins in grain for nutrition of yeast used in brewing	Polizeli et al. (2005)
			Improvement of beer flavor, mouth feel, foam, and color	Polizeli et al. (2005)
Pectinase	Hydrolysis of glycosidic bonds in pectic polymers	Juice extraction	Degradation of pectin that cross-links cellulose and hemicellulose, allowing action of cellulases. Enhancement in the pressing of pulp, resulting in increased juice yield, improved filterability, and reduction in viscosity	Sharma et al. (2017), Ramadan (2019)

		Juice clarification	Reduction of electrostatic repulsion that causes proteinaceous flocculants to aggregate, making them easier to remove	Kashyap et al. (2001)
		Jams, preserves, and jellies	Production of commercial pectin as a by-product of juice extraction and clarification, after treatment of fruit with pectinases	BeMiller (2019), Wang et al. (2013)
		Wine production	Improvement of clarity as well as flavor and color intensity of wine post fermentation, via extraction of anthocyanins, tannins, and phenolic compounds	Kashyap et al. (2001), Garg et al. (2016), Villettaz (1993)
		Coffee production	Removal of mucilaginous coat from coffee beans	Hoondal et al. (2002), Murthy and Naidu (2011)
		Tea production	Pretreatment of tea leaves, in extraction, and in treatment of extract: breakdown of pectin in tea leaf cell wall	Uzuner (2019)
			Reduction of formation of foam on instant tea	Hoondal et al. (2002)
		Paper and pulp production	Reduction of the amount of energy required to remove the bark from the wood	Rättö and Viikari (1996)
Cellulases	Degradation of cellulose into glucose, through the combined action of exoglucanases, endoglucanases, and β-glucosidases	Juice extraction and clarification	Extraction and clarification of fruit and vegetable juices, to produce nectar and purees	Danalache et al. (2018)
		Wine production	Used at grape crushing stage	Kashyap et al. (2001)
			Improvement of wine clarity after fermentation	Villettaz (1993)
		Beer production	Reduction of wort viscosity	Ben Hmad and Gargouri (2017)
			Hydrolysis of glucan, improving filterability	Ben Hmad and Gargouri (2017)
		Coffee production	Removal of mucilaginous coat from coffee beans	Hoondal et al. (2002)
		Tea production	Pretreatment of tea leaves, extraction, and treatment of extract	Uzuner (2019)
			Enhancement of green tea aroma, taste, flavor, and cold-water solubility	Uzuner (2019)
		Biofuel and biochemical production	Complete hydrolysis of the lignocellulosic material for bioethanol production	Dilokpimol et al. (2016), Prasanna et al. (2016), Araujo Silva et al. (2018)

(continued)

Table 4.1 (continued)

Enzyme	Function	Industry	Applications	Reference
β-Glucosidase	Breakdown of glucose oligosaccharides into simple sugars	Wine production	Release of volatile compounds (like terpenes) bound to glycoside fractions in grape skin and juice, resulting in improvement of wine aroma	Francis et al. (1998), Baffi et al. (2013)
		Bioethanol production	Involvement in the final step of cellulose saccharification	Singhania et al. (2013), Benoit et al. (2015)
β-Glucanase	β-Glucan degradation	Animal feed	Breakdown of β-glucans found in barley and oats to improve feed digestibility	Ojha et al. (2019)
Laccases	Cross-link of monomers, degradation of polymers, and ring cleavage of aromatic compounds	Beer production	Improvement of beer stability and shelf life	Osma et al. (2010)
			Removal of chill haze by elimination of polyphenols	Osma et al. (2010)
		Juice clarification, wine production, baking	Removal of undesirable phenolic compounds	Osma et al. (2010)
		Paper and pulp production	Pulp delignification process and elimination of lipophilic extractives known as pitch depositions	Singh et al. (2016a)
		Textile industry	Decolorization of the textile dye indigo	Campos et al. (2001)
			Generation of the stoned-washed look of denim	Pazarlıoğlu et al. (2005)
		Other industrial applications	Production of chromatographic resins, coatings, and adhesives	Mäkelä et al. (2017)
		Leather processing	Use in mixtures during leather processing, along with proteases, amylases, and lipases	Thanikaivelan et al. (2004), Singh et al. (2016b)
Phytases	Degradation of phytic acid	Animal feed	Improvement in absorption/utilization of phosphorus	Ojha et al. (2019), Singh and Satyanatayana (2014)
			Reduction in soil and water contamination by surplus of phosphorus excretion by monogastric animals	Ojha et al. (2019); Singh and Satyanatayana (2014)

α-Galactosidase	Hydrolysis of terminal α-galactosyl moieties from glycolipids and glycoproteins	Animal feed	Removal of raffinose and stachyose via pretreatment with α-galactosidase, to improve digestibility and nutritional uptake	Katrolia et al. (2014)
β-Mannanases	Degradation of mannan	Animal feed	Improvement of feed that results in better digestion and reduction in flatulence in pigs	Kim et al. (2006b), Wu et al. (2005)
			Improvement of feed, resulting in better growth/immunity and higher egg production in chickens	Kim et al. (2006b), Wu et al. (2005)
		Coffee production	Degradation of coffee mannan, in both partially purified and immobilized forms, as well as a soluble crude preparation, resulting in easy concentration of coffee bean extracts by evaporation	Sachslehner et al. (2000), Chauhan et al. (2012)
		Prebiotics	Production of glycomannan, a by-product of mannan digestion, used as prebiotics that have beneficial effects on gut microbiota	Mikkelson et al. (2013)
Feruloyl esterases	Removal of ferulic acid residues and cross-links from polysaccharides	Animal feed	Improvement of access of main chain degrading enzymes, resulting in better digestion and uptake of nutrients	Dilokpimol et al. (2016)
		Biofuel and bio-chemical production	Complete hydrolysis of the lignocellulosic material for bioethanol production	Dilokpimol et al. (2016)
		Pharmaceutical and industrial chemical production	Production of hydroxycinnamic acids during lignin depolymerization that are important in food and cosmetic industries due to their antioxidant and photoprotective properties	Dilokpimol et al. (2016)
			Production of ferulic acid (antidiabetic, antiaging, and anticancer properties), which is important for pharmaceutical companies	Singh et al. (2016b)
			Production of ferulic acid as a precursor of vanillin	Gallage and Moller (2015), Singh et al. (2016b)

(continued)

Table 4.1 (continued)

Enzyme	Function	Industry	Applications	Reference
Tannase	Catalysis of ester and disulfide bonds in hydrolyzable tannins or gallic acid esters, to release glucose or gallic acid	Tea production	Decrease in binding of tea catechins to proteins in tea, reducing aggregation and precipitation during tea storage	Ni et al. (2015)
			Reduction of bitterness, resulting in improved quality and taste and mouth feel of green teas	Chavez-Gonzalez et al. (2012)
			Decrease of insoluble forms of tea cream that result from polyphenols, reducing tea turbidity	Hoondal et al. (2002)
Inulinase	Hydrolysis of the glycosidic linkages in inulin to produce fructose, glucose, and inulooligosaccharides	Production of useful by-products for pharmaceutical industry	Production of inulin-derived fructooligosaccharides (FOS) and inulooligosaccharides (IOS), which are also of great pharmacological value due to their health-promoting properties	Chi et al. (2009)

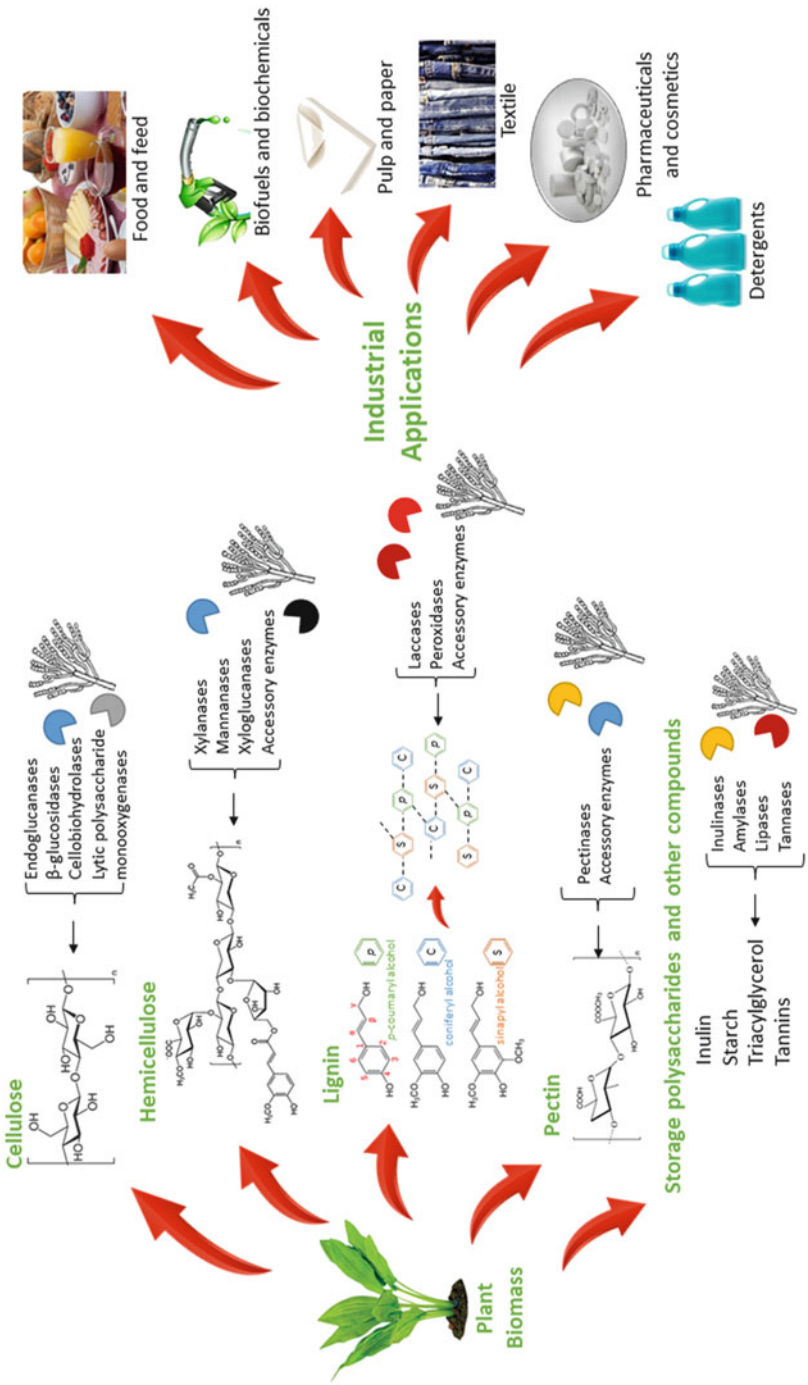

Fig. 4.2 Schematic presentation of the use of fungal enzymes for the conversion of plant biomass in various industrial areas

Table 4.2 Overview of the industrial applications of plant biomass degrading enzymes from ascomycete fungi

Enzyme type	Enzymes	Fungal origin	Industrial applications	References
Cellulases	Glucanases	*T. reesei* *T. harzianum* *A. oryzae* *A. niger* *Aspergillus* sp. *P. roqueforti* *Penicillium* sp. *Thermoascus aurantiacus* *N. crassa*	Food industry Animal feed Textile industry Biofuel production Detergents	Paramjeet et al. (2018) Kaur and Gupta Phutela (2017) Dagaris et al. (2009) Belghith et al. (2001) Singh et al. (2016a, b) Danalache et al. (2018)
	β-Glucosidase	*A. oryzae* *A. niger* *F. oxysporum* *P. roqueforti* *Penicillium* sp. *T. reesei* *T. harzianum* *N. crassa*		
	Cellobiohydrolases	*T. reesei*		
Hemicellulases	Xylanases	*A. niger* *Aspergillus* sp. *Penicillium* sp. *T. reesei* *T. harzianum* *Bispora* sp. *P. roqueforti* *N. crassa* *Talaromyces* sp.	Biofuel production Pulp and paper industry Food industry Animal feed Textile industry	Polizeli et al. (2005) Kim et al. (2006a, b) Rasmussen et al. (2006) Luo et al. (2009) Maitan-Alfenas et al. (2016) Paramjeet et al. (2018) Kaur and Gupta Phutela (2017) Dagaris et al. (2009) Araujo Silva et al. (2018) de Queiroz Brito Cunha et al. (2018)
	Mannanases	*T. reesei*		

(continued)

Table 4.2 (continued)

Enzyme type	Enzymes	Fungal origin	Industrial applications	References
Oxidoreductases	Laccases	*T. harzianum* *A. niger* *Aspergillus* sp.	Bioremediation Adhesives and coatings Pulp and paper industry Food industry Biofuel production Pharmaceutical applications Textile industry Leather industry	Savitha et al. (2009) Campos et al. (2001) Osma et al. (2010) Pazarlıoğlu et al. (2005) Singh et al. (2016b) Rodriguez Couto and Toca Herrera (2006)
	Glucose oxidases	*Aspergillus* sp. *Penicillium* sp.		
Esterases	Feruloyl esterases (FAEs)	*Aspergillus* sp. *F. oxysporum* *P. chrysogenum*	Biofuel production Pulp and paper industry Pharmaceutical applications Food industry Animal feed Cosmetics Detergents	Dilokpimol et al. (2016) Singh et al. (2016b) Rättö and Viikari (1996) Polizeli et al. (2005) Sandri and da Silveira (2018)
	Pectinases	*A. niger* *Aspergillus* sp. *Penicillium* sp. *Bispora* sp. *T. harzianum* *Fusarium* sp.		
Hydrolases	Lipases	*Geotricum* sp. *Aspergillus* sp. *Candida* sp. *Penicillium* sp.	Detergents Biofuel production Pharmaceutical applications Food industry Animal feed Pulp and paper industry Bioremediation Leather industry Textile industry	Chi et al. (2009) Singh et al. (2016b) Yang et al. (2017) Vandam and Hilde (1992) Ni et al. (2015) Adrio and Demain (2014) Chen et al. (2013)
	Cutinases	*Fusarium* sp. *B. cinerea* *A. niger* *A. nidulans* *A. oryzae* *Penicillium* sp.		
	Inulinases	*Aspergillus* sp. *Penicillium* sp.		
	Amylases	*Aspergillus niger* *Aspergillus* sp. *Penicillium* sp.		
	Tannases	*Aspergillus* sp.		
	Proteases	*Aspergillus* sp. *Penicillium* sp. *Fusarium* sp.		

The presence of xylans and arabinoxylans has been shown to affect dough properties and bread quality (Delcour et al. 1991; Michniewicz et al. 1991). The correct balance of water extractable pentosans and water unextractable solids is critical in bread making to achieve the desired properties of the resulting loaf. Xylanases are enzymes that catalyze degradation of (arabino-)xylans and are commonly produced by filamentous fungi. Xylanases break down water-insoluble arabinoxylan to its soluble form by cleaving the main chain of the polysaccharide, which results in a redistribution of water to gluten. This facilitates better gluten coagulation, which improves the rheological properties of bread, such as the volume of the loaf, the uniformity of bread crumb structure, and shelf life (de Queiroz Brito Cunha et al. 2018). The stickiness of the dough is also reduced, ensuring that it does not stick to the machine parts (Camacho and Aguilar 2003; Maat et al. 1992).

In bread making, xylanases act together with other enzymes (α-amylase, malting amylase, glucose oxidase, and protease) to improve the consistency, elasticity, and softness of the dough. For example, bread produced using baker's yeast expressing recombinant lipase 2 from a *Geotrichum* species resulted in a higher loaf volume and a more uniform crumb structure than control (Monfort et al. 1999). Lipases act on lipids in flour, releasing fatty acids that partition to the gluten protein network, increasing its strength, which allows for better dough making. Fatty acids also stabilize the gas cell structure while baking, resulting in better bread load volume and crumb structure (Gerits et al. 2014).

Addition of α-amylase affects the properties of dough, such as structure, as well as dough viscosity, ensuring ease of handling (Vandam and Hilde 1992). α-Amylases degrade starch by hydrolyzing α-1,4 glycosidic bonds, resulting in short-chain dextrins, which in bread baking enhances taste, crust color, and toasting qualities of the resulting bread (van der Maarel et al. 2002). α-Amylases (e.g., from *Aspergillus oryzae*) act on damaged starch, reducing its ability to immobilize water, thus increasing dough mobility, resulting in better dough handling. In addition, the enhanced production of fermentable sugars via amylase activity increases yeast growth and thus its ability to produce carbon dioxide, leading to larger loaves (Martinez Anaya and Jimenez 1997). The appropriate concentration of this enzyme ensures the proper rising of dough; e.g., the combined expression of *Aspergillus nidulans* endoxylanase and *A. oryzae* α-amylase showed a significant improvement in loaf volume and density, possibly due to a synergistic interaction (Monfort et al. 1996).

Proteases from fungi (e.g., *Aspergillus usamii*) have been shown to improve the viscoelastic properties of dough, resulting in decreased mixing times, easier use with machinery, and better bread crumb quality. They do this by weakening the gluten structure, and hence softening it, via breaking down its peptide bonds, and they are used primarily to regulate gluten structure in dough (Deng et al. 2016).

Biscuits are also subject to various treatments with fungal enzymes. Xylanase, for example, is used in biscuit dough and results in lighter cream crackers, with an improved texture, palatability, and uniformity (Polizeli et al. 2005). Similarly, the addition of proteolytic enzymes as well as other hemicellulases also improves these qualities of biscuits, crackers, and waffles.

2.1.2 Juice Clarification

Natural juice produced from the edible portion of fruits, generally extracted by pressure or other mechanical means, is turbid, bitter, and viscous and has a tendency to develop haze due to a high concentration of pectin. Pectic substances make up about 0.5–4% of ripe fruit, and these are released in the liquid phase as cloudy particles when fruit tissue is ground, making the resulting juice viscous and pulpy (Kashyap et al. 2001). Other contributors to juice cloudiness are cellulose, starch, proteins, tannins, and lignins. Commercial production of fruit and vegetable juices requires extraction, clearing, and stabilization to ensure a consistent and palatable product. To this end, macerating enzymes are used to process fruit juice for less pulp, haze, and consistency, although standardization of this process can be difficult due to the broad variability in the specific quantities of pectin, hemicellulose, and cellulose each fruit has (Grassin and Fauquembergue 1996). Therefore, it is important to choose the right enzyme combination depending on the fruit composition and the desired final product. Juice clarification and extraction are carried out using a combination of pectinases, xylanases, mannanases, cellulases, and amylases, resulting in improved yield, stabilization of fruit pulp, reduction of viscosity, and clearing of juice (Polizeli et al. 2005).

Pectins are polymers of D-galacturonic acid, which are commonly found in cell walls of plants. To process pectin in juices, pectinases from *A. niger* are commonly used, which have been produced either in submerged or solid-state cultivation (Sandri and da Silveira 2018; Sandri et al. 2011). Pectinases are a complex family of enzymes that hydrolyze glycosidic bonds in pectic polymers and can be broadly divided into esterases, which catalyze the de-esterification of pectin by the removal of methoxyl and acetyl esters, and depolymerases, which consists of different groups depending if they act on pectin, polygalacturonic acid, or rhamnogalacturonan. Depolymerases can be either hydrolases or lyases, breaking the glycosidic bond by two different mechanisms, introducing water across the oxygen bridge or lysis by trans-elimination, respectively.

In the fruit juice industry, acidic pectinases are used in extraction and clarification of sparkling clear juices from apples, pears, and grapes, as well as the cloudy juices, sourced from prunes, citrus fruits, and tomatoes (Sharma et al. 2017). Pectinases can be used in both extraction and clarification of juice, resulting in enhanced coloring and concentrated juice flavor. During mechanical extraction, fruits with a high level of pectin are treated with pectinases, degrading the pectin that cross-links cellulose and hemicellulose, allowing (hemi-)cellulases to act on these substrates. This improves pressing of pulp and results in an increase in the juice yield, improved filterability, and reduction in viscosity, as has been shown in grape, peach, pear, plum, and apricot (Ramadan 2019). Pectinases also aid with juice clarification by degrading the negative charge carrying pectin, that forms a coat around the positively charged proteins, causing them to repel each other. The degradation of pectin reduces the electrostatic repulsion, causing the flocculants to aggregate, making them easier to remove (Kashyap et al. 2001).

Cellulases are enzymes that degrade cellulose into glucose, through the combined action of exoglucanases, endoglucanases, and β-glucosidases. These enzymes are used to extract and clarify fruit and vegetable juices, to produce nectar and purees (Danalache et al. 2018). Xylanases and other hemicellulases, e.g., from *Aspergillus* sp. and *Trichoderma* sp., are also used in combination with cellulases for clarifying juices.

Other potential contributors to turbidity in juices are starch and arabinans (side chains from pectin). These make juices difficult to filter, foul membranes, promote gelling after juice concentration, and contribute to post-concentration haze (Dey and Banerjee 2014). Starch can be removed from juice at the same time as pectin, using amylases, which prevent starch molecules from accumulating with pectins and proteins, thus eliminating haze.

2.1.3 Modification of Pectin in Jams

Pectin is used to generate water-soluble galacturonoglycan preparations of varying methyl ester contents and degrees of neutralization that are capable of forming gels (BeMiller 2019). It is this property of pectins that is harnessed to form spreadable gels, like jams, jellies, marmalade, and preserves. High methoxyl pectins are used to make jams, either by rapid gelation (to prevent settling of fruit pieces) or slower gelation (in preparation of jellies that allow for the escape of air bubbles) (BeMiller 2019). Commercial pectin is obtained as a by-product of juice extraction and clarification, after the treatment of fruit with pectinases. Pectin acetylesterase is an enzyme that catalyzes the transacylation reaction between pectin molecules, which was shown to be feasible to make fruit jam with a reduced sugar content (Wang et al. 2013).

2.1.4 Production of Wine/Beer/Beverages

The production of wine is similar to fruit juice, in that grapes have a high pectin content that makes them difficult to press. Enzymes are used for wine clarification, color extraction, and protein stabilization (Uzuner 2019). Enzymatic treatment also reduces gelling and hazing of grape juice as wine is being prepared. Enzymes from fungi like *A. niger*, *Penicillium notatum*, or *Botrytis cinerea*, including pectinases, cellulases and hemicellulases, are used during all three stages of wine production: the crushing stage, the free run juice stage prior to fermentation, and after fermentation is complete (Kashyap et al. 2001). At the crushing stage, commercial enzyme preparations are used to macerate the berries and increase the juice yield, reducing also the pressing time (Villettaz 1993). Because the maceration step releases colloidal substances into the juice, the second stage is a clarification step, where suspended particles settle along with undesirable microorganisms. Addition of pectinases after wine fermentation increases clarity (Kashyap et al. 2001).

Some enzyme preparations have been reported to increase the color intensity/stability and flavor of wines. For example, treatment with pectinases post fermentation increases the extraction of anthocyanins and tannins, phenolic compounds that increase the flavor and color intensity of wine (Garg et al. 2016). A xylanase (XlnA) from *A. nidulans* was used to make wine with a more pronounced aroma (Ganga et al. 1999).

β-Glucosidase is an enzyme that breaks down glucose oligosaccharides into D-glucose. In wine making, volatile compounds like terpenes are bound to glycoside fractions derived from grape skin and juice. These are released when these fractions are enzymatically treated (Francis et al. 1998). For example, β-glucosidase from *Aureobasidium pullulans* has been shown to improve wine aroma (Baffi et al. 2013). An important aspect of red wine making is color extraction. Addition of enzyme cocktails with a broad range of activities, including hemicellulases, cellulases, and pectinases, during the extraction process, give the best results (Villettaz 1993).

The most important enzymes for malting and brewing of beer are amylases, proteases, peptidases, β-glucanases, and xylanases. These enzymes have several roles in the production of beer and malted liquor, primarily in fermentation, control of viscosity, and chill proofing (protection of beer clarity/brightness at low temperatures). The first stage of fermentation requires the release of fermentable sugars from starch, the carbohydrate storage in grain, which is achieved by adding amylases, xylanases, and β-glucanases. During mashing and primary fermentation, cellulases are added to reduce the viscosity of wort and hydrolyze glucan, which improves the filterability (Ben Hmad and Gargouri 2017). In addition, proteins in grains are essential for nutrition of the yeast used in brewing, as well as for flavor, mouth feel, foam, and color, and are therefore modified using proteases and peptidases. Xylanases are also used to hydrolyze arabinoxylans that are released when the cell wall of barley is hydrolyzed, which results in decreased beer viscosity and muddiness (Polizeli et al. 2005).

Laccases are enzymes found in fungi, plants, insects, bacteria, and archaea that belong to the blue multicopper oxidases. Laccases cross-link monomers, degrade polymers, and carry out ring cleavage of aromatic compounds (Shraddha et al. 2011). In food industry, laccases are used to eliminate undesirable phenolic compounds, including for baking, juice processing, and wine stabilization. In beer making in particular, laccases not only improve beer stability but also increase its shelf life (Osma et al. 2010). Chill haze occurs when proteins are precipitated at low temperatures, stimulated by small quantities of naturally occurring proanthocyanidins polyphenols. Addition of laccase at the end of the brewing process removes this haze effect, by removing the polyphenols.

2.1.5 Animal Feed

Feed ingredients for pigs and poultry can contain indigestible components, because the animal does not produce the proper endogenous enzymes to digest them. To ensure maximum uptake and efficiency, immunological health of the animals, and a

good feed conversion ratio (the ratio of the weight of feed consumed to the weight gained by the animal), enzymes are used to increase the availability of essential nutrients. Treatment with enzymes either produces nutrients by hydrolysis or liberates nutrients blocked by these fibers, increasing their absorption (Hoondal et al. 2002). In addition, these enzyme cocktails can reduce unwanted residues in excreta and thus protect the environment (Polizeli et al. 2005). Usually these enzymes complement what is already present in the gut of the animals. There are four main categories of enzymes that are used in the feed sector: enzymes targeting phytates, enzymes targeting viscous cereals like triticum, enzymes targeting nonviscous cereals like maize and jowar, and enzymes targeting noncereals/legumes (Ojha et al. 2019). Combinations of xylanases with other enzymes like glucanases, pectinases, cellulases, proteases, amylases, phytase, galactosidases, and lipases help with processing grain to highly digestible feed for animals.

Fiber is a major component of plant-based material. Xylanases are used in the treatment of fiber in animal feed, acting on arabinoxylan and its by-products, found in grains (Polizeli et al. 2005). In its soluble form, arabinoxylan can increase the viscosity of ingested feed, leading to mobility issues and less efficient uptake of nutrients. The addition of xylanase can help to produce a high energy, better digestible food mixture, by releasing nutrients trapped inside macromolecules and improving the access of digestive enzymes to their substrate. A commercial preparation, Avizyme, consisting of xylanase, protease, and amylase, was added to poultry feed, and it was shown that birds raised on this feed obtained higher net energy (Cafe et al. 2002). Along with xylanase, β-glucanase is the other major fiber-digesting enzyme used for feed production, which acts on β-glucans found in barley and oats. Taken together, these enzymes act on the cell walls and release nutrients from grain endosperm and the aleurone layer of cells. Starch in grain and grain by-products is degraded by α-amylases, increasing the energy derivation from feed for chickens and pigs. This results in an improved pork/chicken and egg production (Ojha et al. 2019). For example, an α-amylase-treated corn/soybean diet improved the nutritional digestibility of broilers, as well as their performance (Gracia et al. 2003).

Phytic acid is a form of organic phosphorus found in plant-derived food like cereals, legumes, soybean, and others. It is not available to nonruminants such as pigs, poultry, and humans, because their gastrointestinal tracts lack phytase. Phytic acid chelates important metal ions that are required for digestive enzymes to work, thus inhibiting their activity. Phytases added to feed prior to animal consumption improve the absorption/utilization of phosphorus and also decrease the contamination of soil and water by the surplus of phosphorus excretion by monogastric animals (Ojha et al. 2019; Singh and Satyanatayana 2014).

Nonruminant animals lack α-galactosidase, which hydrolyzes the terminal α-galactosyl moieties from glycolipids and glycoproteins (Ademark et al. 2001). In order to process the high amount of soybean meal that is present in feed, pretreatment with α-galactosidase to remove raffinose and stachyose can improve digestibility and nutritional uptake (Katrolia et al. 2014).

Meal supplements high in mannan can result in indigestion and sticky droppings in chickens and flatulence in pigs, because pigs cannot digest mannans or manno-

oligosaccharides. When the high mannan containing feed is treated with β-mannanases, broiler chickens showed improved body weight, and pigs showed reduced flatulence (Kim et al. 2006b; Wu et al. 2005). The use of mannanases in feed has shown improved utilization of nutrients, higher egg production, better growth and immunity, as well as improved digestibility and reduced uric acid in poultry. Similar effects were also seen in fish and goats (Wu et al. 2005).

Feruloyl esterases are responsible for removing ferulic acid residues and cross-links from polysaccharides. Feruloylation in foraging feed can inhibit the ruminant digestive system. Addition of feruloyl esterases (in an enzyme cocktail) improves the access of main chain degrading enzymes, resulting in better digestion and uptake of nutrients (Dilokpimol et al. 2016).

2.1.6 Tea and Coffee

The polysaccharide fraction of green coffee beans consists of arabinogalactan, mannan, and cellulose, the presence of which complicates processing the beans. These compounds, in particular mannans, increase the viscosity of coffee, impede its industrial processing, and therefore need to be processed using enzymes, many of which are derived from fungi. For example, mannanases extracted from *Sclerotium rolfsii* were shown to effectively degrade coffee mannan, in both partially purified and immobilized form, as well as a soluble crude preparation (Sachslehner et al. 2000). As a result of this treatment, coffee bean extracts can be easily concentrated using evaporation (Chauhan et al. 2012). The fermentation of coffee is accelerated using pectinase treatment, which removes the mucilaginous coat from the coffee bean, which could be helped along by cellulases and hemicellulases (Hoondal et al. 2002). For example, Robusta coffee fermentation was shown to be improved using pectinases derived from *A. niger* (Murthy and Naidu 2011). The degradation of mucilage improves the quality of the coffee bean.

The processing of green tea requires the usage of cellulases, hemicellulases, as well as pectinases, during pretreatment of tea leaves, extraction, and treatment of extract (Uzuner 2019). Enzymatic treatment of tea enhances the aroma, taste, flavor, and cold-water solubility of green tea. The formation of tea haze as well as cream formation are the biggest issues encountered during tea processing, causing discoloration and precipitation of substances. Tannase, derived from *Aspergillus* sp., is the most common enzyme used in tea processing. Tannase is a key enzyme that catalyzes ester and disulfide bonds in hydrolyzable tannins or gallic acid esters, to release glucose or gallic acid (Ni et al. 2015). The hydrolytic action of tannase decreases tea catechins binding to proteins in tea, reducing aggregation and precipitation during tea storage. Tannase has also been shown to reduce bitterness and result in improved quality and taste and mouth feel of green teas (Chavez-Gonzalez et al. 2012). Insoluble forms of tea cream that result from polyphenols can be reduced by addition of tannases, reducing tea turbidity. The formation of foam on instant tea can be reduced by the addition of alkaline pectinases, which break down pectin present in the cell wall of tea leaves (Hoondal et al. 2002). This also results in

change in color of tea during processing, resulting in the characteristic tea aroma. In particular cellulase together with laccase has been shown to increase the quality of black tea (Murugesan et al. 2002). Interestingly, crude enzyme from *Aspergillus* sp. was more effective in improving tea quality than purified pectinase enzyme, and this was because the crude extract contained a combination of, e.g., cellulases, hemicellulases, pectinases, and proteinases (Garg et al. 2016).

2.1.7 Prebiotics

Some by-products of fungal enzymes are beneficial as prebiotics in functional foods for both human and animal consumption. Xylo-oligosaccharides are by-products of xylan metabolism, released during xylanase treatment, and possess prebiotic effects. Xylo-oligosaccharides encourage the growth of beneficial bacteria in the human gut, such as bifidobacteria, while restricting harmful bacteria (Aachary and Prapulla 2011). They are added to foods (e.g., desserts, confectionary products, breakfast cereals, chocolate), as well as beverages (e.g., soymilk, coffee, tea, alcoholic beverages) and milk products (e.g., powdered milk, instant milk, and ice cream) (Kumar et al. 2018). Another example of a prebiotic compound is a by-product of wheat bran processing, arabinoxylo-oligosaccharides, which have been shown to stimulate bifidobacterial growth in human fecal samples (Gullon et al. 2014). The same effect has been shown in chickens that are on feed that is supplemented with these oligosaccharides (Courtin et al. 2008).

Dietary fiber comprises of soluble oligosaccharides, as well as polysaccharides that cannot be digested in the mammalian small intestine. Glucomannans are structural polymers in plant cell walls and carbohydrate storage compounds in seeds. Linear glucomannans are used as thickening agents in food and beverages. These can also be used as prebiotics that have beneficial effects on gut microbiota and human health. Konjac flour glucomannan in particular has been shown to produce manno-oligosaccharides at the industrial level (van Zyl et al. 2010). Traditionally, the breakdown of mannan to manno-oligosaccharides is done by a bacterial endo-β-mannanase but can also be efficiently done by mannanases from *T. reesei* (Mikkelson et al. 2013).

2.2 Applications in Paper and Pulp Production

The pulp and paper industry is one of the largest industries in the world. Nowadays, bleached Kraft pulp is the most important pulp obtained for paper production. However, this industry uses a wide variety of chemicals that pose a risk to the environment due to the possible formation of dioxins and other toxic compounds (Polizeli et al. 2005). The first stage of the pulp production process involves chemical wood pretreatment and the subsequent degradation of the recalcitrant lignin. After this, the colored pulp obtained must be bleached in order to be suitable

for paper production (Mette Nissen et al. 1992). The bleaching process traditionally involves the utilization of many different chemicals, such as chlorine dioxide, sodium hydroxide, hydrogen peroxide, and chlorine peroxide, with the disadvantages of high gas emission rates and the high economic costs associated with the process (Polizeli et al. 2005). In this context, plant biomass degrading enzymes from fungi have been implemented as environmentally friendly alternatives in the pulp pretreatment and bleaching process (Pérez et al. 2002).

The use of lignocellulolytic enzymes, particularly xylanases, decreases the amount of chemicals needed to obtain good quality pulp for paper production (Pérez et al. 2002). Cellulose degradation is of great concern during the pulping process, as it affects the final quality of the paper (Walia et al. 2014). Cellulose-free xylanases from filamentous ascomycetes, mainly produced by the genus *Aspergillus* (de Vries 2003; Maitan-Alfenas et al. 2016), are applied for the removal of lignin linked to xylan with little or no detrimental effect to the pulp, since xylanases have no cellulolytic activity (Ferreira et al. 2016; Walia et al. 2014). Pretreatments with fungal xylanases improve chemical extraction of lignin from pulp, minimizing the amount of chemicals needed and reducing economic and environmental costs (Walia et al. 2017; de Vries and Visser 2001). In addition, xylanases have been reported to help increase pulp brightness and thickness (Savitha et al. 2009).

Ligninolytic enzymes, e.g., laccases, play a role in the pulp delignification process and the elimination of lipophilic extractives known as pitch depositions, although to a lesser degree than lipases (Singh et al. 2016a). Lipases are essential in the paper and pulp industry for the control of pitch (Singh and Mukhopadhyay 2012), which is normally generated from lipophilic extractives containing alkanes, fatty acids, resin acids, sterols, triglycerides, and waxes, and represent a serious problem in the paper industry because pitch deposits are usually associated with lower production yields and quality of the final product (Gutiérrez et al. 2009). Fungal lipases are of great interest due to their stability, selectivity, and broad specificity and are widely applied in the paper industry (Singh and Mukhopadhyay 2012). The main lipase-producing ascomycete fungi are from the genera *Geotrichum, Aspergillus, Candida,* and *Penicillium.* On the other hand, another alternative for the (bio)control of pitch is the application of some pitch-metabolizing fungi, such as the ascomycete *Ophiostoma piliferum,* directly to the pitch deposits as a pretreatment to improve pulping efficiency (Farrell et al. 1997).

Fungal pectinases, on the other hand, are more often applied in the food industry (see Sect. 2.1.2), but they also play a role in pulp and paper industry, since they can be added during the debarking process, reducing the amount of energy required to remove the bark from the wood (Rättö and Viikari 1996). α-Amylases, predominantly from *Aspergillus (A. niger*) and *Penicillium*, are also applied in the paper industry to produce starch with improved properties (e.g., lower viscosity, higher molecular weight) for paper coating and to improve the writing quality of the paper (de Souza and de Oliveira Magalhães 2010).

2.3 Applications in Production of Biofuels and Biochemicals

Fossil fuels are the most widely used energy sources worldwide. However, these have many drawbacks, since they are nonrenewable and are associated with environmental and health risks (Voloshin et al. 2016). Biofuels are sustainable and safer energy resources that have become an alternative to replace the rapid depletion of fossil fuels.

Biofuels, such as bioethanol or biomethanol, can be produced from lignocellulosic biomass obtained principally from forest and agricultural crop residues, including forest woody feedstocks, corn stovers, rapeseed residues, sugarcane bagasse, and fruit peels. However, also several waste streams can be used for bioethanol production, such as paper waste, household food and kitchen waste, or wine and coffee residues (Jeihanipour and Bashiri 2015). Lignocellulose is mainly composed of cellulose, hemicellulose, and lignin. Its complex and compact structure makes lignocellulose extremely resistant to fragmentation. Thus, the conversion of lignocellulosic biomass into biofuel is an economically challenging task, since many pretreatments are required in order to transform lignocellulosic material into fermentable mono- and oligosaccharides, increasing the costs associated with biofuel generation (Araújo et al. 2017).

Lignocellulose-degrading fungi have received much attention due to the fact that fungal pretreatments during industrial biofuel production imply low energy consumption and little or no impact to the environment (Paramjeet et al. 2018). Many filamentous ascomycetes, specially from the genera *Aspergillus*, *Penicillium*, and *Trichoderma*, but also *Fusarium* and *Neurospora* (Ferreira et al. 2016) naturally produce extracellular enzymes that are able to degrade lignocellulose, which include cellulases (endoglucanases, cellobiohydrolases, and β-glucosidases), hemicellulases (e.g., endoxylanases, β-xylosidases, α-L-arabinofuranosidases) (Araujo Silva et al. 2018), oxidoreductases (e.g., laccases, glucose and/or galactose oxidases, lytic polysaccharide monooxygenases) (Mäkelä et al. 2017; Johansen 2016), and the so-called accessory enzymes feruloyl esterases (FAEs), which are necessary for complete hydrolysis of the lignocellulosic material for bioethanol production (Dilokpimol et al. 2016). FAEs are widely produced by ascomycete fungi (Dilokpimol et al. 2016). *A. niger*, *A. oryzae*, *Penicillium roqueforti*, *T. reesei*, and *Trichoderma harzianum* have been reported to secrete high amounts of different hemicellulases and cellulases, including β-glucosidases (Paramjeet et al. 2018). These last enzymes, however, represent a bottleneck in bioethanol production since they are involved in the final step of cellulose saccharification and get inhibited by glucose, their final product (Singhania et al. 2013). For this reason, many efforts are currently being made in order to optimize the production yield of cellulases in filamentous ascomycetes (Prasanna et al. 2016; Araujo Silva et al. 2018). Approaches that are used for this are the use of genetically modified fungi to produce higher amounts of more effective cellulases (Murray et al. 2004; Kovács et al. 2008) and the generation of mixed fungal populations to improve saccharification efficiency (Benoit et al. 2015). In addition, plant pathogenic ascomycetes, such as *Botrytis cinerea* or *Fusarium* sp., have been

recognized as very efficient lignocellulolytic fungi, becoming excellent sources for plant-degrading enzymes for biofuel production (Mäkelä et al. 2014a).

Biodiesel also represents an ecological alternative to fossil fuels. Biodiesel can be chemically or enzymatically synthesized from plant and algal oils by transesterification reactions. However, enzymatic synthesis is less energy-consuming and generates fewer undesired by-products, being a promising alternative to chemical synthesis (Szczęsna Antczak et al. 2009). In this context, fungal lipases have attracted the attention in the last decades for biodiesel production, since their application results in high production yields and easier downstream purification steps (Gog et al. 2012). The main problems regarding the application of lipases for biodiesel generation are their sensitivity to glycerol, which is the main side product of the transesterification reaction, and their production costs (Gog et al. 2012). For this reason, different approaches are used to optimize the enzymatic activity, stability and shelf life of lipases, such as immobilization (Mohamed and Bornscheuer 2003). Currently, the major lipase-producer ascomycete is *Candida antarctica*, but other species (e.g., *A. oryzae*) are being genetically modified to produce high amounts of different cocktails of lipases for biodiesel production (Adachi et al. 2011). Some commercial lipases used for biodiesel production have been reviewed previously (Gog et al. 2012).

Apart from biofuel generation, plant cell wall degrading enzymes from ascomycetes can also be used for the production of pharmaceutically and industrially relevant chemicals with different applications. For instance, FAEs release considerable amounts of hydroxycinnamic acids, including ferulic acid, during lignin depolymerization (Dilokpimol et al. 2016). These compounds are very interesting in food and cosmetic industries due to their antioxidant and photoprotective properties. In addition, antidiabetic, antiaging, and anticancer properties have been associated with ferulic acid, which makes this compound very interesting for pharmaceutical companies (Singh et al. 2016b). Moreover, ferulic acid acts as a precursor for the synthesis of vanillin, one of the principal and most demanded flavor and aroma compounds in the market (Gallage and Moller 2015; Singh et al. 2016b).

Storage polysaccharides from plant biomass can also be degraded by fungal enzymes for multiple applications. Inulin, for example, can be hydrolyzed by fungal inulinases to produce glucose and fructose, which are mainly used in food industry, but can also be used for bioethanol production. Inulin-derived fructooligosaccharides (FOS) and inulooligosaccharides (IOS) are also of great pharmacological value due to their health-promoting properties (Chi et al. 2009). Another example is lactic acid. Soluble sugars obtained from lignocellulosic material by fungal enzymes can also be used for lactic acid production through direct yeast, bacterial, or fungal fermentation (Castillo Martinez et al. 2013). Lactic acid has been traditionally used in food industry, but it is also used as a precursor of many industrially and economically relevant compounds, such as propylene glycol (Castillo Martinez et al. 2013) for plastic production, among other applications (Datta and Henry 2006).

2.4 Other Applications

Fungal plant biomass degrading enzymes from ascomycetes can be additionally applied in many different fields, including bioremediation, textile, and pharmaceutical industry, and some examples of this are presented here.

Fungal hydrolases, laccases, lyases, and peroxidases have been proposed for their application in bioremediation due to their wide capacity to degrade a wide range of organic contaminants and xenobiotics (Singh et al. 2016b; Yang et al. 2017).

Oxidoreductases such as polyphenol oxidases and laccases are also used to synthesize 3,4-dihydroxylphenyl alanine and actinocin, respectively, both with important pharmaceutical applications (Singh et al. 2016b; Mäkelä et al. 2017). In the textile industry, laccases can be used for the decolorization of the textile dye indigo (Campos et al. 2001), as well as for the generation of the stoned-washed look of denim (Pazarlıoğlu et al. 2005). The latter application also uses fungal cellulases to generate this stoned-washed look in an environmentally friendly manner (Belghith et al. 2001). Laccases can also be applied for the production of chromatographic resins, coatings, and adhesives, among other industrial applications (Mäkelä et al. 2017). In leather industry, laccases, together with fungal proteases, amylases, and lipases, are applied alone or in mixtures during leather processing (Thanikaivelan et al. 2004; Singh et al. 2016b). Additionally, in detergent industries, fungal amylases, lipases, proteases, cellulases, and cutinases are used as additives to increase the efficiency of the detergents (Belhaj et al. 2010; Kirk et al. 2002; Singh et al. 2016b).

3 Applications of Fungal Algal Biomass Degrading and Modifying Enzymes

Seaweeds include red (Rhodophyceae), green (Chlorophyceae), and brown (Phaeophyceae) algae. They have a unique chemical composition and represent a source of highly valuable components, such as proteins, polysaccharides, carotenoids, vitamins, minerals, and sterols (Fernand et al. 2017). This composition of seaweeds makes their utilization as food, feed, and medicinal additives attractive. Recent developments in seaweed biorefineries have focused on seaweed polysaccharides as a potential source for biofuel production (Masarin et al. 2016; Bruhn et al. 2011; Adams et al. 2011). In addition, seaweeds are used to control eutrophication in coastal waters, for example, when they are incorporated into mariculture systems (Wu et al. 2015). The use of seaweeds as raw materials in various industrial applications or as a remediation agent for eutrophication leads to an increased amount of seaweed waste. Therefore, it is critical to recycle seaweed waste to improve conditions of marine environments and preserve them. Seaweed biomass degrading enzymes play a crucial role in extracting high-value components from seaweeds as well as in processing seaweed waste. Microorganisms, particularly derived from marine environments, are capable of producing seaweed-specific enzymes that have

wide applications in food, pharmaceutical, and cosmetic industries (Balabanova et al. 2018). Agarases, alginate lyases, and carrageenases are among the most promising industrial enzymes currently. The majority of seaweed-specific enzymes have been reported from bacteria such as *Pseudomonas* sp., *Bacillus* sp., *Vibrio* sp., *Agarivorans* sp., *Thalassomonas* sp., and *Alteromonas* sp., while studies on fungal algal biomass degrading and modifying enzymes are limited (Li et al. 2011; Harshvardhan et al. 2013; Zhu et al. 2018b; Yoon et al. 2017; Zhang et al. 2018; Jouanneau et al. 2010) (Table 4.3). Fungal species that have abilities to produce algae-specific enzymes with interest in industry have been mainly identified from marine habitats (Furbino et al. 2018; Solis et al. 2010; Schaumann and Weide 1990; Hifney et al. 2018; Rodriguez-Jasso et al. 2010).

Certain polysaccharides commonly found in terrestrial plant biomass, cellulose and hemicellulose, also constitute an important part of seaweed biomass. In addition to these polysaccharides, seaweeds also contain specific polysaccharides, such as agar and carrageenan found in red seaweeds; alginate, laminarin, and fucoidan in brown seaweeds; and ulvan in green seaweeds. The enzymatic mechanisms to degrade and modify these seaweed polysaccharides are poorly understood compared to plant polysaccharides. This section collates current knowledge on the fungal enzymes needed for the conversion of seaweed-specific polysaccharides into valuable products (Fig. 4.3).

3.1 Applications of Red Seaweed Degrading and Modifying Enzymes

Agar is a well-known polymer synthesized by red seaweeds such as *Gracilaria* and *Gelidium* and is degraded by agarases classified into α-agarases (E.C. 3.2.1.158) and β-agarases (E.C. 3.2.1.81). α-Agarases belong to glycoside hydrolase (GH) family GH96 of the Carbohydrate-Active Enzyme (CAZy) database (www.cazy.org) and cleave α-1,3 linkages in agarose, while β-agarases hydrolyze β-1,4 linkages in agarose and belong to GH16, 50, 86, and 118 families (Ohta et al. 2005; Wang et al. 2006). Agarases have wide applications in food, cosmetics, and nutraceuticals industries (Chi et al. 2012; Jahromi and Barzkar 2018). They are used to produce oligosaccharides from agar that possess antioxidant activities and moisturizing and whitening effects on human skin (Kim et al. 2017). Agar-derived oligosaccharides are able to inhibit bacterial growth, slow down starch degradation, and improve food quality (Giordano et al. 2006). Moreover, agarases are also commonly used in microbiological, cytological, and physiological research. So far, only a few studies have shown agarase activities produced by fungi (Gomaa et al. 2015, 2017; Furbino et al. 2018; Fawzy et al. 2018). Agarases producing fungal strains have been isolated from seawater (*Cladosporium* sp. and *Phoma lingam*) (Solis et al. 2010) and different types of seaweeds (*Cladosporium* sp., *Doratomyces* sp., *Penicillium chrysogenum*, *Penicillium citrinum*, *Penicillium* sp., *Aspergillus flavus, Curvularia lunata*, *Dendryphiella arenaria*, etc.) (Furbino et al. 2018).

Table 4.3 Overview of the algal biomass degrading enzymes from ascomycete fungi

Enzyme type	Enzymes	Fungal origin	Polymeric substrate	References
Lyases	Glucuronan lyase	*T. reesei*	Ulvan	Delattre et al. (2006)
	Ulvan lyase	*P. longicolla*	Ulvan	Li et al. (2017)
	Alginate lyase	*C. intermedia* *A. cruciatus* *D. salina* *D. arenaria* *A. niger* *E. chevalieri* *S. chartarum* *A. nidulans*	Alginate	Schaumann and Weide (1990) Wainwright (1980) Wainwright and Sherbrock-Cox (1981)
Hydrolase	Laminarinase	*A. niger* *P. claviforme* *T. viride* *D. salina* *A. japonicas* *R. miehei* *P. rolfsii* *T. amestolkiae*	Laminaran	Lee et al. (2014) Grant and Rhodes (1992) Kulminskaya et al. (2001) Chaari and Chaabouni (2018) Méndez-Líter et al. (2018)
	Fucoidanase	*Mucor* sp. *A. niger* *P. purpurogenum* *Fusarium* sp. *E. chevalieri* *D. arenaria* *E. chevalieri* *A. nidulans* *C. funicola* *S. chartarum*	Fucoidan	Rodriguez-Jasso et al. (2010) Hifney et al. (2018)
	Carrageenase	*A. ochraceus* *A. terreus* *Phoma* sp. *P. chrysogenum* *Penicillium* sp. *B. bassiana* *Pseudogymnoascus* sp. *Doratomyces* sp.	Carrageenan	Solis et al. (2010) Furbino et al. (2018)
	Agarase	*Cladosporium* sp. *P. lingam* *Doratomyces* sp. *P. chrysogenum* *Penicillium* sp. *A. flavus* *C. lunata* *D. arenaria* *Acrophialophora* sp.	Agar	Solis et al. (2010) Furbino et al. (2018) Gomaa et al. (2015, 2017) Fawzy et al. (2018)

(continued)

Table 4.3 (continued)

Enzyme type	Enzymes	Fungal origin	Polymeric substrate	References
		Acremonium sp. *A. terreus* *C. pruinosum* *C. salinae* *C. lunata* *D. arenaria* *L. thalassiae* *M. trigonosporus* *S. brevicaulis* *S. candida* *S. rostrata* *S. racemosum*		

Carrageenases are enzymes involved in the degradation of carrageenan obtained from different red seaweeds, for instance, *Kappaphycus*, *Eucheuma*, and *Chondrus* (Rhein-Knudsen et al. 2015). They are classified in three types, κ- (EC 3.2.1.83, GH16), ι- (EC 3.2.1.157, GH82), and λ- (EC 3.2.1.162) carrageenases, which hydrolyze β-1,4 glycosidic linkages of carrageenan and release oligosaccharides with various biological activities (Chauhan and Saxena 2016). It has been demonstrated that carrageenan-derived oligosaccharides have antitumor, anti-inflammation, antiviral, anticoagulation, antioxidant and immunomodulatory activities, and potential biomedical and pharmaceutical applications (Haijin et al. 2003; Talarico and Damonte 2007; Zhu et al. 2018a). Carrageenases are also used in detergent industries (Chauhan and Saxena 2016), where they are added to detergents to remove gum containing stains. The application of carrageenases in combination with other enzymes for the removal of thickeners and excess dye after textile printing reduces time and use of energy and water (Chauhan and Saxena 2016). Commercially available carrageenases are currently mainly produced by bacterial strains. Limited knowledge is available about fungal strains that have abilities to produce carrageenases. For instance, seawater-derived fungi (*Aspergillus ochraceus*, *Aspergillus terreus*, and *Phoma* sp.) (Solis et al. 2010) and fungal strains isolated from seaweeds (*Penicillium chrysogenum*, *Penicillium* sp., *B. bassiana*, *Pseudogymnoascus* sp., and *Doratomyces* sp.) were reported as a potential sources of carrageenases (Furbino et al. 2018).

3.2 *Applications of Brown Seaweed Degrading and Modifying Enzymes*

Brown seaweed polysaccharides including alginate, fucoidan, and laminarin have a wide variety of potential applications due to their broad range of biological properties. These beneficial activities are related to the chemical composition and structure of these

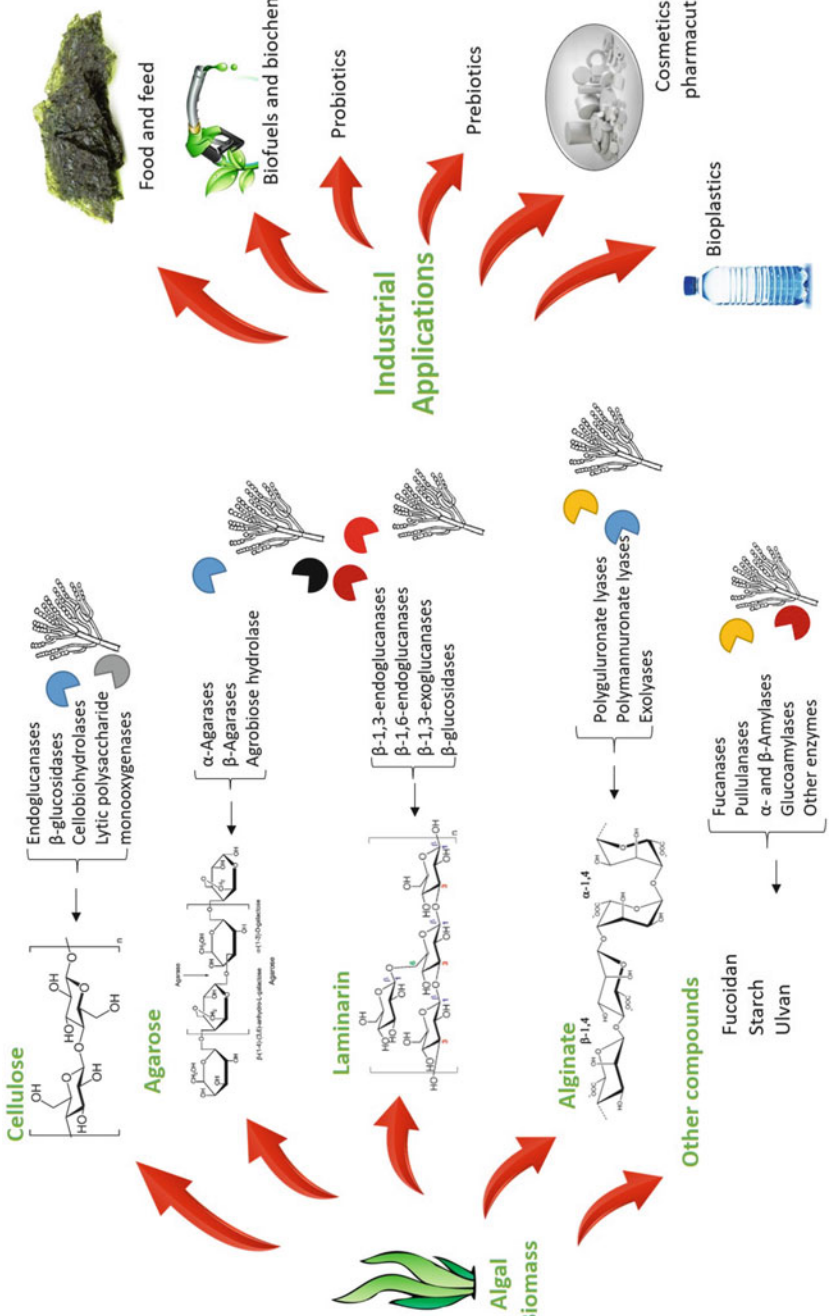

Fig. 4.3 Schematic presentation of the use of fungal enzymes for the conversion of algal biomass in various industrial areas

polysaccharides. Alginate is present in most brown seaweed species, but the amounts of alginate vary. Commercially, alginates are mainly produced in *Laminaria hyperborea*, *Laminaria digitata*, *Laminaria japonica*, *Ascophyllum nodosum*, *Macrocystis pyrifera*, and *Sargassum* spp. (Rhein-Knudsen et al. 2015). Depolymerization of alginate is catalyzed by alginate lyases (EC 4.2.2.3), which hydrolyze alginate by the β-elimination reaction to cleave the glycosidic bond (Li et al. 2011). These enzymes belong to seven polysaccharide lyase (PL) families (PL5, 6, 7, 14, 15, 17, 18) of the CAZy database. Alginate and alginate-derived oligosaccharides produced by alginate lyases play an important role in food, feed, pharmaceutical, nutraceutical, and biofuel industries. They have gelling, emulsifying, and film-forming properties (Gomaa et al. 2018a, b). Furthermore, oligoalginates produced by alginate lyases have potential applications in protection against pathogens and as therapeutic agents such as anticoagulants and tumor inhibitors (An et al. 2009). These oligosaccharides also have applications in the field of agriculture as growth promoters for plants (Hu et al. 2004). Monomers released from alginate degradation by alginate lyases are essential for bioethanol production in biofuel applications (Takeda et al. 2011; Lee and Lee 2016). In addition, alginate lyases are important for the determination of alginate composition by using alginate lyase fingerprinting and enzymatic assay and for the preparation of protoplasts of brown algae (Inoue et al. 2011). Most of the characterized alginate lyases originate from alginate-degrading bacteria (Cantarel et al. 2009), but alginate lyases were also found in several fungi (*Corollospora intermedia*, *Asteromyces cruciatus*, *Dendryphiella salina*, *Dendryphiella arenaria*, *A. niger*, *Eurotium chevalieri*, *Stachybotrys chartarum*, and *A. nidulans*) that were isolated from seaweeds (Schaumann and Weide 1990; Wainwright 1980; Wainwright and Sherbrock-Cox 1981). However, there has been relatively little research reported on these enzymes, and the genes encoding these enzymes have not yet been sequenced or cloned.

Fucoidan is another complex polysaccharide found in various species of brown seaweeds such as *Undaria*, *Macrocystis*, *Laminaria*, *Sargassum*, etc. Many studies have shown that fucoidans possess antioxidant, antiviral, anticoagulant, anticancer, and anti-inflammatory activities and can act as an immunomodulator (Chevolot et al. 1999; Zhuang et al. 1995; Zhao et al. 2018). Despite these numerous beneficial activities, fucoidan molecules have high molecular weight, are structurally different, and have a viscous nature, which inhibits their pharmaceutical and therapeutic applications. Therefore, oligosaccharides with low molecular mass derived from fucoidan have a large potential for applications (Silchenko et al. 2013; Holtkamp et al. 2009; Berteau and Mulloy 2003). Fucoidanases (EC 3.2.1._) are key enzymes to hydrolyze the complex structure of fucoidan and produce fuco-oligosaccharides (Silchenko et al. 2013; Holtkamp et al. 2009) and are also an important tool to structurally characterize fucoidan. Only few characterized fucoidanases (GH107) have been reported, and these were isolated from marine bacteria (Silchenko et al. 2013; Colin et al. 2006; Silchenko et al. 2018). Fucoidanases have been also found in marine fungi, and it has been demonstrated that *Mucor* sp., *A. niger*, *Penicillium purpurogenum*, *Fusarium* sp., *E. chevalieri*, *D. arenaria*, *E. chevalieri*, *A. nidulans, C. funicola,* and *S. chartarum* have the potential to produce fucoidanase (Rodriguez-Jasso et al. 2010; Hifney et al. 2018). Furthermore, fungal treatment of the brown

seaweed *Cystoseira trinodis* increased the antioxidant properties of fucoidan through the generation of fucoidan with a lower molecular weight and looser structure (Hifney et al. 2018).

Besides unique polysaccharides such as alginate and fucoidan, brown seaweeds (*Laminaria*, *Saccharina*, *Ascophyllum*, *Fucus*, and *Undaria* species) produce the storage polysaccharide laminarin which is a β-glucan with β-1,3- and β-1,6-linkages (Garcia-Vaquero et al. 2017). Laminarinases are enzymes that catalyze the hydrolysis of laminarin and include endo-β-1,3-1,4 glucanase (EC 3.2.1.6; GH3, 16, 26), β-1,3-glucanase (EC 3.2.1.39, GH16, 17, 55, 64, 81), β-1,6-glucanase (EC 3.2.1.75, GH5, 13, 30), pullalanase (EC 3.2.41, GH13), exo-β-1,3/1,6-glucanase, and endo-β-1,4-glucanase (GH131) (Balabanova et al. 2018). β-1,3-glucanases have a key role in the efficient degradation of laminarin. Laminarin and its derivatives were reported to exhibit antioxidant, anticancer, anti-apoptotic, and immune-stimulating activities, have a protective function against pathogens, and have potential for bioethanol production (Kim et al. 2006a; Yin et al. 2014; Kadam et al. 2015; Harris et al. 2014). Therefore, laminarinases are promising biocatalysts in the degradation of laminarin for various applications, such as generation of biochemicals and bioenergy. Laminarinases with activity against laminarin were isolated from several ascomycete fungi such as *A. niger*, *Penicillium claviforme*, *Trichoderma viride*, *D. salina*, *Aspergillus japonicus*, *Rhizomucor miehei*, and *Penicillium rolfsii* (Lee et al. 2014; Grant and Rhodes 1992; Kulminskaya et al. 2001). Laminarinase from *P. rolfsii* was purified and characterized (Lee et al. 2014; Chaari and Chaabouni 2018). Based on the enzymatic hydrolysis activity to produce fermentable sugars, this laminarinase has potential for bioethanol production. In addition, the acidophilic and broad pH stability as well as good thermostability of the purified enzyme has advantages for feed, food, pharmaceutical, biochemical, and biofuel industries (Lee et al. 2014). Another efficient laminarinase for saccharification of laminarin has been purified and characterized from *Talaromyces amestolkiae* (Méndez-Líter et al. 2018).

3.3 Applications of Green Seaweed Degrading and Modifying Enzymes

Ulvan is the most abundant carbohydrate synthesized by green seaweeds (*Ulva* and *Enteromorpha*) (Lahaye and Robic 2007). Ulvan and oligosaccharides released from it have recently gained attention for a variety of applications in food, feed, and chemical industries. They also have antioxidant, anticoagulant, immunomodulator, antiviral, and antitumoral activities that are interesting for pharmaceutical and nutraceutical applications (Qi et al. 2005; Mao et al. 2006; Leiro et al. 2007; Ivanova et al. 1994; Kaeffer et al. 1999). In addition, it has been demonstrated that ulvan has plant defense and plant resistance activities with a potential to be used in agricultural applications (Jaulneau et al. 2010; Paulert et al. 2010). Furthermore, biomaterials such as ion exchanger hydrogels, nanofibers, membranes, and microparticles can be

built using ulvan polymers (Toskas et al. 2011; Alves et al. 2012; Morelli and Chiellini 2010). Despite these promising applications of ulvan and its derivatives, identification and characterization of enzymes involved in ulvan degradation and release of oligo- and monosaccharides have been poorly investigated, in contrast to the enzymes that degrade agars and carrageenan from red seaweeds and alginates from brown seaweeds. Enzymes that have been identified to have ulvanolytic activities are ulvan lyase (EC 4.2.2._, PL24, 25, and 28), β-glucuronidase (EC 3.2.1.31, GH1, 2, 30, 79, 154), β-1,4-glucuronan lyase (EC 4.2.2.14, PL14, 20), and unsaturated β-glucuronyl hydrolase (EC 3.2.1._, GH105) (Nyvall Collen et al. 2011; Quemener et al. 1997; Delattre et al. 2006; Nyvall-Collén et al. 2014; Kopel et al. 2016). There are only a few reports on ulvanolytic enzymes from fungi. An extracellular glucuronan lyase was isolated and purified from *Trichoderma* sp. GL2 (Delattre et al. 2006). It was active toward ulvan producing various low molecular weight ulvans (Delattre et al. 2006). Another study identified an ulvan lyase (PL24) encoding gene in *Phomopsis longicolla*, which is a seed-borne fungus causing *Phomopsis* seed decay in soybean (Li et al. 2017). However, the role of ulvan lyases in *P. longicolla* is unknown.

4 Conclusions and Future Prospects

This chapter provided an overview of the applications of fungal enzymes naturally involved in the degradation of plant and algal biomass. This presents one of the best examples of the implementation of a highly efficient and diverse biological system, degradation of biomass by fungi for their growth and reproduction, into human-designed processes. The long history and subsequent broadening of these applications highlight their importance for human society, which is likely to grow even further as we are moving to a biobased renewable society. Implementation of plant biomass conversion using fungal enzymes has already occurred in many industrial sectors (Fig. 4.2), while the conversion of algal biomass is more in its infancy, in part due to the highly diverse cell wall structure and composition of the different algae.

The availability with an ever-growing number of fungal genomes (Grigoriev et al. 2014) has supplied us with a collection of (putative) enzymes that could never have been foreseen in the pre-genomics era, and this number will continue to grow exponentially. While traditionally only well-studied industrial fungi (e.g., *A. niger*, *T. reesei*) were considered as enzyme suppliers, now also other fungi have shown high potential as enzyme sources (Espagne et al. 2008; Peng et al. 2017). This resource can be mined not only for novel enzymes or activities but also for similar enzymes with more advantageous properties. It has already been shown that orthologous enzymes from related fungi can have strongly different properties with respect to proteolytic (de Vries et al. 1997) or temperature stability (Culleton et al. 2014).

In addition to the discovery of novel enzymes, another issue to be solved is the production of these enzymes. Current production yields are still hampering their

application in some industrial processes. In this context, the biotechnological production in higher amounts of enzymes with improved physicochemical properties will increase the future perspectives for their application in these and other unexpected industrial processes yet to be exploited.

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