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REVIEW ARTICLE

Cellulases, Hemicellulases, and Pectinases: Applications in the Food and Beverage Industry

Thaiza S. P. de Souza[1] · **Haroldo Yukio Kawaguti**[1,2]

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Abstract

Enzymes are present in all naturally occurring forms of life, including plants, animals, and microorganisms. Enzymes have been used in the food industry to transform a raw material into a main product, to modify the functional characteristics of a product, and/or to control or improve food processes. The cell wall of plant cells is composed of a complex network of polysaccharides, including cellulose, hemicelluloses, and pectin, with interactions between these structures. Selective enzymes for the degradation of cell wall components, such as cellulases, hemicellulases, and pectinases, are used to perform hydrolytic actions on the respective cell wall components. Cellulases and hemicellulases play a predominant role in the hydrolysis of lignocellulosic substrates, and pectinolytic enzymes are used to degrade pectic structures. Along with this, cellulolytic, hemicellulolytic, and pectinolytic enzymes have been used in the food industry in different processes such as in fruit and vegetable processing industries, wine production, baking process, essential oil recovery, and vegetable oil extraction. This review discusses the major applications of cellulases, hemicellulases, and pectinases and their cleavage characteristics, sources (mainly microbial), and features of the substrates in the food and beverage industries.

Keywords Bakery products · Fruit juice clarification · Oligosaccharides · Industrial applications

Introduction

The world market for enzymes regarding industrial applications has been increasing annually. In 2015, the marketed value was approximately 8.18 billion dollars and projections show an increase of 17.5 billion dollars in 2024 (Cipolatti et al., 2019). Although this market shows promising prospects, the market for enzymatic biocatalysts is not diversified (Cipolatti et al., 2019). The use of enzymes in 2015 was distributed as follows: 35% were destined to the food and beverage manufacturing industries, including dairy, bakery, fruit and vegetable processing, and beer making; 25% for the detergents, cleaning materials, and personal care industries; 20% used in agriculture and animal feed production; 10% directed to the bioenergy sector; and 10% included enzymes for technical applications, pharmaceutical industries, and others (Guerrand, 2018).

Biocatalysts are obtained from several natural sources, such as plants and animals; however, microbial sources have been the most used due to a series of advantages compared to other sources, such as the greater metabolic diversity of microorganisms, the regular availability due to the absence of seasonal fluctuations, the higher yield in production, the greater susceptibility to genetic manipulation, and the shorter development and production time of these catalysts. The microorganisms most cited in enzyme production are filamentous fungi, bacteria, and yeasts (Bilal & Iqbal, 2019; Cipolatti et al., 2019; Singh & Kumar, 2019; Singh et al., 2019b; Ventura-Sobrevilla et al., 2015).

The application of enzymes in agro-industrial processes, particularly in the food industry, is becoming increasingly attractive. This is owing to several benefits of using enzymes over traditional chemical reagents. Enzymes can replace the addition of synthetic catalysts in different processes; lead to the use of smaller amounts of toxic reagents, which generates less energy

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✉ Haroldo Yukio Kawaguti
hkawaguti@gmail.com

[1] Food and Nutrition Graduate Program, Federal University of the State of Rio de Janeiro, Rio de Janeiro, RJ 22290-240, Brazil

[2] Department of Food Science, Federal University of the State of Rio de Janeiro, Pasteur Avenue, 296, Rio de Janeiro, UrcaRJ 22290-240, Brazil

consumption and less environmental impacts; they can be incorporated directly into food safely; improve product functionality, such as texture and appearance; lead to increased nutritional quality, shelf life, and safety of food; and the generation of new products of commercial interest as a fundamental part of the evolution of certain processes. In this context, enzymes are used in a wide range of applications, such as in bakery, dairy manufacture, starch processing, fruit juice, wine and beer production, and other drinks (Singh & Kumar, 2019).

The structural constituents of a plant cell wall are complex polysaccharides mainly cellulose, hemicellulose, and pectic substances (Danalache et al., 2018). These components are present in large amounts in dietary fibers and the primary cell wall of major fruits and vegetables (Toushik et al., 2017). During processing of vegetables and fruits to the corresponding final food and beverage products, the complex polysaccharides of the cell wall are hydrolyzed by different enzymes (Toushik et al., 2017). The most frequent enzymes employed to break down the native carbohydrate-matrix are cellulases, hemicellulases, and pectinases (Danalache et al., 2018).

Cellulases and hemicellulases play a fundamental role in the hydrolysis of lignocellulosic substrates. Cellulolytic enzymes hydrolyze the beta-1,4-glucosidic bonds of cellulose, a homopolysaccharide composed of glucose. For the complete hydrolysis of cellulosic material, three different types of cellulases are required, endoglucanase, exoglucanase (cellobiohydrolase), and beta-glucosidase (cellobiase). Hemicelluloses are heteropolysaccharides composed of different hexoses and pentoses (Bilal & Iqbal, 2019; Singh et al., 2019a), and the efficient degradation of the polymer requires the synergistic action of many hemicellulolytic enzymes such as xylanases, mannanases, arabinofuranosidases, glucuronidases, xylosidases, and hemicellulolytic esterases (Shallom & Shoham, 2003). Pectinolytic enzymes are an enzyme complex with the property of degrading pectic structures that are produced naturally by plants, bacteria, and fungi (Ruiz et al., 2017). Pectin is a complex polysaccharide composed in its main structure of galacturonic acid residues connected by alpha-1,4 bonds, which may contain substituent groups in its main structure, and side chains containing several other sugars. Pectinolytic enzymes can be applied in various industrial sectors where degradation of pectin is desired, and about 25% of global enzyme sales are attributed to pectinases (Haile & Kang, 2019b; Kashyap et al., 2000; Kaur et al., 2004).

This current review article provides an overview of the carbohydrases cellulase, hemicellulase, and pectinase, highlighting their applications in the food industry including baking, brewing, beverages, as well as sweeteners and oils.

Cellulase, Hemicellulase, and Pectinase Main Sources

Currently, there is a strong need for methods that could replace the use of chemical solvents, in order to avoid toxic chemical residues in the final products. With the increasing pressure on food industries to develop sustainable chemical processes, including extraction methods, the search for new approaches to these processes has become essential. In this sense, the biological catalyst is a method with great potential as the enzymes can catalyze reactions like hydrolysis, with a high level of selectivity that reduces or eliminates the need for the use of solvents (Puri et al., 2012).

The cell wall of plant cells is composed of a complex network of polysaccharides, including cellulose, hemicelluloses, and pectin with interactions between these structures. Selective enzymes for the degradation of cell wall components, such as cellulases, hemicellulases, and pectinases with minimal pectinolytic activity, are often used to perform hydrolytic actions on the respective cell wall components. However, this requires a good knowledge of the catalytic action of the selected enzymes and the ideal conditions for their use. Enzyme-based use depends on the intrinsic ability of the enzymes to catalyze reactions with exquisite specificity and the ability to function under moderate processing conditions. Microorganisms represent an attractive resource of these biocatalysts due to their biodiversity, rapid growth, and susceptibility to genetic manipulations. To date, a large number of different genera of bacteria, fungi, and yeasts have been recognized for the production of these enzymes that degrade the cell wall components of plants as relevant to the industry (Danalache et al., 2018).

Cellulases are produced by different genera of microorganisms such as anaerobic bacteria in the digestive tract of ruminants (*Clostridium* spp., *Ruminococcus* spp.), aerobic bacteria (*Bacillus* spp., *Cellulomonas* spp.), filamentous fungi (*Aspergillus nidulans*, *A. niger*, *A. oryzae*, *Fusarium* spp., *Trichoderma viride*, *T. reesei*), and actinomycetes (*Microbispora* spp., *Thermomonospora* spp., *Streptomyces* spp.) (Kumar et al., 2019; Sampathkumar et al., 2019; Shida et al., 2016; Singhania et al., 2017; Soni et al., 2018). Most bacterial cellulases act at neutral and alkaline pH, while the optimal pH values for most fungi are between 4 and 6 (Hmad & Gargouri, 2017; Singhania et al., 2017). Among the several microorganisms that can produce cellulases, fungi are its main producers. *Trichoderma reesei* is the fungal strain most widely used for cellulase production. Other fungi such as *Humicola* spp., *Penicillium* spp., and *Aspergillus* spp. are also high enzyme producers (Kumar et al., 2019; Ramesh et al., 2020). Generally, fungi produce cellulases in the presence of cellulose, whereas bacteria constitutively produce cellulase. Besides fungi, extremophiles bacteria can survive in harsh conditions and may produce cellulases with other characteristics, as high stability (Kumar et al., 2019). The main bacteria producing cellulases are from the genus *Bacillus* such as *B. amyloliquefaciens*, *B. licheniformis*, *B. circulans*, and *B. subtilis*, and from the genus *Clostridium* such as *C. acetobutylicum*, *C. cellulovorans*, and *C. thermocellum* (Soni et al., 2018).

Different hemicellulolytic enzymes act on the different structures of hemicellulose. Microorganisms such as the genus *Trichoderma* and *Aspergillus* secrete at high concentrations a large variety of hemicellulases that work synergistically. Aerobic bacteria, like the *Bacillus* genus, secret a more moderate number of polysaccharide-backbone-degrading enzymes, which produce relatively large oligosaccharide products (Shallom & Shoham, 2003). The main microbial hemicellulases are xylanases, glucuronidases, arabinofuranosidases, galactosidases, and mannanases that act on glycosidic bonds, while acetyl or feruloyl esterases hydrolyze ester bonds of side groups of acetate or ferulic acid in the structure of the plant cell wall. Hemicellulases are produced by *Aspergillus nidulans*, *A. niger*, *Trichoderma reesei*, *T. viride*, *Penicillium chrysogenum*, among others (Shallom & Shoham, 2003; Thomas et al., 2017).

Pectinolytic enzymes can be obtained from different microorganisms such as yeasts, bacteria, actinomycetes, and mainly by filamentous fungi that are considered one of the most effective producers of pectinases (Jacob, 2009; Jahan et al., 2017; Sieiro et al., 2012). Fungal pectinases are extracellular enzymes, in which polygalacturonase is the most relevant type among them. Pectinases are produced by different fungi, including *Aspergillus* spp., *Fusarium* spp., *Penicillium* spp., *Rhizopus* spp., *Trichoderma* spp., *Rhizomucor* spp., *Aureobasidium* spp., *Thermotoga* spp., *Saccharomyces* spp., *Candida* spp., *Pichia* spp., *Kluyveromyces* spp., and bacteria such as *Bacillus* spp., *Klebsiella* spp., and *Pseudomonas* spp., have been documented as producers of alkaline pectinases (Jayani et al., 2005; Kashyap et al., 2001; Kavuthodi & Sebastian, 2018; Patidar et al., 2018; Ruiz et al., 2017). Generally, pectinolytic enzymes derived from fungi are acidic, while alkaline enzymes are mainly secreted by bacterial strains. *Aspergillus* spp. is the most common genus of fungus used for the industrial production of these enzymes and presents considerable differences between species concerning the substrate specificity, cleavage rate, optimum pH, and temperature for its activity (Favela-Torres et al., 2006; Lang & Dörnenburg, 2000; Ruiz et al., 2017). A review showing the main pectinase-producing microorganisms can be seen in Amin et al. (2019), Samanta (2019), Rebello et al. (2017), and Garg et al. (2016). Table 1 summarizes different applications of commercial microbial pectinase, cellulase, and hemicellulase in food and beverage industries, and Fig. 1 presents an overview of the application of those carbohydrases in the same industrial sectors.

The knowledge of the structure of the raw material, such as the composition of cellulose, hemicellulose and pectin, as well as the mode of action of each biocatalyst on a particular substrate, will contribute to the choice of the method and type of enzyme that will be applied for a better conduction of a process to obtain a product, or to modify the native structure of the substrate, in order to optimize costs or produce higher added value compounds.

Cellulose

Cellulose is the most abundant natural polysaccharide in nature that is located mainly on the secondary wall of plant cells, corresponding to approximately 35–50% of the plant. Thus, it is found naturally in wood, fruit husks, corn straw, grain bran, and cereals, such as wheat and rice. Cellulose is considered a sustainable resource that is present in agricultural and agro-industrial wastes and, currently, its use and application are valued. Fruit and vegetable cell wall polysaccharides contain approximately 20–35% cellulose. Cellulose is a linear polysaccharide composed of an organized and partially crystalline structure, insoluble at room temperature in organic solvents, in diluted acids and alkalis; which consists exclusively of glucose connected by beta-1,4 glycosidic bonds, and the smallest repetitive unit is called cellobiose (Gouveia & Passarinho, 2017; Toushik et al., 2017; Urbaniec & Bakker, 2015; Zhong et al., 2019).

The spatial conformation of cellulose is a consequence of beta-1,4 glycosidic bonds, which are organized in a linear structure with a strong tendency to form intramolecular hydrogen bonds between hydroxyl groups of the same molecule and, intermolecular bonds, between hydroxyl groups of adjacent chains, leading to the formation of the elementary fibril, which is insoluble in water and has a high degree of crystallinity. The fibrils are grouped by a hemicellulose monolayer and wrapped in a matrix containing lignin and hemicellulose, associated with each other through physical interactions and covalent bonds. The structure resulting from this association is called cellulosic microfibril (Bonechi et al., 2017; Carvalho et al., 2009; Toushik et al., 2017; Zhong et al., 2019). Microfibrils have some regions in which the cellulose molecules are arranged in a disordered way, called amorphous regions; in other regions, they are ordered, forming micelles of crystalline structure, showing that the cellulose chain has a strong tendency to form intra- and intermolecular hydrogen bonds between the internal hexoses subunits and between the cellulose chains, respectively, promoting the aggregation in a crystalline structure (Carvalho et al., 2009; Lynd et al., 2002; Meng et al., 2016; Toushik et al., 2017; Zhong et al., 2019). Cellulose fiber consists of a mixture of

Table 1 Application of diverse commercial microbial carbohydrases (pectinase, cellulase, and hemicellulase) in food and beverage processing and its results

Enzyme	Enzyme concentration and conditions	Application	Result	Reference
Pectinex Ultra® SP-L and Viscozyme® L	0.1% (Pecinex:Viscozyme, 70:30), 40 °C, 120 min	Improvement of red dragon fruit juice processing	Extraction yield increased from 54.04 to 86.35%, relative viscosity reduced from 1.42 to 1.09, the total acidity increased from 0.47 to 0.75 (g/100 mL), the total phenolic compounds from 13.68 to 14.16 (mgGAE/100 g puree), and the vitamin C content from 27.94 to 32.29 (mg/100 g puree)	Truong and Dang (2016)
Pectinex® Yeld Mash, Pectinex® Smash XXL	1 mL/L, 25 °C, 24 h	Influence of enzymes on quality parameters of chokeberry juice	Pectinex Yeld Mash increased (13%) the phenolic compounds, and Pectinex Smash XXL decreased turbidity (96%) and viscosity (76%) in juice	Lachowicz et al. (2018)
Pectinex® Ultra Clear, Lallzyme® Beta	0.75 U/g (Pectinex/Lallzyme ratio 0.52), 51 °C, 52 min	Grape juice extraction from *Vitis labrusca* L. variety Concord	Juice yield increased 75.8%, quercetin 3-*O*-glucoside and total anthocyanins were improved up to 112% and 41%, respectively	Dal Magro et al. (2016)
Rohapect® UF, Rohament® CL, Colorase® 7089	2% (equal mass proportions of enzyme cocktail), 54 °C, 15.4 h	Pumpkin oil recovery preceded by enzymatic maceration of seeds	Extraction of 36.0% of pumpkin oil (72.6% of total available lipids), oil extracted by the aqueous enzymatic extraction was more abundant in sterols, tocopherols, and squalene	Konopka et al. (2016)
Celluclast® 1.5L	2% of substrate concentration, 20 endoglucanase units of cellulase, 200 MPa, 50 °C, 15 min	Valorization of the apple by-product using high hydrostatic pressure assisted by enzyme	A synergistic effect produced the hydrolysis of the insoluble dietary fiber of apple by-product, increased the release of water-soluble polysaccharides (1.8-fold) and oligosaccharides (3.8-fold)	De la Peña-Armada et al. (2020)
Pectinex® Ultra SP-L, Viscozyme® L	Enzyme:sample (1:5), 50 °C, 120 min	Influence of enzymes on the extraction yield and the quality of mulberry juice	Pectinex Ultra SP-L increased the juice yield (15.8%), extraction yield (87.1%), total soluble solids (11.9°Bx), titratable acidity (1.4%), L-ascorbic acid content (35.5 mg/100 mL), total phenolic content (160.6 mg GAE/100 mL), and antioxidant capacity (82.6%)	Nguyen and Nguyen (2018)
Pectinex® Ultra SP-L, Celluclast® 1.5 L	2.5%, 50 °C, 2.5 h	Enzymatic maceration and liquefaction of pumpkin flesh for the preparation of a suitable base feed for spray drying	Pectinex were used to prepare macerated pumpkin prior to combine treatment with Celluclast to produce a puree, and macerated pumpkin showed no significant differences in the spray drying feed characteristics in terms of color, viscosity, and solids concentration	Shavakhi et al. (2020)

Table 1 (continued)

Enzyme	Enzyme concentration and conditions	Application	Result	Reference
Pectinex AR®, Celluclast® 1.5 L	1 mg/kg (each), 50 °C, 18 h	Enzymatic pre-treatment to reduce the consistency of the pepper pulp and increase the yield of the extract used in the sauce formulation	The enzymes association increased the extract yield by 17.5% without impairing the sensory acceptability of the formulated sauce, release of carotenoids and capsaicinoids were not observed, and the macerated sauce presented fruity notes	Farias et al. (2020)
Celluclast®, POWERBake® 960	55 °C, 90 min	Improvement of the baking quality of whole wheat meals prepared from flour–bran blends and prehydration of wheat bran with enzymes	Bran hydration with a mix of cellulase and xylanase increased the soluble sugar and decreased the insoluble fiber, bran hydrated with cellulase or a mixture of cellulase and xylanase showed delayed or inhibited starch gelatinization and decreased water absorption for dough development, and a higher loaf volume was observed in bread containing bran hydrated with a low dose of xylanase or a mix of cellulase and xylanase in hard red wheat, and bread containing bran hydrated with low-dose xylanase in hard white wheat	Park et al. (2018a)
Celluclast BG®, Pentopan Mono BG®	Celluclast (70, 130, and 195 ppm), Pentopan (20, 50, and 75 ppm)	Improvement of whole wheat bread properties using different enzymes	Enzymes, including amylase, cellulase, glucose oxidase, and xylanase, showed promise at improving the quality of whole wheat bread by increasing the loaf volume, the greatest improvement in loaf volume was 13%, which was obtained with the highest dose of xylanase, and also showed a trend of decreasing crumb hardness and slowing the rate of crumb firming	Tebben et al. (2020)
Pectinex® Ultra SP-L	0.93%, 45 min of soaking time, 600 mmHg of vacuum pressure	Application of enzymatic peeling aided with vacuum infusion to ease the peeling process of key lime (*Citrus aurantifolia*) fruit	The vacuum-aided enzymatic treatment has not significantly affected the physicochemical characteristics (pH, titratable acidity, total soluble solids, moisture content, and ascorbic acid content) of peeled key lime compared to the conventional method, and the intensity of puree color was significantly improved	Hussain et al. (2019)

Table 1 (continued)

Enzyme	Enzyme concentration and conditions	Application	Result	Reference
Pectinex® Ultra SP-L, Celluclast® 1.5 L	Pectinase (1.5%), 50 °C, 2 h	Application of enzyme preparations to liquefy soursop fruit pulp to yield puree	Pectinase produced the best result in liquefaction, a liquefied puree with a reduced viscosity of up to 50% was obtained when pectinase was used in combination with cellulase, and the addition of cellulase did not lead to significant changes in pH, titratable acidity, and ascorbic acid but caused significant increases in total soluble solid and total sugar content	Chang et al. (2018)
Pectinex Ultra SP-L®, Crystalzyme®	0.15 mL/kg (each), 45 °C, 2 h,	Enzyme treatment of the fruit macerate to improve physicochemical and antioxidant properties of extracted blueberry juice	Enzyme treatments resulted in significantly higher juice yield (Pectinex-87.29 mL/100 g, Crystalzyme-86.91 mL/100 g, control-79.45 mL/100 g), higher juice clarity (Pectinex-52.47%, Crystalzyme-55.10%, control-33.05%), and titratable acidity (Pectinex-0.298 g/100 g, Crystalzyme-0.294 g/100 g, control-0.278 g/100 g), and lower extraction loss (Pectinex-0.92 g/100 g, Crystalzyme-1.01 g/100 g with, control-4.49 g/100 g), and total anthocyanins were significantly higher (Pectinex-12.78 mg/100 mL, Crystalzyme-11.80 mg/100 mL, control-9.69 mg/100 mL)	Siddiq et al. (2018)
Pectinex®Ultra SP-L	500 µL/50 g of seeds with the pulp, 45 °C, 15 min	Enzymatic maceration with pectinases on cocoa pulp	Pectinase increased the yield by more than 100% (22.45%) when compared to the control (11.18%), and the content of polyphenols was higher for enzyme treatment (7.47 mg/100 g), which also showed the best antioxidant activity	Oliveira et al. (2020)

Pectinex Ultra® SP-L: a blend of pectinases, hemicellulases, and beta-glucanases; Viscozyme® L: a blend of beta-glucanases, pectinases, hemicellulases, and xylanases; Pectinex® Yeld Mash: pectinases; Pectinex® Smash XXL: mash enzyme based on pectin lyase; Pectinex® Ultra Clear: a blend of pectinases, hemicellulases, and arabinanases; Lallzyme® Beta: a blend of beta-glucosidases and polygalacturonases; Rohapect® UF: a blend of pectinases and arabanases; Rohament® CL: cellulases; Colorase® 7089: endopeptidases; Celluclast®: cellulases; Pectinase AR: mainly pectinase activity, but with secondary activities, such as hemicellulases and cellulases; POWERBake® 960: xylanases; Celluclast BG®: cellulases; Pentopan Mono BG®: xylanases; Crystalzyme: pectinases microfibrils of different sizes, and the degree of polymerization and molecular mass of this polysaccharide depends on the plant species. The polysaccharide structure is strongly resistant to enzymatic, chemical, and physical treatments (Bonechi et al., 2017; Keshwani, 2010). The microfibrillar structure of cellulose remains unknown or controversial due to little information about the molecular size and the distribution of crystalline and non-crystalline structures.

The efficient hydrolysis of cellulose is catalyzed by a complex mixture of enzymes called cellulase complex, which act synergistically, composed of endoglucanase, exoglucanase, cellobiohydrolase, and beta-glucosidase. Endoglucanases hydrolyze glucosidic bonds within the structure of cellulosic substrates, while cellobiohydrolases act at the ends of the cellulosic chain to produce cellobiose, which is later converted into glucose molecules by the action of beta-glucosidases (Garcia-Galindo et al., 2019; Sindhu et al., 2016).

Cellulolytic Enzymes

Cellulases are hydrolytic enzymes efficient in breaking beta-1,4 glycosidic bonds between glucose units. The conversion of cellulose into cello-oligosaccharides and glucose can be carried out by chemical or enzymatic hydrolysis. Chemical hydrolysis uses inorganic acids under extreme conditions; thus, the formed products contain sugars of lower molecular weight and other degradation products. In the enzymatic hydrolysis of cellulose, endoglucanase and exoglucanase act synergistically to transform cellulose into small cello-oligosaccharides and, subsequently, beta-glucosidase hydrolyzes cello-oligosaccharides into simple sugars or glucoses (Sindhu et al., 2016).

Endoglucanase or carboxymethylcellulase (endo-1,4-beta-*D*-glucanase/endo-beta-1,4-*D*-glucan-4-glucanhydrolase, EC 3.2.1.4) acts on the cellulose amorphous region, randomly breaking beta-1,4 glycosidic bonds, inside the molecule, releasing long-chain cello-oligosaccharides. Many endoglucanases are unable to act on crystalline cellulose, acting only on the amorphous fraction of the polymer and performing incomplete hydrolysis. Exoglucanase or cellobiohydrolase (exo-beta-1,4-glucan cellobiohydrolase/1,4-beta-*D*-glucan cellobiohydrolase, EC 3.2.1.91) breaks cellulose and cello-oligosaccharides from the end, releasing glucose and cellobiose. Exoglucanases can be classified into two types, which are cellobiohydrolases-type I, which act preferentially in the reducing end of the cellulose chain, in contrast to type II, which act actively on the non-reducing end of the chain. Beta-glucosidase or cellobiase (1,4-beta-glucosidase, EC 3.2.1.21) disrupts cellobiose by releasing glucose and also acts as exoenzymes on beta-1,4 oligosaccharides like cellodextrins (Kuhad et al., 2016; Lynd et al., 2002; Sajith et al., 2016). Figure 2 show the performance of the main cellulases.

Thermophilic fungi such as *Sporotrichum thermophile*, *Thermoascus aurantiacus*, *Humicola grisea*, are also known to produce cellulases and are interesting for industrial application due to their ability to produce thermostable enzymes. These microorganisms produce cellulases with high stability at highly acidic or alkaline pH, as well as at temperatures up to 90 °C (Singhania et al., 2017; Srivastava et al., 2018). Although these microorganisms are extremely efficient in cellulose degradation, the enzymatic extracts produced are not as efficient as those obtained in vivo. Therefore, for satisfactory results, pretreatment of the cellulose, with acid or base, is desirable to break down the crystalline portions of the polymer, which can cause an increase in the cost of the process. Due to this difficulty, cellulases are used in conjunction with pectinolytic and hemicellulolytic enzymes, in the extraction of juices and olive oil and the treatment of coffee (Soni et al., 2018).

Industrial Application of Cellulolytic Enzymes

Cellulolytic enzymes in the food industry are used to contribute to the release of antioxidant compounds from fruit and vegetable bagasse; increase the yield in the extraction of starch and proteins; improve the maceration, pressing, and color extraction processes of fruits and vegetables; act as an adjuvant in the clarification of fruit juices; improve the texture and quality of bakery products; change the viscosity of fruit purees; improve the texture, flavor, aroma and volatile properties of fruits and vegetables; control the bitterness of citrus fruits; extracting olive oil, treating wines, and improving the quality of bakery products (Bilal & Iqbal, 2019; Karmakar & Ray, 2011; Kuhad et al., 2011; Kumar & Sharma, 2017; Singh et al., 2019a; Toushik et al., 2017).

Cellulolytic enzymes are used in combination with pectinases for the extraction and clarification of fruit and vegetable juices, to produce nectars and purees, to extract oil from oil seeds, and in the production of oligosaccharides as functional ingredients of food. Table 2 summarizes several recent publications reporting different characteristics and applications of cellulolytic enzymes.

Cellulases to Obtain Fermentable Sugars

Several studies have been conducted to saccharify cellulose to obtain fermentable sugars, which can be used and transformed into different products such as organic acids, natural pigments, and alternative sweeteners. The process of converting cellulose to glucose includes several steps such as chemical and physical pretreatments, enzymatic hydrolysis, and the fermentation process. Pretreatment is an important and necessary step to break down cellulose and allow enzymes to access the polysaccharide. Chemical treatments

Fig. 1 Schematic illustration of cellulase, hemicellulase, and pectin applications in the food and beverage industries

with acids or bases promote partial hydrolysis and improve the yield of obtaining glucose from cellulose, in addition to removing hemicellulose and partially lignin. Pretreatment, from an economic point of view, in addition to making cellulose more accessible to attack by enzymes, should be carried out in a moderate way to avoid the formation of inhibitors to the enzymatic and fermentative processes (Chandrasekaran, 2012; Kuhad et al., 2011).

In the enzymatic process, enzymes that degrade cellulose (exoglucanases, endoglucanases, and glucosidases) need to act synergistically. As cellulose is linked to other structural polysaccharides, it is also suggested adding other enzymes to

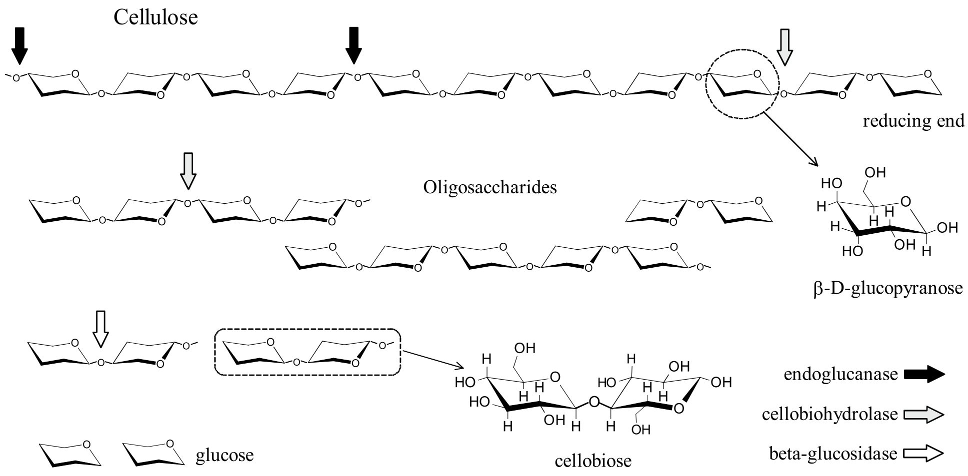

Fig. 2 Schematic representation of the mode of action of cellulolytic complex enzymes on cellulosic material with the release of oligosaccharides and monosaccharides: endoglucanase randomly cleaves the internal beta-1,4 glycosidic bonds of cellulose; cellobiohydrolase hydrolyzes cellobiose from the reducing or non-reducing end of the cellulose chains; cellobioses released as a result of these activities are converted into glucose by the action of beta-glucosidase releasing glucose

improve the yield of the enzymatic step, such as hemicellulases, lignin-peroxidases, and pectinases (Kumar & Sharma, 2017; Kumar et al., 2009; Soni et al., 2018).

Cellulases in the Beverage Industry

Cellulases and hemicellulases are used alone or synergistically with other enzymes in beverage production processes. Some cellulolytic and hemicellulolytic enzymes are applied in the extraction and clarification processes of fruit and vegetable juice. In the production of fermented beverages, such as beer, endoglucanases can be included to promote the hydrolysis of glucan, which results in a decrease in the viscosity of the wort, thus increasing its filterability. Cellulases, hemicellulases, and pectinases can be used in the red wine production process and, when used together, they are called maceration enzymes, as they act on the polysaccharide fraction of the cell wall of the grape skin cells, allowing for better maceration of the skin, an increase in the extraction of color and phenolic compounds, improving the clarification and filtering processes, the stability, and the overall quality of the wine (Ramesh et al., 2020; Sharma et al., 2016; Toushik et al., 2017). Enzymes of the cellulolytic and hemicellulolytic complex can be used to obtain aroma precursors in wine and tea, such as the synergistic action of beta-glucosidase and beta-xylosidase to produce instant green tea infusions with high aroma quality. The glycosides of monoterpene alcohols (linalool, linalool oxides, and geraniol), aromatic alcohols, and aliphatic alcohols are some of the important aroma precursors of tea products. The sugar fraction of the glycosides is typically a monosaccharide or disaccharide. The aglycone portion is linked to beta-*D*-glucopyranose and, in most glycosides, the glucose portion connects to another monosaccharide such as alpha-*L*-arabinofuranose, alpha-*L*-arabinopyranose, alpha-*L*-ramnopyranose, beta-*D*-glucopyranose, and beta-*D*-xylopyranose. After enzymatic cleavage, some released aglycones may have aromatic potential or be precursors to flavor compounds. Hemicellulolytic enzymes can act on the glycosides by cleaving the link between sugars, releasing the beta-glycoside which can subsequently undergo the action of beta-glucosidases releasing the aglycone and glucose (Ho et al., 2015).

Cellulolytic Enzymes in Baking

Cellulases can be used in dough formulation to provide good texture and quality. Endoglucanases are used due to their ability to assist in the hydrolysis of pentosans. Although pentoses are a minor part of wheat flour, due to their high-water holding capacity, they are one of the main determinants of dough rheology and bread quality. The greater the number of soluble pentosans, the greater the elasticity of the mass (Ramesh et al., 2020).

Hemicellulose

In cell walls, cellulose is linked to pectic substances by hemicellulose which comprises approximately 15–19% of the polysaccharides in the cell wall of fruits and vegetables (Toushik et al., 2017). Hemicelluloses make the primary cell walls of plants stronger through their interactions with cellulose and are constituted by an amorphous, heterogeneous, and complex carbohydrate structure, and are highly branched polymers that contain different monomers of pentoses as beta-*D*-xylose and alpha-*L*-arabinose, and hexoses such as beta-*D*-glucose, alpha-*D*-galactose, and beta-*D*-mannose. All hemicelluloses have side chains composed of acetic acid, pentoses, hexuronic acids, and deoxyhexoses such as alpha-*L*-rhamnose and alpha-*L*-fucose, which are responsible for the solubility of hemicelluloses in water or alkalis (Bonechi et al., 2017; Toushik et al., 2017).

Based on the composition of the polymer structure, hemicelluloses are classified as xylans, mannans, arabinans, xyloglucans, arabinoxylans, glucomannans, and arabinogalactans. Xylans and mannans are the main constituents of hemicelluloses in higher plants. Thus, xyloglucans are composed of glucose molecules with beta-1,4 glycosidic bonds and xylose branches in alpha-1,6 bonds, and xylans are xylose chains in beta-1,4 bonds. The main chains have branches composed of xylose or arabinose, glucuronic acid, mannose, galactose, and rhamnose. These polysaccharides are the predominant constituents in primary and secondary walls, respectively. In hardwoods and various agro-industrial residues, the hemicellulose is composed of a high content of xylans. Mannans are more prominent in the hemicelluloses of softwood, plant seeds, and fruits. Mannans are a group of polymers that comprise linear mannans, composed of beta-1,4 linked mannose units; glucomannans, which consist of the main chain containing beta-1,4-linked mannose and glucose residues; galactomannans, composed of a main chain formed by mannoses and branches with galactoses linked in alpha-1,6; and galactoglucomannans, which have the main chain containing beta-1,4 linked mannoses and glucoses and alpha-1,6 linked galactose branches. Hemicellulose is the most sensitive structure, thermally and chemically, and connects lignin to cellulose fibers, providing greater stability, flexibility and elasticity to the cellulose-hemicellulose-lignin structure (Bonechi et al., 2017; Sachslehner et al., 1998; Toushik et al., 2017; Zhong et al., 2019). Figure 3 shows the performance of the main hemicellulases.

The hydrolysis of hemicellulose by hemicellulases is important not only for the degradation of the cell wall structure, but also to improve the hydrolysis of the cellulose that

Table 2 Characteristics and applications of some microbial cellulolytic enzymes

Enzyme microorganism	Effect of the pH	Effect of the temperature	Km, Vm, substrate, molecular weight	Application	Reference
Endoglucanase *Eubacterium cellulosolvens* sp.	Optimal value of 4.0 and stable at pH 3.0–9.0	Optimal value of 50 °C	14.05 mg/mL, 45.66 µmol/min/mg, CMC, -	-	Park et al. (2018b)
Endoglucanase *Penicillium roqueforti* ATCC1011	Optimal value of 5.0 and stable at pH 5.0–7.0	Optimal value of 50 °C and stable at 40–50 °C	1.17 mg/mL, 0.90 mg/mL/min, CMC, -	-	Oliveira et al. (2019)
Endoglucanase *Tricholoma matsutake* NBRC30605	Optimal value of 4.0 and stable at pH 3.0–6.0	Optimal value of 60 °C and stable at 4–40 °C	-, -, -, 40 kDa	Cello-oligosaccharides production from barley beta-glucan	Onuma et al. (2019)
Endoglucanase *Bacillus subtilis* CBS31	Optimal value of 7.5	Optimal value of 50 °C	0.0183 mg/mL, 1293 U/mg, CMC, 35 kDa	Cello-oligosaccharides production, mainly cellobiose, and wheat bran hydrolysis	Regmi et al. (2020)
Endoglucanase *Aspergillus terreus* JL1	Optimal value of 5.0 and stable at pH 4.0–8.0	Optimal value of 60 °C	-, -, -, 56 kDa	Saccharification of macroalgal biomass	Jmel et al. (2020)
Exoglucanase *Trichoderma harzianum*	Optimal value of 5.0	Optimal value of 60 °C	2.8 mM, 1.32 IU/mL/min, avicel, -	-	Butt et al. (2018)
Exoglucanase, *Schizophyllum commune* KMJ820 (CBH1)	Optimal value of 5.0	Optimal value of 55 °C	2.0 mM, 51.4 U/mg, pNPC, 50 kDa	-	Kondaveeti et al. (2020)
Exoglucanase *Penicillium digitatum* RV 06	Optimal value of 5.2	Optimal value of 70 °C and relatively stable at 60 °C	11.2 mg/mL, 0.13 µmol/min, CMC, 74 kDa	Cellobiose and glucose production from CMC	dos Santos et al. (2020)
Beta-glucosidase *Issatchenkia terricola*	-	-	4.35 mmoL/L, -, pNPG, 48 kDa	Wine aromatic precursors hydrolysis and liberation of norisoprenoids and phenols	de Ovalle et al. (2018)
Beta-glucosidase *Aspergillus flavus*	Optimal value of 4.5 and stable at pH 3.5–9.0	Optimal value of 60 ºC and relatively stable at 55 °C	0.38 mM, 36.92 mmol/min/mg, pNPG, 94.2 kDa	Saccharification of soybean meal	Chen et al. (2019)
Beta-glucosidase *Mucor ardhlaengiktus* RSC1	Optimal value of 4.8 and stable at pH 4.6–5.0	Optimal value of 50 °C and stable at 20–30 °C	78.2 µmol/L, 28.5 µmol/L/min, salicin, -	-	Yang et al. (2019)

CMC carboxymethylcellulose, *pNPC* *p*-nitrophenyl-*D*-cellobiopyranoside, *pNPG* 4-nitrophenyl β-*D*-glucosidase is strongly bounded. Hemicellulases are classified based on their catalytic activity into glycosyl hydrolases, esterases, and carbohydrate liases, which catalyze the hydrolysis of glycosidic bonds, hydrolysis of ester bonds of lateral groups of acetate or ferulic acid, and cleavage of glycosidic bonds, respectively. Hemicellulases include a group of enzymes composed of xylanase, glucuronidase, mannanase, beta-glucanase, arabinase, and acetyl-xylanesterase (Sindhu et al., 2016; Toushik et al., 2017).

Hemicellulolytic Enzymes

Hemicellulases are part of a group of enzymes efficient in the hydrolysis of polysaccharides classified as hemicelluloses. Due to the complexity and heterogeneity of its structure, the complete degradation of hemicellulose requires the action of several hemicellulases. Xylan is the largest component of the structure of hemicellulose. Among the most important hemicellulolytic enzymes are endoxylanases (endo-beta-1,4-xylanase/1,4-beta-*D*-xylan xylanohydrolase, EC 3.2.1.8) which hydrolyze the glycosidic bonds of the xylan structure, releasing small oligosaccharides, and xylosidases (1,4-beta-*D*-xylan xylohydrolase, EC 3.2.1.37) that hydrolyze beta-1,4-type bonds releasing xylose from the non-reducing end of the xylooligosaccharides (Lopes et al., 2018; Polizeli et al., 2005; Thomas et al., 2017). Beta-mannanase (endo-1,4-beta-mannanase/1,4-beta-*D*-mannan mannanohydrolase, EC 3.2.1.78) hydrolyzes hemicelluloses composed mainly of mannans and release short mannooligomers, which can be hydrolyzed releasing mannose by beta-mannosidases (beta-*D*-mannosidase/1,4-beta-*D*-mannoside mannohydrolase, EC 3.2.1.25) (Bonechi et al., 2017; Shallom & Shoham, 2003).

There are also debranching enzymes that remove side groups or substituents like alpha-*L*-arabinofuranosidase (EC 3.2.1.55) that cleaves the alpha-*L*-1,2-, alpha-*L*-1,3-terminal and alpha residues -*L*-1,5-arabinofuranosyl; alpha-*D*-glucuronidase (EC 3.2.1.139) that cleaves the alpha-1,2 bonds between glucuronic acid residues and the main chain in glucuronoxylan; acetylxylan esterase (EC 3.1.1.6) that removes the *O*-acetyl groups from acetylxylan; alpha-1,6-*D*-galactoside galactohydrolase that removes alpha-1,6-linked *D*-galactopyranosyl substituents from the mannan main chain; and phenolic acid esterases, feruloyl esterase (EC 3.1.1.73) and *p*-coumaryl esterase (EC 3.1.1.73) that hydrolyze the ester bond between arabinose and monomeric or dimeric ferulic acid and the bonds between arabinose and *p*-cumaric acid, respectively (Kawaguti & Koblitz, 2019; Moreira et al., 2011; Polizeli et al., 2005).

Xylanases of fungal origin are generally more active at pH from 3.5 to 6.5 and a temperature between 40 and 60 °C (Thomas et al., 2017). Xylanases of bacterial origin are more active at pH between 5.0 and 8.0 and temperature ranging from 50 to 80 °C (Polizeli et al., 2005). As well as xylanases, most fungi xylosidase have an optimal activity at acidic pH range, between 4.0 and 5.0, and an optimum temperature that can vary from 40 to 80 °C (Polizeli et al., 2005). Hemicellulases are produced concurrently with pectinases by different microorganisms, where filamentous fungi are particularly interesting as they excrete the enzymes into the environment at higher levels, being the most important strains of *Aspergillus niger*, *Trichoderma* sp., and *Humicola* sp. (Gírio et al., 2010; Hamid et al., 2015).

Industrial Application of Hemicellulolytic Enzymes

Hemicellulases are mostly used by the bakery industry and in the production of prebiotic oligosaccharides (Danalache et al., 2018; Toushik et al., 2017). Depending on the raw material and processing technology, hemicellulolytic enzymes can be used simultaneously with cellulases and pectinases as macerating enzymes. Table 3 summarizes various recent publications concerning different characteristics and applications of hemicellulolytic enzymes.

Hemicellulases in the Beverage Industry

When used in conjunction with cellulases, xylanases can be applied to reduce viscosity and clarify fruit juice, and also to hydrolyze hemicellulose in fruit peels. The progressive degradation of the middle lamella between cells can be carried out by hydrolytic enzymes, which weaken the cell wall, resulting in the release of intracellular components, including water, improving the recovery of the juice. When fruit juices are treated with xylanases, carbohydrate reducing units are released, allowing better processing of the pulp, and increasing the yield of the substances contained in the fruit. Thus, the amount of reducing sugars released is the indicator of the decomposition of hemicellulosic materials by the enzyme (Adiguzel et al., 2019; da Silva et al., 2019a, 2019b).

Oligosaccharides Obtained from Xylan and Mannan

Xylooligosaccharides, oligomers made up of xylose units containing beta-1–4 bonds, are used as sweeteners or additives in foods. These oligomers are considered prebiotics that stimulates the growth of probiotic microorganisms like *Lactobacillus* sp. and *Bifidobacterium bifidum* and inhibits the proliferation of pathogenic bacteria in the intestine, such as *Clostridium* sp. and *Escherichia coli*. Thus, they are metabolized in the large intestine, stimulate the production of short-chain fatty acids, enabling health and wellness (Aachary & Prapulla, 2011; Gibson, 2004; Kawaguti & Koblitz, 2019; Lachke, 2006). In addition, studies indicate that supplementation of food with xylooligosaccharide improves intestinal

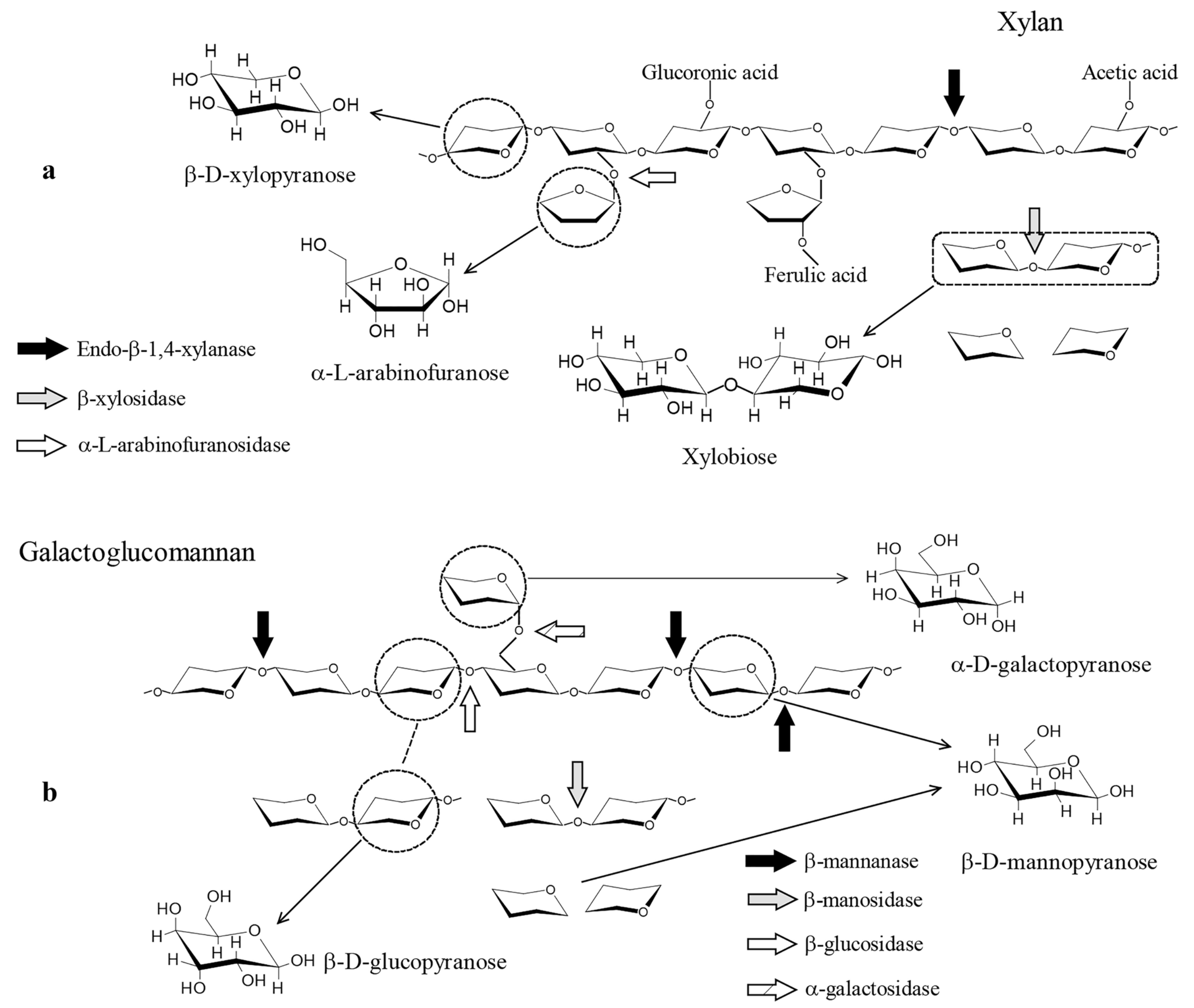

Fig. 3 Schematic representation of the mode of action of some hemicellulolytic enzymes on hemicellulosic material with the release of oligosaccharides and monosaccharides. **a** Xylan—endoxylanase cleaves the xylan backbone to release shorter xylooligosaccharides, which are hydrolyzed by accessory enzymes; beta-xylosidases release xylose monomers from xylobiose; arabinofuranosidase activity release *L*-arabinose from the xylan chain. **b** Galactoglucomannan—beta-mannanase cleave β-1,4 linkages between either mannose and glucose or mannose and mannose sugars within the backbone chain; alpha-galactosidase release galactose residues which are appended to hydroxyl groups of main chain mannose or glucose residues; beta-glucosidase enzymes cleave glucose residues from the non-reducing ends of oligosaccharides produced by the action of β-mannanase enzymes

function and calcium absorption, providing positive effects on the immune and cardiovascular system, stimulating antiallergic and anti-inflammatory activities (Aachary & Prapulla, 2009; Chung et al., 2007; Grootaert et al., 2007).

The production of xylooligosaccharides from lignocellulosic materials can be obtained directly by acid hydrolysis and further purification or in two steps: (1) extraction of hemicellulose from lignocellulosic material by self-hydrolysis processes, or by acidic hydrolysis and pre-treatment with alkalis and (2) acidic hydrolysis with the enzymatic treatment of hemicellulose using xylanases (Qing et al., 2013; Vázquez et al., 2000). The endo-beta-1,4-xylanase acts on the main chain generating xylooligosaccharides with a low degree of polymerization. The enzymatic pathway is the most desirable due to the absence of by-products generated during hydrolysis and the low formation of sugar monomers; besides that, it is considered a sustainable process, which occurs under mild pH and temperature conditions, with the possibility of reusing enzymes in some cases. However, the enzymatic process is easily inhibited by compounds present in lignocellulosic biomass, which demands the need for pretreatment to remove these compounds related to plant defense; another important

Table 3 Characteristics and applications of some microbial hemicellulolytic enzymes

Enzyme microorganism	Effect of the pH	Effect of the temperature	Km, Vm, substrate, and molecular weight	Application	Reference
Xylanase *Aspergillus flavus* L4	Optimal value of 5.5	Optimal value of 70 °C	-	Orange juice clarification* and dough rising of bread by 58.12–74.22% and 1.87–2.2-fold, respectively	Elegbede and Lateef (2018)
Xylanase *Thermomyces lanuginosus*	Optimal value of 3.0 and stable at pH 3.0–5.0	Optimal value of 60 °C and relatively stable at 50–60 °C	138.1 mg/mL, 24.05 µmol/min/mL, beechwood xylan, -	Xylan hydrolysis	Souza et al. (2018)
Xylanase *Pichia stipitis*	Optimal value of 6.0 and relatively stable at pH 3.0–5.0	Optimal and stability values at 50 °C	4.52 mg/mL, 9.17 µmol/min/mL, xylan, 31.6 kDa	Xylooligosaccharides production, mainly xylotetroase (14%), xylotriose (49%), and xylobiose (29%)	Ding et al. (2018)
Xylanase *Anoxybacillus kamchatkensis* NASTPD13	Optimal value of 9.0 and relatively stable at pH 6.0–9.0	Optimal value of 65 °C and relatively stable at 30–65 °C	0.7 mg/mL, 66.64 µM/min/mg, beechwood xylan, 37 kDa	Xylan hydrolysis, xylooligosaccharides, and xylose production	Yadav et al. (2018)
Xylanase *Phoma* sp. MF13	Optimal value of 5.0 and relatively stable at pH 5.0–10.0	Optimal value of 45 °C and stable at 40 °C	3.16 mg/mL, 2688.17 µmol/mg/min, beechwood xylan, 27 kDa	Steamed bread characteristics quality improving (specific volume and elasticity) and decreasing hardness and chewiness. Production of xylooligosaccharides (xylobiose, xylotriose, xylotetraose, and xylopentaose) from corncob xylan	Wu et al. (2018)
Xylanase *Bacillus pumilus* K22	Optimal value of 8.0 and stable at pH 5.0–10.0	Optimal value of 50 °C and stable at 40–70 °C	-, -, -, 24 kDa	Tomato juice clarification** increasing the juice yield (30%), clarity (9%), and reducing sugars (69%)	Ullah et al. (2019)
Xylanase *Penicillium roqueforti* ATCC 10,110	Optimal value of 3.0 and stable at pH 3.0–5.0	Optimal value of 60 °C and stable at 50–60 °C	1.96 mg/mL, 16.23 µmol/min/mL, beechwood xylan	-	de Almeida Antunes Ferraz et al. (2020)
Endoxylanase *Myceliophthora thermophila*	Optimal value of 6.0	Optimal value of 60 °C	8.80 mg/mL, 2.38 U/mg, RBB xylan, -	Corn stover saccharification	Basit et al. (2018)
Endoxylanase *Pediococcus acidilactici* GC25	Optimal value of 7.0 and relatively stable at pH 2.0–9.0	Optimal value of 40 °C and stable at 40–50 °C	3.10 mg/mL, 4.66 U/mg, birchwood xylan, 48.15 kDa	Fruit juice clarification*** (peach-24.47%, apricot-15.32%) and reducing the haze	Adiguzel et al. (2019)
Endoxylanase *Aspergillus japonicus* UFMS 48.136	Optimal values of 5.0–6.0 and relatively stable at pH 3.0–8.0	Optimal values of 50–60 °C and stable at 40–45 °C	2.59 mg/mL, 467.4 µmol/min/mg, birchwood xylan, 32 kDa	Fruit juice clarification** (mango-51.11%, banana-9.99%, tangerine-8.54%), and fruit peel waste hydrolysis	da Silva et al. (2019a, 2019b)

Table 3 (continued)

Enzyme microorganism	Effect of the pH	Effect of the temperature	Km, Vm, substrate, and molecular weight	Application	Reference
Endoxylanase *Bacillus licheniformis* DM5	Optimal value of 6.5	Optimal value of 50 °C and stable at 50–60 °C	1.5 mg/mL, 2.7 U/mL, birchwood xylan, 38 kDa	Xylooligosaccharides production from beechwood xylan and preprocessed corncob. Mixed xylotriose and xylobiose showed prebiotic activity	Ghosh et al. (2019)
Endoxylanase *Bacillus velezensis* AG20	Optimal value of 7.0	Optimal value of 50 °C and stable at 50–60 °C	1.25 mg/mL, 21.0 U/mL, pNPX, 45 kDa	Xylooligosaccharides production from sugar cane bagasse. Mixed xylobiose, xylotriose, and xylotetrose showed prebiotic and anti-inflammatory activities	Ghosh et al. (2020)
Beta-xylosidase *Aspergillus niger* ADH-11	Optimal value of 4.0	Optimal value of 65 °C	1.17 mM, 24.39 μmol/mL/min, pNPG, 120.48 kDa	Lignocellulosic biomass saccharification	Patel et al. (2018)
Beta-xylosidase *Thermogemmatia sp.* T81	Optimal value of 5.0	Optimal value of 65 °C and relatively stable at 50–65 °C	0.25 mM, 889.47 U/mg, beechwood xylan	Xylooligosaccharides hydrolysis from beechwood xylan and rye arabinoxylan	Tomazini et al. (2019)
Beta-mannanase *Trichoderma longibrachiatum* RS1	Optimal value of 5.7	Optimal value of 75 °C	3.33 mg/mL, 6.2 U/mg/min, LBG, -	Manooligosaccharides production from locust bean gum and guar gum	Ismail et al. (2019)
Beta-mannanase *Microbacterium* sp. CIAB417	Optimal value of 6.0	Optimal value of 50 °C	-	Manooligosaccharides production from locust bean gum (a mixture of mannobiose to mannohexose)	Purohit and Yadav (2020)
Beta-mannanase *Aspergillus oryzae*	Optimal value of 5.0	Optimal value of 60 °C	2.7 mg/mL, 1388.8 μmol/min/mg, LBG, 34 kDa	Manooligosaccharides production	Jana et al. (2018)
Beta-mannanase *Aspergillus niger* F12	Optimal value of 4.8	Optimal value of 69 °C	-	Enzymatic hydrolysis of coffee residue	Favaro et al. (2020)
Beta-mannanase *Lactobacillus casei* HDS-01	Optimal value of 5.0 and relatively stable at pH 5.0–7.0	Optimal value of 40 °C and relatively stable at 30–60 °C	2.68 mg/mL, 400.03 μmol/min/mg, LBG, 37 kDa	Fruit juice clarification**** (orange-47.55%, apple-72.3%, and pear-66.25%) and increasing the juice yield (orange-188.20%, apple-150.96%, and pear-172.62%)	Zhao et al. (2020)

Table 3 (continued)

Enzyme microorganism	Effect of the pH	Effect of the temperature	Km, Vm, substrate, and molecular weight	Application	Reference
Beta-mannanase *Kitasatospora* sp.	Optimal value of 6.0 and stable at pH 6.0–9.0	Optimal value of 60 °C	-, -, -, 37.0 kDa	Manooligosaccharides and mannose production from various mannan polymers (porang potato, palm sugar fruit, coconut cake, palm cernel cake, LBG, β-mannan, konjac, and ivory nut)	Yopi et al. (2020)

RBB xylan Remazol brilliant blue-xylan, *pNPX* 4-nitrophenyl β-*D*-xylopyranoside, *pNPG* *p*-nitrophenyl-β-*D*-glucopyranoside, *LBG* locust bean gum

*Clarification yield (%) was calculated as (volume of clear juice/volume of sample) × 100; **% Transmission at 650 nm between control and sample; ***% Decrease in absorbance at 660 nm between control and sample; ****% Transmission at 660 nm between control and sample

factor is the cost of enzymes compared to chemical reagents (Aachary & Prapulla, 2011; Qing et al., 2013).

Mannans are the second fraction present in greater quantity in hemicellulose. Different enzymes, including endo beta-mannanase, beta-mannosidase, beta-glucosidase, and alpha-galactosidase, can be used in the hydrolysis of different classes of mannans. Depending on the type of enzyme that acts on the mannans, the release of oligosaccharides of different sizes, manooligosaccharides, may occur. Manooligosaccharides, generated due to the random action of endo-beta-mannanase, are used as prebiotics to promote the health of the intestinal microbiota (Srivastava et al., 2017; van Zyl et al., 2010). The preparation of manooligosaccharides has been carried out from the coffee spent ground, guar gum, and konjac flour (Jana et al., 2018; Yopi et al., 2020).

Hemicellulolytic Enzymes in Baking

Wheat can form a viscoelastic mass and the gluten-forming proteins, gliadin, and glutenin are primarily responsible for the formation of this film and the retention of gas, produced during the fermentation process of the dough and in the early stages of baking bread and, consequently, the dough growth (Costa, 2008; Wieser, 2007). Wheat flour generally contains approximately 80% starch, 12% protein, and 2–3% arabinoxylan (Goesaert et al., 2005). Arabinoxylan in wheat flour consists of a water-soluble fraction and another non-soluble fraction, formed due to the combination of covalent and non-covalent interactions with adjacent molecules of arabinoxylans and other cell wall components, such as proteins or cellulose molecules. The non-soluble fraction harms the quality of the dough, interfering in the formation of the gluten network. This fraction has a great capacity for water retention, competing for it with other flour components, decreasing its availability for the development of gluten; still contribute to the destabilization of gas bubbles, by forming physical barriers in gluten during the development of the dough, resulting in decreased bread volume (Courtin et al., 2001; Fallahi et al., 2018; Kawaguti & Koblitz, 2019; Primo-Martín et al., 2005).

The endoxylanases act on the non-water-soluble fractions, solubilizing the arabinoxylan, leading to a loss of the ability to retain water and an increase in the viscosity, flexibility, and stability of the dough system. Furthermore, it is expected that the addition of endoxylanases during the dough processing, increase the concentration of arabinoxyloligosaccharides in bread, which should serve as a prebiotic and, therefore, have additional beneficial effects on human health. However, the excess of endoxylanase can result in fragile and inconsistent doughs, and bread with undesirable characteristics concerning the crumb structure, distribution of gas bubbles, and color of the crust. This is due to the excessive degradation of arabinoxylans and, consequently, the decrease in the water retention capacity of the mass (Fallahi et al., 2018; Sanromán & Deive, 2017; Sorensen, 2003; Vardakou et al., 2003).

Pectic Substances

Pectic substances are composed of high molecular weight structural polysaccharides, being the major constituents of the middle lamella, and components of the primary wall of young cells of higher plants. The primary wall is formed mainly by cellulose and hemicellulose, surrounded by the middle lamella, responsible for keeping cells united to each other (Cosgrove & Jarvis, 2012; Jayani et al., 2005; Zhong et al., 2019). When the vegetable stops growing, it reaches the stage of maturation and the cell starts to deposit material between the plasma membrane and the primary wall, forming the secondary wall. This is more rigid and thicker than the primary, as it contains higher proportions of cellulose and less pectic substances and hemicellulose (Zhong et al., 2019). In the secondary wall, deposition of lignin usually occurs, which gives the plant tissue greater rigidity and impermeability. Thus, the cell wall protects the plant cell without interfering with the permeability of the membrane, becoming responsible for maintaining the turgidity of the plant tissue. Fruits and vegetables contain approximately 35–40% of pectic substances (Toushik et al., 2017).

In immature fruit, pectic substances are linked to cellulose microfibrils on the cell wall; however, during the ripening of the fruit, the structure of pectic substances is altered by endogenous enzymes, which promotes the rupture of their chains, making them soluble and resulting in the softening of the plant tissue (Caffall & Mohnen, 2009). The exact chemical structure of pectic substances is still controversial, varying depending on the source and different extraction methods (Kaya et al., 2014). The pectic substrates are composed of a colloidal complex of acid polysaccharides, in which the main chain consists of residues of galacturonic acid connected by alpha-1,4 glycosidic bonds. The carboxylic groups are partially esterified by methyl ester groups and are partially or completely neutralized by one or more bases with sodium, potassium, or ammonium ions (Adetunji et al., 2017; Caffall & Mohnen, 2009; Jayani et al., 2005; Mohnen, 2008; Molina et al., 2013; Uenojo & Pastore, 2007). Side groups of the molecule chain consist of rhamnose, arabinose, galactose, and xylose. Based on the type of modification of the main chain, pectic substances are classified into protopectin, pectin, pectinic acid, and pectic acid (Bhardwaj et al., 2017; Molina et al., 2013; Ramadan, 2019).

The predominant pectic substance in immature fruits is called protopectin, and it is composed of chains of methoxylated galacturonic acids, esterified with methanol, that is linked by divalent metal ions (Ca^{2+}, Mg^{2+}); by chains of other carbohydrates such as arabinose, galactose, rhamnose, and xylose, mainly; by phosphate groups; and by hydrogen bonds. Protopectin is insoluble in water and one of the responsible for the firm texture of the fruits. During maturation endogenous pectinases, such as protopectinases (EC 3.2.1.99), act on protopectin, generating soluble pectin and contributing to the softening of the fruit (Bhardwaj et al., 2017; Kaya et al., 2014; Ramadan, 2019).

Pectin is the general term used for pectic substances capable of forming gels. These pectic substances are commercially extracted from fruits and vegetables that can present different degrees of methoxylation in the polymer, which interferes with its gel formation capacity. The pectinic acid is a group of substances that includes pectin and contains up to 75% of methoxylated galacturonate units and under suitable conditions, are capable of forming gels in the presence of a high concentration of sugars, like sucrose, in an acidic medium and are stabilized by intermolecular hydrogen bonds and hydrophobic bonds between methyl esters (Adetunji et al., 2017; Bhardwaj et al., 2017; Jayani et al., 2005; Oakenfull & Scott, 1984; Ruiz et al., 2017; Sila et al., 2009; Wang et al., 2018). The pectic acid is mainly composed of colloidal polygalacturonic acid (free or with very low content of methyl ester groups). The demethoxylated pectin is known as polygalacturonic acid or pectic acid. Pectic acids form a gel in the presence of divalent ions, such as Ca^{2+}, which causes the crosslinking between two carboxylates of two different chains through ionic strength, without the need to add sucrose. Pectic acid salts are also called pectates (Axelos & Thibault, 1991; Bhardwaj et al., 2017; Jayani et al., 2005; Ramadan, 2019; Ruiz et al., 2017).

Pectins are composed of distinct polysaccharides classified as homogalacturonans or polymers of galacturonic acid and rhamnogalacturonans, in which galacturonic acid residues are partially replaced by rhamnose residues joined by alpha-1,2 bonds. Rhamnogalacturonans have ramifications such as arabinans or arabinose polymers, galactans or galactose polymers, and arabinogalactans or mixed arabinose and galactose polymers (Danalache et al., 2018; Nighojkar et al., 2019; Sila et al., 2009). The pectin structural composition has already been reviewed by several authors (Caffall & Mohnen, 2009; Celus et al., 2018; Mohnen, 2008; Sila et al., 2009; Wang et al., 2018). The diversity of structural and molecular properties of pectin forms the basis for its various food applications, which include its health-promoting benefits and bioactivities. Low molecular weight pectin and chemically modified structures stimulate satiety-inducing effects, improves cardiovascular health, and reduces the blood glucose (Adetunji et al., 2017; Lara-Espinoza et al., 2018; Sila et al., 2009; Wicker et al., 2014).

Pectinolytic Enzymes

Pectinolytic enzymes constitute a diverse group of enzymes that catalyze the degradation of pectic substances through de-esterification reactions, by esterases and depolymerization reactions, by the action of hydrolases and lyases. Pectinases can be classified according to the preference of the substrate used, being able to act in pectin, pectic acid, protopectin, or oligo-*D*-galacturonate. According to the cleavage mechanism, pectinases can be called depolymerases or esterases. These enzymes can further be named according to the mode of action; if they hydrolyze the substrate randomly, they are endoenzymes, which lead to liquefaction and depolymerization; if they hydrolyze from the ends, they are exoenzymes of saccharification (Bhardwaj et al., 2017; Ramadan, 2019).

Pectinases, in terms of the substrate they act on, are mainly classified into three types: protopectinases, which catalyze the solubilization of protopectin, since they degrade the insoluble substrate producing a highly polymerized soluble pectin (Tapre & Jain, 2014); esterases, which catalyze de-esterification of pectin by removing methoxy esters; and depolymerases, which include hydrolases and lyases, that catalyze the hydrolytic cleavage of alpha-1,4 glycosidic bonds in the *D*-galacturonic acid of pectic substances (Garg et al., 2016; Jayani et al., 2005; Kashyap et al., 2001; Ramadan, 2019). Figure 4 shows the performance of the main pectinolytic enzymes.

De-esterifying Enzymes

The main esterase is known as pectin-esterase (EC 3.1.1.11) or pectin-methylesterase, a hydrolase that acts on the ester bond, demethoxylating galacturonic acids esterified with methanol. The result of its action is pectin molecules with low content of methoxylation or polygalacturonic acid, in addition to the release of methanol (Pedrolli et al., 2009). The action of pectin esterases on pectic substances has two important consequences: the increased susceptibility of the polysaccharide to be attacked by certain depolymerizing enzymes; and the susceptibility of the polysaccharide to precipitate in the presence of Ca^{2+} ions, by the generation of calcium pectate. The successive presence of carboxylic groups throughout the polymer allows the formation of cross bonds mediated by Ca^{2+} ions, and other divalent ions, which causes their insolubilization or precipitation (Bhardwaj et al., 2017; Ramadan, 2019).

Pectin esterases are produced by plants and microorganisms. The activity of pectin esterase is correlated with the plant physiological processes such as fruit maturation, cambial cell differentiation, and seed germination (Kohli et al., 2015). Pectin esterase of plant origin act on the non-reducing end of the polysaccharide chain, in the case of exoenzymes, or in regions close to free carboxylic groups, for the endoenzymes, and follow the demethoxylation along the molecule by a simple chain mechanism, which generates long segments of galacturonic acids in the molecule, making it highly sensitive to calcium ions precipitation. Irregularities in the chain, such as the presence of branched regions and acetylations, inhibit the action of this enzyme. Its activity is higher on substrates with a high degree of polymerization, and it is inactive on substrates of three monomer units or less. They are highly specific enzymes that hydrolyze other esters at extremely slow rates. They have optimal pH values ranging from 4 to 8 and an optimal temperature of 40 to 50 °C (Uenojo & Pastore, 2007). Fungal pectin-esterases differ from plant enzymes because they act through a multichain mechanism, promoting demethoxylation at random and, therefore, generates pectin with low methoxylation content, however, they are quite resistant to calcium precipitation, and are mainly applied in the manufacturing of jams with low sugar content (Kohli et al., 2015). The main microorganisms that produce pectin methylesterases are filamentous fungi such as *Aspergillus niger*, *A. japonicus*, *Fusarium oxisporum*, and *Penicillium nonatum*; bacteria like *Xhantomonas* spp. and *Bacillus* spp.; and yeasts like *Saccharomyces cerevisiae* (Jayani et al., 2005; Patidar et al., 2018; Ruiz et al., 2017; Uenojo & Pastore, 2007).

Depolymerizing Enzymes

Depolymerases act on alpha-1,4 glycosidic bonds between the constituent units of pectic substances and may act as hydrolases or lyases. Lyases cleave the glycosidic bond on carbon 4 with the release of hydrogen on carbon 5, via beta-elimination, with the formation of a double bond between carbons 4 and 5 of the uronide. Both enzymes can present a mode of action of endo- or exocarbohydrases (Sharma et al., 2016; Uenojo & Pastore, 2007).

Regarding the substrate, depolymerizing enzymes are characterized by acting preferentially in the bonds between galacturonic acids, in pectin with low methoxylation content or pectic acids (group 1), or between methoxylated galacturonic acids, in high methoxylated pectin (group 2). In the first group, there are polygalacturonases, which can be endopolygalacturonases (EC 3.2.1.15) or exopolygalacturonases (EC 3.2.1.67) and pectate lyases, whose activity decreases with the increase in the degree of substrate methoxylation (Jayani et al., 2005; Rebello et al., 2017). The exception is bacterial pectate lyases, endo (EC 4.2.2.2), or exopectate lyases (EC 4.2.2.9), which presents greater activity on low methoxylation pectins and not on polygalacturonic acid. In the second group, there are only pectin lyases (EC 4.2.2.10) that are strongly activated in the presence of Ca^{2+} ions and other divalent ions (Yadav et al., 2009).

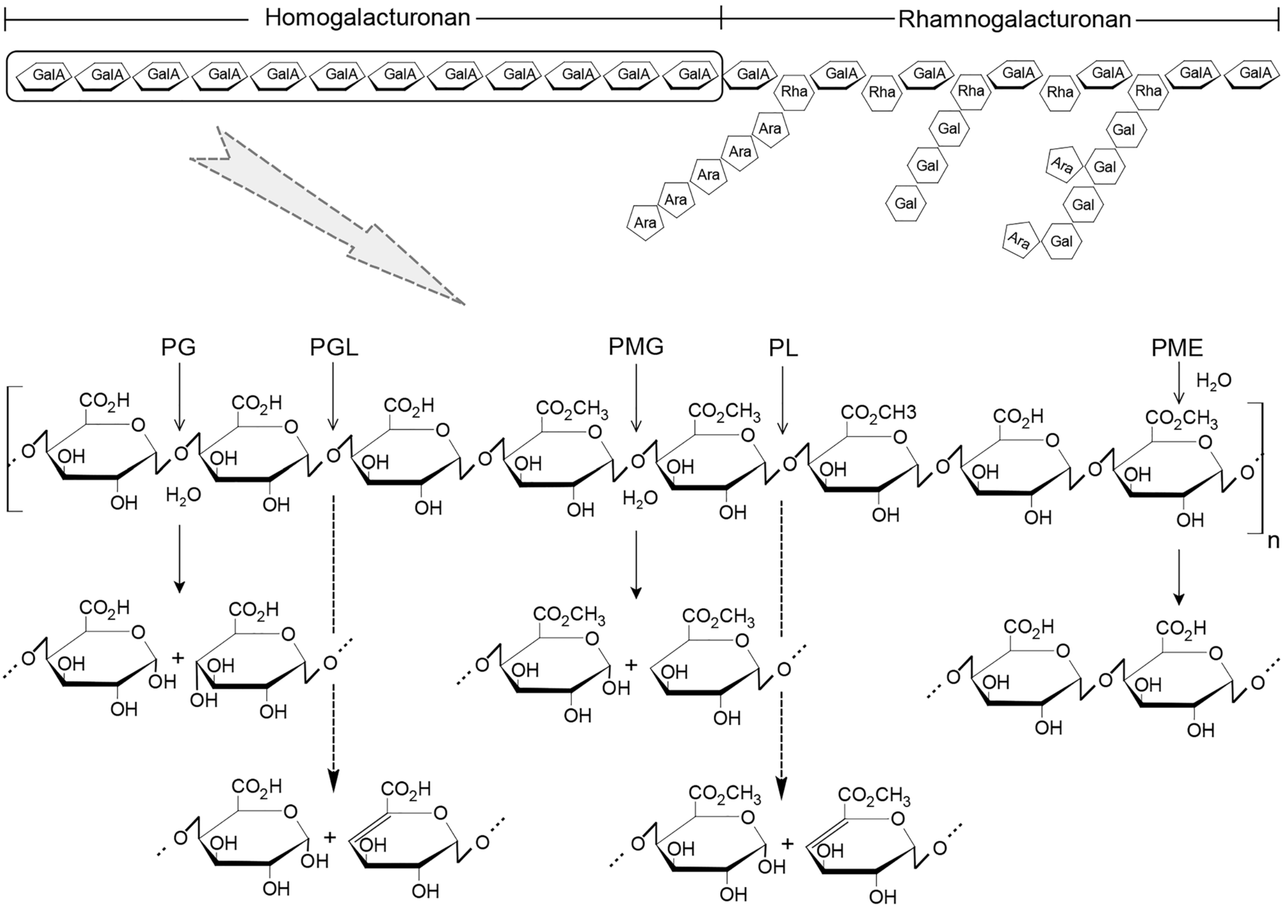

Fig. 4 Schematic representation of the mode of action of pectinolytic enzymes on pectic material with the release of oligosaccharides and monosaccharides. GalA galacturonic acid, Rha rhamnose, Gal galactose, Ara arabinose, PG polygalacturonase, PGL polygalacturonase lyase, PMG polymethyl galacturonases, PL pectin lyase, PME pectin-methyl-esterase

The presence of microbial polymethyl galacturonases is not common. However, the hydrolysis of highly methoxylated pectin can be easily achieved by the combined action of pectin esterases and polygalacturonases, and/or pectate lyases. Microbial esterases have an optimum temperature between 40 and 60 °C and an optimum pH ranging from 4.0 to 8.0. Most commercial pectinases are mixtures of fungal pectinolytic enzymes, generally from *Aspergillus* spp., containing pectin esterase, polygalacturonase, and pectin lyase activities in addition to cellulolytic activity, due to the presence of beta-endoglucanases, and hemicellulases, all enzymes produced by the same microorganism. In some cases, exocellulases from other microbial sources are added (Kavuthodi & Sebastian, 2018; Uenojo & Pastore, 2007).

Microbial enzymes have different characteristics based on the mechanism of action, biological and physicochemical properties. Fungal polygalacturonases are useful due to their high enzymatic activity. Its optimal pH of activity is in the acidic region at pH 3.5–5.5 and optimum temperature between 30 and 55 °C (Ma et al., 2016; Pan et al., 2015). However, polygalacturonases obtained from *Bacillus licheniformis* and *Fusarium oxysporum* have an optimum pH of 11 (Hassan & Ali, 2016). Pectin lyases usually have an optimum pH of 4.0–5.0 and pectin lyase from *Aspergillus* spp. (*A.oyae*, *A. japonicus*, *A. niger*, *A. ficcun*) have an optimum pH around 5.5 and optimum temperature between 40 and 50 °C. Pectate lyases usually have pH in the alkaline region, between 7.5 and 10, but in some cases, those obtained from *Erwinia* sp. are active at pH 6 and *B. licheniformis* at pH 11. This enzyme requires calcium ions for activity and optimum temperature between 40 and 50 °C (Kavuthodi & Sebastian, 2018; Uenojo & Pastore, 2007; Yadav et al., 2009).

Another group of enzymes that can be present in pectinases mixtures are the rhamnogalacturonases, which can hydrolyze the glycosidic bonds between rhamnose and galacturonic acids in the branched regions of pectic substances. Its action releases oligomers composed of galacturonic acid and neutral sugars such as rhamnose but also arabinose, galactose, and xylose, among others. This type of activity was detected in preparations of commercial pectinases produced by filamentous fungi (Kashyap et al., 2001).

Industrial Application of Pectinolytic Enzymes

Pectinases are important and potentially useful biocatalysts in several industrial sectors, including the food industry (Amin et al., 2019; Kashyap et al., 2001). A great diversity of pectinases, produced by fungal, bacterial, and yeast cultures, are available on a commercial scale. The main applications of pectinases in food industry are to be used in the fruit and vegetable juice industry to increase extraction yields and also to facilitate its clarification; to increase the level of total soluble solids; to act on the liquefaction of the pulp and reduce turbidity and viscosity; to intensify flavor and color in wine; to aid in the extraction and washing of vegetable fibers like cotton, and in the extraction of vegetable oil (e.g., olive oil); to increase the speed of tea fermentation and removing the mucilaginous layer of coffee beans; and to aid the production of alcoholic beverages and other food products of plant origin (Garg et al., 2016; Haile & Kang, 2019b; Ramadan, 2019; Ruiz et al., 2017; Sharma et al., 2016; Singh et al., 2019b; Tapre & Jain, 2014). Table 4 shows recent publications regarding the characteristics and applications of pectinases in the food and beverage industries.

Maceration

The combination of pectinases, cellulases, and hemicellulases, collectively called maceration enzymes, is used to produce pulps, nectars, cloudy or transparent juices, and their concentrates. Pectinases are used in the process of hydrolysis and solubilization of the middle lamella of plant tissues, generating fruit and vegetable pulps containing intact cells, applied in the production of baby foods, puddings, yogurts, and purees (Nighojkar et al., 2019). This process has several advantages over conventional products, such as the absence of degenerative reactions that cause enzymatic browning and the destruction of aromas and vitamins that are caused by the action of endogenous enzymes released by cell disruption. The use of enzymes also provides the maintenance of high fiber content, in which only the middle lamella is hydrolyzed and the cell walls remain an integral part of the product (Bhardwaj et al., 2017).

The use of maceration enzymes increases the extraction yield and improves processing, without increasing costs. The addition of alpha-amylase and amyloglucosidase, active at acidic pH, is used in the processing of starch-containing fruits, especially apples, to prevent turbidity (Kashyap et al., 2001; Sharma et al., 2016; Uenojo & Pastore, 2007). These enzymes are used after cutting the raw material to macerate the pulp until partial or total liquefaction of the fruit, reducing processing time, and improving the extraction of the components of the fruits. After extraction, pectinases are added for clarification and viscosity reduction to facilitate filtration and concentration (Danalache et al., 2018; Nighojkar et al., 2019).

To obtain the pulps, the vegetable and fruits are subjected to a mild mechanical disintegration and is added with polygalacturonases or pectate lyases. The action of these enzymes is moderate, in the absence of pectin esterases, causing only the middle lamella to solubilize. Thus, there is a loss of cohesion between the cells with pulp formation, in addition to the generation of oligomers, which contribute to produce a creamy product. This process can be applied in the production of carrot puree for infant food formulation and instant potato puree. In the latter, the starch must be previously gelatinized and the use of maceration prevents it from spilling out of the cells, avoiding the sticky texture in the reconstituted product (Bhardwaj et al., 2017; Garg et al., 2016; Nighojkar et al., 2019).

Extraction of Fruit Juices

The fruit juice production process consists of the separation of the liquid fraction (constituted by the vacuolar contents of the cells) from the insoluble solid fraction, that is, the fruit pulp (composed of the components of cell walls, mainly cellulose and protopectin). This separation, in general, is achieved by pressing the fruit pulp; in this case, the removal of the liquid part depends on the mechanical disruption of the cell walls and membranes (Sieiro et al., 2012). The use of maceration enzymes contributes to the rupture of the walls, consequently aiding in the separation of precipitated flocculants by filtration, sedimentation, or centrifugation (Ramadan, 2019).

In addition to pectinases, other enzymes such as cellulases, hemicellulases, amylases, and proteases are used in the juice industry as processing aids to increase the efficiency of the operation, and the quality and stability of manufactured juices (Singh et al., 2016). As tropical fruits contain a higher content of components such as cellulose and hemicellulose compared to other fruits, the use of pectinases combined with hemicellulases and/or cellulases is recommended not only for the maceration of fruits but also to develop adequate turbidity, texture, and concentration of nectars and purees in the final product reducing viscosity (Garg et al., 2016; Toushik et al., 2017). Some fruit pulps, especially those with a high content of soluble pectin such as papaya, bananas, and guava are especially difficult to press, leading to low juice yield. In these cases, the addition of pectinases to the pulp promotes hydrolysis of the pectin generating less viscous juices, easier to extract, improving the pressing characteristics, and increasing the yield (Singh et al., 2019a; Tapre & Jain, 2014).

Table 4 Characteristics and applications of some microbial pectinases

Enzyme microorganism	Effect of the pH	Effect of the temperature	Km, Vm, substrate, molecular weight	Application	Reference
Pectinase *Bacillus subtilis* Btk 27	Optimal value of 7.5	Optimal value of 50 °C	1,879 mg/mL, 149.6 U/mL, citrus pectin, -	Coffee beans demucilation	Oumer and Abate (2017)
Pectinase *Bacillus subtilis* ZGL14	Optimal value of 8.6 and stable at pH 8.0–10.0	Optimal value of 50 °C and stable at 40–50 °C	-, -, -, 65 kDa	-	Yu et al. (2017)
Pectinase *Trichoderma viride*	Optimal value of 6.0 and stable at pH 6.0–7.0	Optimal and stability values of 50 °C	-	Orange juice clarification	Mahmoud et al. (2018)
Pectinase *Chryseobacterium indologenes* SD	Optimal value of 8.0	Optimal value of 40 °C	-	Fruit juice clarification (apple and grape)	Roy et al. (2018)
Pectinase *Schizophyllum commune*	Optimal value of 8.0	Optimal value of 45 °C	-	Apple juice clarification	Mehmood et al. (2019)
Pectinase *Bacillus tequilensis* SALBT	-	-	-, -, -, 35 kDa	Demucilation of coffee beans and juice clarification	Koshy and De (2019)
Polygalacturonase *Aspergillus niger* AN07	Optimal value of 5.0 and stable at pH 4.0–7.0	Optimal and stability values of 55 °C	2.6 mg/L, 181.8 µmols/mL/min, polygalacturonic acid, 64.5 kDa	Oligosaccharides and galacturonic acid formation from polygalacturonic acid	Patidar et al. (2017)
Pectin methylesterase *Aspergillus tubingensis*	Optimal value of 4.6	Optimal value of 50 °C	-	Pineapple juice clarification* (19%)	Patidar et al. (2016)
Pectin methylesterase *Aspergillus niger*	Optimal value of 11.0	Optimal value of 55 °C	-	-	Pili et al. (2018)
Pectin lyase *Aspergillus niger* WHAK1	Optimal value of 8.0	Optimal value of 40 °C	5.2 mg/mL, 0.2 mmol/mL/min, citrus pectin, 23.3 kDa	Fruit juice clarification** (apple-219.74%, orange-206.38%, pomegranate-203.48%)	Poturcu et al. (2016)
Pectin lyase *Fusarium lateritum* MTCC 8794	Optimal value of 10.0 and stable at pH 6.0–10.0	Optimal value of 40 °C and stable at 10–50 °C	0.79 mg/mL, 0.57 U/mL, citrus pectin, 16 kDa	-	Yadav et al. (2017)
Pectin lyase *Penicillium digitatum*	Optimal value of 5.0	Optimal value of 35 °C	0.3 µmol/mL, 100 U/mL, citrus pectin, -	Apple juice yield improving	Siddiqa et al. (2018)
Pectate lyase *Bacillus subtilis* PB1	Optimal value of 9.5 and stable at pH 5.0–11.0	Optimal value of 50 °C	0.312 mg/mL, 1,248 U/mL, polygalacturonic acid and citrus pectin, 43.1 kDa	-	Zhou et al. (2017)
Polygalactorunase *Saccharomyces cerevisiae*	Optimal value of 4.5 and stable at pH 4.0–6.0	Optimal value of 40 °C and stable at 30–60 °C	0.31 mg/mL, 3.15 mmols min/mg, citrus pectin	-	Poondla et al. (2017)
Polygalacturonase *Penicillium notatum*	Optimal value of 6.0	Optimal value of 50 °C	40 mg/mL, 6.66 µmols/mL/min, citrus pectin, -	Fruit juice clarification (apple-94.22%, grape-74.32%, peach-92.71%)	Amin et al. (2017)
Polygalactorunase *Aspergillus niger* MTCC 478	Optimal value of 4.0 and stable at pH 3.0–11.0	Optimal value of 50 °C and stable at 10–40 °C	2.3 mg/mL, -, polygalacturonic acid, 124 kDa	Orange juice clarification*** (27%)	Anand et al. (2017)

Table 4 (continued)

Enzyme microorganism	Effect of the pH	Effect of the temperature	Km, Vm, substrate, molecular weight	Application	Reference
Polygalacturonase *Calonectria pteridis*	Optimal value of 4.0 and relatively stable at pH 3.6–6.0	Optimal value of 60 °C and stable at 50 °C	0.52 mg/mL, 5.86 U/mL, polygalacturonic acid, 64.5 kDa	Apple juice clarification and volume yield improvement (11.92%)	Ázar et al. (2020)
Polygalactorunase *Penicillium janczewskii*	Optimal value of 6.0	Optimal value of 45 °C	10 mM, 41.67 U/mL, citrus pectin, -	Fruit juice clarification*** (apple-83.64%, mango-92.73%, peach- 89.33%)	Amin et al. (2020)

*% Transmittance at 650 nm between control and sample; **% Transmittance at 600 nm between control and sample; ***% Transmittance at 660 nm between control and sample

Pulp liquefaction

The process of transforming pulp into juice does not require pressing. In this case, the pulp is practically all liquefied by the hydrolysis of the middle lamella and the pectin of the cell walls in vegetables and fruits (Uenojo & Pastore, 2007). For the process to be efficient, pectinases such as polygalacturonases, pectin methylesterases, and pectin lyases, should be used together, in addition to cellulases and hemicellulases that, due to the synergism of their activities, are capable of hydrolyzing up to 80% of the polysaccharides present in the pulp. The degree of hydrolysis obtained to produce clear, cloudy, or viscous juices depends on the access of enzymes to the substrate and is mainly related to the presence and concentration of lignin in the product. Papaya juices obtained in this way are completely clear, while apple juices are cloudy and carrot juices are viscous (Kashyap et al., 2001; Kohli et al., 2015).

Enzymatic hydrolysis of cell walls increases the extraction yield and decreases the content of sugars, soluble dry matter, galacturonic acids, and titratable acidity. The resulting pulp has low viscosity and the residue content of the pulp is reduced (Kashyap et al., 2001). Liquefaction is a relevant process in several aspects because it increases the solids content of the juice, which is of interest to the concentrated juice industry; reduces the production of waste because there is no bagasse generation; and can be successfully applied to fruits that are not adapted well to the conventional extraction process by pressing such as banana, mango, and guava (Garg et al., 2016; Kashyap et al., 2001; Kohli et al., 2015; Ramadan, 2019; Uenojo & Pastore, 2007).

Clarification of Fruit Juices

The clarification of fruit juices is the largest and oldest application of commercial pectinases. After extraction, most fruit juices have high viscosity and turbidity. In juices such as orange, turbidity is desired and must be preserved by inactivating the pectin methylesterases, naturally present in the juice. This enzyme removes the methoxylated groups forming partially methylated pectin which, in the presence of calcium ions, forms insoluble calcium pectate leading to precipitation, being an undesirable effect of the particles. However, grape, apple, and pear juices are marketed clarified and must be subjected to a filtration or centrifugation process to remove turbidity. To degrade pectin, pectin methylesterase is used in combination with other pectinases, such as polygalacturonase and pectate lyase (Patidar et al., 2018; Uenojo & Pastore, 2007).

The addition of pectinases reduces the viscosity and causes precipitation of the turbid particles, facilitating their removal by the filtration and centrifugation processes, increasing the yield of the clarified juice and the useful life of equipment such as filters (Kohli et al., 2015; Ramadan, 2019; Sieiro et al., 2012). Turbidity in juices is caused by proteins from the plant cytoplasm, positively charged in the acidic pH of the juices, covered by a negatively charged pectic substance. These particles remain in suspension due to the repulsion of their negative surface charge. The partial pectin degradation of these particles leads to the exposure of the protein nucleus, containing a positive charge, promoting the attraction of the nucleus of some particles by the layer of others. This attraction generates very large particles that precipitate (Kawaguti & Koblitz, 2019; Kohli et al., 2015; Sorrivas et al., 2006).

The viscosity of the juicy is caused by dissolved pectin and hemicellulose, not compromised with the protein particles. When these particles are hydrolyzed into smaller chains, due to depolymerization, the viscosity is significantly reduced. Clarification and viscosity reduction can be achieved by the combined use of pectin esterases and polygalacturonases, indicated for all juices and mainly for grape juice, whose pectin has a low methoxylation content, or by the addition of pectin lyases, indicated for apple juices, whose pectin is highly esterified. It is important to note that the juice pH must be such that the protein particles assume a positive charge. In juices with artificially high pH, the action of pectinases does not affect the removal of turbidity (Nighojkar et al., 2019; Toushik et al., 2017). The review work by Nighojkar et al. (2019) and Ramadan (2019) shows a summary of the results of research on the application of pectinases in the clarification of fruit juice. Table 5 presents the application of pectinases in the processing of fruit juice.

Enzymatic Peeling

The peel removal of the fruits is obtained by hydrolysis of the fruit albedo, mainly orange, and grapefruit, between the peel and the pulp and between segments of the pulp, to separate the fruit into segments. The process depends on the application of pectinases, under pressure or vacuum, to whole fruit. After the hydrolysis time, the skin must be removed manually. The fruit slices are then cooled and packaged for sale as minimally processed products. The concentrated mixture of pectinases, hemicellulases, and cellulases is used as an enzymatic treatment to peel apricots, nectarines, and stone fruits, like peaches. To remove orange peel, only pectinases or a mixture of hemicellulases with polygalacturonases and arabinase showed good results in mild temperatures (Kohli et al., 2015; Sharma et al., 2016).

Release of Aroma Precursors in Wines

Three main exogenous enzymes, pectinases, beta-glucanases, and hemicellulases, have been widely used to hydrolyze the cell wall polysaccharides to improve the maceration and extraction process of grape skin pigments, to optimize the processes of clarification and filtration, and to improve the quality and stability of wine (Chaudhri & Suneetha, 2012). Monoterpene alcohols are considered extremely important substances in the aroma formation of different types of wine (Uenojo & Pastore, 2007). The release of these alcohols depends on the hydrolysis of the glycosylated terpenes present in the fermented wort and which is obtained by the action of beta-glucosidases and hemicellulases, such as arabinosidase, rhamnosidase, among others (Kawaguti & Koblitz, 2019). Currently, pectinase from *Aspergillus niger* and *Penicillium notatum* are used during wine preparation to improve the opacity condition and the extraction capacity of the soluble components of grapes, by reducing the filtration time and increasing the must volume. Consequently, the addition of pectinase increases the amount of extractable phenolic components, such as polymeric anthocyanins and tannins, which are responsible for the improvement of taste and color intensity in wines (Jayani et al., 2005; Kawaguti & Koblitz, 2019; Uenojo & Pastore, 2007).

Commercial pectinase preparations with high pectin lyase activity and low pectin methylesterase activity are preferred as they minimize methanol release from methoxylated polygalacturonic acids during wine production. The hydrolysis of cell wall components favors the release of pigments into the juice. This effect is especially desired in the production of red wine, reducing the time of maceration of the skin in the must, necessary for the extraction of anthocyanins. In these procedures, the combination of applied enzymes can be the same as the used for clarification, where the degree of esterification of the pectin of the used fruit should also be considered (Hüfner & Haßelbeck, 2017; Nighojkar et al., 2019; Toushik et al., 2017).

Elimination of Bitterness in Citrus Juices

The bitterness in citrus juices is mainly due to the presence of naringin, a flavanone glycosylated by a disaccharide composed of rhamnose joined to glucose by an alpha-1,2 bonds. The release of aglycone by specific carbohydrases provides the elimination of a bitter taste and is achieved by the successive removal of residues of *L*-rhamnose and *D*-glucose through the action of naringinase (EC 3.2.1.40), a heterodimeric complex, composed of two subunits with specific activities of alpha-*L*-rhamnosidase (EC 3.2.1.40) and beta-glucosidase (EC 3.2.1.21). Removal of rhamnose

Table 5 Applications of pectinases and modification of some characteristics of fruit juice

Enzyme microorganism	Extract/enzyme concentration	Turbidimetry/viscosity/clarification (%)	Effect	Reference
Exo-Polygalacturonase *Penicillium notatum*	Apple juice/- Grape juice/- Peach juice/-	73.78/69.02/94.22* 71.10/85.24/74.32* 88.25/82.61/92.71*	Juices of apple, grape, and peach were highly turbid and viscous, after enzymatic treatment, a significant reduction in turbidity and viscosity was recorded, a considerable amount of clarity was achieved following treatment of juice samples with enzyme	Amin et al. (2017)
Exo-polygalacturonase *Penicillium janczewskii*	Apple juice/- Mango juice/- Peach juice/-	-/72.94/83.64** -/57.25/92.73** -/72.67/89.33**	Enzyme treatment showed promising results in yield and clarity improvement, viscosity reduction, and also improved the total antioxidant (95% increase in the case of apple) and total phenolic (9% increase in case of apple) contents of the fruit juices	Amin et al. (2020)
Pectinase *Aspergillus niger*	Apple juice/-	-/7.20/-	The concentration of soluble sugar, clarity, and viscosity of the juice as well as the juice extraction yield was significantly improved by pectinolytic activity	Mahmoodi et al. (2017)
Pectinase *Trichoderma viride*	Orange juice/0.573 mg protein/mL	98.80/86.14/-	A decrease in the viscosity and turbidity values with the removal of suspended particles	Mahmoud et al. (2018)
Pectinase *Aspergillus niger* LB-02-SF	Strawberry juice/ 1 U/mL	60.00/40.00/-	Enzymatic treatment resulted in no significant difference in terms of turbidity or a viscosity decrease, and did not affect the content of total phenolic compounds, anthocyanins, and antioxidant activity	Sandri and Silveira (2018)
Pectinase *Aspergillus* sp.	Orange juice/1%	-/-/21.00***	The yield of the juice, the total soluble solid, and clarity was increased as the concentration of the pectinase increased	Kc et al. (2020)
Pectin lyase *Aspergillus niger*	Orange juice Pomegranate juice Apple juice	54.17/-/206.38**** 71.43/-/203.48**** 57.45/-/219.74****	Enzyme induced viscosity reduction in fruit juice samples, and it was effective for clarification, and also showed that apple juice had a lower viscosity and higher transmittance values as compared to orange and pomegranate juices	Poturcu et al. (2016)
Polygalacturonase *Aspergillus niger* MTCC 478	Orange juice/ 50 µL/mL	-/-/27.00**	The transmittance of the treated juice increased because of the removal of colloidal and suspended particles in the juice	Anand et al. (2017)

*Reduction in absorbance at 660 nm; **Transmittance increasing at 660 nm between control and sample; ***Transmittance at 540 nm; ****Transmittance at 600 nm

generates prunin that reduces bitterness since prunin is about three times less bitter than naringin (Singh et al., 2019a).

Most commercial preparations, generally called naringinases, have both alpha-*L*-ramnosidase and beta-glucosidase activities and are produced mainly by filamentous fungi, especially of the *Aspergillus* genus (Kawaguti & Koblitz, 2019; Singh et al., 2019a). Another flavanone of importance in concentrated citrus juices is hesperidin (Singh et al., 2019a). Its glycosylated form, by the same disaccharide as naringin, can crystallize in concentrated juices, especially from tangerine, causing undesirable changes in appearance and mouthfeel. However, aglycone of the hesperedin is much more soluble and does not crystallize under normal processing and storage conditions for these products. Commercial naringinases are efficiently applied to hydrolyze hesperidin, preventing the occurrence of crystals (Kawaguti & Koblitz, 2019; Singh et al., 2019a).

Essential Oil Recovery and Vegetable Oil Extraction

Aqueous enzymatic extraction is a technique that uses enzymes to assist the extraction of oil from plant structures such as fruit peels, pulps, and seeds. The selection of enzymes depends on the structure and composition of the cell plant wall. The aqueous enzymatic extraction is considered an eco-friendly process since it reduces the chemical load generated by organic solvents. The main function of the enzymes is to degrade and break the cell wall of a plant structure to facilitate the release of oil from the matrix. The enzyme application can be isolated or by combining different enzymes with a positive effect on oil yield (Mwaurah et al., 2019). Pectinases are used in combination with cellulases to extract oil in different cultures, by liquefying the structural components of their cell walls. Citric oils, such as lemon, can be extracted with pectinase (Jayani et al., 2005). Essential oils are located especially in the cells of citrus fruit albedo and contain hydrocarbons like terpenes and sesquiterpenes, oxygenated compounds such as aldehydes, esters, alcohols, ketones, and phenols, and non-volatile residues like waxes, flavonoids, and fatty acids (Kashyap et al., 2001). Pectinase hydrolyzes pectin–protein complexes, eliminating the emulsifying properties of the pectin, which interferes with the extraction, turning the obtention of citrus peel oils possible.

Pectinase preparations are also used in the olive oil industry to increase oil extraction production and to improve oil quality indicators. Commercial enzymatic preparations containing pectinases, cellulases, and hemicellulases started to be used for the extraction of olive oil, being added during the pressing of olives to improve the extraction process (Bhardwaj et al., 2017; Kashyap et al., 2001; Kawaguti & Koblitz, 2019; Kohli et al., 2015). The extraction of olive oil was evaluated by Al-Rousan et al. (2019) and the yield increased 4.38% (at 0.08% of enzyme concentration), 3.29% (at 0.10%), and 5.25% (at 0.12%) in olives Nabali Baladi cultivar treated with cellulase, pectinase, and 1:1 (cellulase:pectinase), respectively. Regarding the extraction of oil from oil seeds, the selection of enzymes depends on the anatomy of the seed, the type of enzyme in use, and its constituents. Generally, the best conditions for the enzymatic extraction of oil from different oilseeds are an enzyme to substrate ratio of 1% to 8%, temperature between 40 and 55 °C, and a pH of 4 to 8 (Mwaurah et al., 2019).

New techniques are applied to increase the yield and quality of oil extraction, such as microwave-assisted enzymatic extraction that uses microwave radiation as the main extraction agent and enzymes as auxiliary agents. This technique uses the properties of enzymes such as high selectivity, its ability to catalyze specific reactions, and great specificity, to increase the efficiency of the extraction of the entire process. In addition, the application of microwave energy produces synergistic effects, increases the rate at which enzymatic reactions occur, decreases the effects of enzyme denaturation, therefore, increases its stability profile. This method was used to extract cherry seed oil with a 2.7% concentration of enzymatic cocktail composed of cellulase, hemicellulase, and pectinase (1/1/1, w/w) (Hu et al., 2018); extraction of tiger nut oil (*Cyperus esculentus* L.) with a concentration of 2% of an enzyme mixture containing cellulase, pectinase, and hemicellulase (1/1/1, w/w) (Hu et al., 2020); and extraction of oil from Buriti (*Mauritia flexuosa*) using cellulases, pectinases, and proteases in different concentrations (Silva et al., 2019a, 2019b).

Fermentation of Coffee

Coffee fermentation is essential to remove mucilage from the bean, which is composed of polysaccharides such as pectin, cellulose, and starch. Mucilage can prolong the time needed for drying the beans and can lead to the development of fungi, which reduces the final quality of the coffee. The fermentation process is facilitated by enzymes that occur naturally in the coffee fruit and the microflora acquired from the environment; thus, microorganisms play an important role in the degradation of mucilage, producing various enzymes, alcohols, and acids during the fermentation process. The most important enzymes produced by microorganisms to degrade pectin substances during coffee fermentation are pectin lyase, polygalacturonase, and pectin methylesterase. Currently, studies demonstrate that the use of initial cultures collaborates with the microbiota in the fermentation of coffee. A culture starter is a microbiological culture previously selected and added to the coffee beans that can accelerate the fermentation process in addition to better uniformly controlling the process, thus improving the physical, chemical, and sensory profile of the coffee (Haile & Kang, 2019a; Siridevi et al., 2019). Another process that can also be used is the addition of pectinases to remove the mucilage layer from pulped coffee seeds (Koshy & De, 2019). Pectinase removes the mucilaginous coating of the bean, preventing the appearance of an astringent flavor in the final product, after drying and roasting (Bhardwaj et al., 2017; Haile & Kang, 2019a; Kashyap et al., 2001; Koshy & De, 2019).

Modification of Pectin for Use in Food

Pectin produced from apple and orange peels has wide applications in the food industry as gelling, thickening, and stabilizing agents. The degree of esterification (DE) of the pectin molecule induces its functional properties, which can vary from 0 to 100% and, based on DE, pectin can be classified into two groups: pectin with a high methoxylation content, with DE greater than 50% and low methoxylation pectin, with DE less than 50%. Pectin can be modified by pectin methylesterase to obtain the desired DE value. Low DE pectin is particularly useful for obtaining gels without the use of sugar and acid (Kohli et al., 2015). Pectin with a high methoxylation content is used for the preparation of jellies where the pectin gelling mechanism is based on hydrophobic interactions and dehydration at low pH, less than 4.0. In these gels, the presence of high concentrations of sugar, greater than 60%, is essential for gelation. Low methoxylation pectin produces gels by ionic interactions in which calcium or other divalent cations interact with the free carboxylic acid of two adjacent chains and promote crosslinking of these chains. In this gelling mechanism, the sugar concentration is not very important. Thus, low methoxylation pectin is suitable for the production of low-sugar jellies (Kohli et al., 2015; Sila et al., 2009; Wang et al., 2018).

Other Applications

Pectinolytic and cellulolytic enzymes can be used as process aids to improve the yield of cassava starch extraction. After the extraction of starch from cassava, a considerable amount of starch granules is retained in the residual pulp of the cassava. The remaining granules are aggregated and retained in a fibrous network that can be broken by enzymatic methods, which is based on the synergistic action of pectinase and cellulase that destroy the structural integrity of the matrix responsible for the retention of the granules, exposing and releasing the starch (Sriroth et al., 2000; Uenojo & Pastore, 2007).

Pectic polysaccharides are being studied as bioactive food ingredients. The pectin modified by pectinase finds application as functional ingredients in different food products for probiotic applications. These pectic oligosaccharides and their products modified by pectinases are classified as probiotics, as they are not digestible, that is, they are not hydrolyzed in the upper part of the gastrointestinal tract, and can be used as health promoters by selectively stimulating the growth or activity of bacteria beneficial in the intestinal colon. The non-degraded modified pectin in the human intestine is applied as dietary fiber, increasing the viscosity in the intestinal tract, which leads to reduced cholesterol absorption and the excretion of bile acids and neutral sterols. De-esterified pectin is fermented more quickly by intestinal bacteria, producing short-chain fatty acids that protect the intestine against inflammatory diseases and modulate the release of hormones (Khan et al., 2013; Uenojo & Pastore, 2007).

Conclusion

The application of cellulolytic, hemicellulolytic, and pectinolytic enzymes in the degradation of the cell wall and medium lamella of fruits and vegetables improves the quality of products and increases the performance of processes in the food and beverage industries. Pectinolytic enzymes in combination with cellulases and hemicellulases have been extensively used in various fruit and vegetable processing industries. The sensory attributes of quality that can be improved in the production of fruit and vegetable products are color and appearance, flavor, aroma, texture, and turbidity. Bioactive compound availability, including phytochemicals and phenolics, are also important quality parameters depending on the product. Cellulase, hemicellulase, and pectinase, in combination with other types of enzymes, are helping many industrial processes to provide better products for human consumption. However, there is still a need to improve novel and sustainable production processes. Enzymatic applications have increased due to rapid progress in developing native enzymes and discover new enzymes from microbial resources. This trend should continue due to engineered enzymes obtained by many molecular techniques such as genomics, metagenomics, recombinant DNA technology, directed evolution, and synthetic microbiology that are becoming routine. Microbial enzymes have been used as processing aids to improve product quality parameters and increase the efficiency of fruit and vegetable processing operations. The optimization of processes leads to an increase in product yield and a shorter processing time. The main parameters to be considered in any enzymatic reaction are pH, temperature, amount of enzyme, treatment time, and presence of inhibitors. The enzymatic treatment conditions depend heavily on the type of raw material employed. Novel enzyme activity and stability should be designed and developed under challenging processing conditions.

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Declarations

Conflict of Interest The authors declare no competing interests.

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