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REVIEW

Fungal pectinases: an insight into production, innovations and applications

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Abstract

The fungal system holds morphological plasticity and metabolic versatility which makes it unique. Fungal habitat ranges from the Arctic region to the fertile mainland, including tropical rainforests, and temperate deserts. They possess a wide range of lifestyles behaving as saprophytic, parasitic, opportunistic, and obligate symbionts. These eukaryotic microbes can survive any living condition and adapt to behave as extremophiles, mesophiles, thermophiles, or even psychrophile organisms. This behaviour has been exploited to yield microbial enzymes which can survive in extreme environments. The cost-effective production, stable catalytic behaviour and ease of genetic manipulation make them prominent sources of several industrially important enzymes. Pectinases are a class of pectin-degrading enzymes that show different mechanisms and substrate specificities to release end products. The pectinase family of enzymes is produced by microbial sources such as bacteria, fungi, actinomycetes, plants, and animals. Fungal pectinases having high specificity for natural sources and higher stabilities and catalytic activities make them promising green catalysts for industrial applications. Pectinases from different microbial sources have been investigated for their industrial applications. However, their relevance in the food and textile industries is remarkable and has been extensively studied. The focus of this review is to provide comprehensive information on the current findings on fungal pectinases targeting diverse sources of fungal strains, their production by fermentation techniques, and a summary of purification strategies. Studies on pectinases regarding innovations comprising bioreactor-based production, immobilization of pectinases, in silico and expression studies, directed evolution, and omics-driven approaches specifically by fungal microbiota have been summarized.

Keywords Pectinases · Microbial enzymes · Fungal enzymes · Purification metagenomics · Omics · Immobilisation · Directed evolution

Introduction

The idea of sustainable and innovative bio-economical use of science is the basis for scientific advancements. With more than 4000 different enzymes reported, an average of 200 enzymes has the potential for commercialization, although only 10% can be industrially produced. There is huge potential in the enzyme market, which was reported to be around 6.3 billion dollars in 2017 and has a projection of a compound annual growth rate (CAGR) of 6.8% until 2024. Over the next five years, the food enzyme market is expected to grow by 7.5%, the highest rate of any market projected in the industry (Food enzyme trend gminsight). The thrust to uplift the production of renewable resources is greatly impregnated with the requirement of low-cost yet highly efficient systems (Joshi et al. 2018; Raveendran et al. 2018). White biotechnology is dedicated to harnessing biocatalysts i.e., enzymes and microorganisms at an industrial scale (Meyer et al. 2020, Cairns et al. 2021). The mandate of white biotechnology is to provide pure and replenishable sources as potential alternatives for industrial acceleration resulting in improved, bio-economical, and highly sustainable products (Hyde et al. 2019).

The microbial system is the foundation of biotechnological applications and innovations. The fungal community is a highly exploited eukaryotic system that can be applied directly or by acting as the source to produce industrially important products (Joshi et al. 2018). Filamentous fungi

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are efficient decomposers that can feed on and break down organic materials and polymeric compounds. Industrial production of commercial citric acid marks the stepping stone of fungal biology as an important commercial industrial product. Enzymes are the backbone of sustainable environments and harnessed industrially for centuries. The fungal system has been a pioneer source of these commercially applicable enzymes. Cellulases, amylases, pectinases, laccases proteases, and lipases are secreted by fungal cells (Hyde et al. 2019; Meyer 2019). These enzymes hydrolyse plant polysaccharides such as cellulose, starch, pectin, proteins, and lipids respectively. Their wide substrate interaction leads to microbial enzymatic intervention in food and feed, pulp and paper, detergent, fuel, pharmaceutical, and chemical sectors (Ahmed et.al. 2021, Kordi et al. 2022).

Pectin alone constitutes approximately 35% of the plant cell wall composition and shows structural complexity and diversity. Pectin polysaccharide gives plant tissues their tensile strength and rigidity. Pectin is frequently employed in the food sector as a gelling agent, thickening, emulsifier, or stabilizer. It can also be used in the pharmaceutical industry as a blood pressure stabilizer, cholesterol controller, and detoxifier (Gawkowska et al. 2018). Natural sources of pectin include fruit waste from pomegranate, banana, lemon, orange, pineapple, wheat bran, malt sprout, and rice bran. Their physiological properties though isolated from different sources remain similar and are beneficial to humankind (de Souza and Kawaguti 2021).

Pectinases are the group of hydrolases, depolymerase, esterases, and lyases enzymes. These act on pectin, protopectin, pectic acid, and galacturonate (Yadav et al. 2009a). Based on the mode of action, specificity of the substrate, and cleavage mechanism there exists a diverse family of pectinolytic microbial enzymes. In this emerging era of biotechnological innovations, fungal pectinase accelerates its way as a promising natural biotechnological innovative agent (Nighojkar et al. 2019; Anand et al. 2020). Microbial pectinases have a broad range of applications and high catalytic effectiveness has significantly raised the global demand. Microbes are natural sources of pectinases that are often employed due to their simplicity of manufacture and distinctive physicochemical features. With a 25% share in the market for food and beverage enzymes, the pectinases family of enzymes is a great part of the biotechnological industry. They are on top of the list of industrial enzymes made for commercial production. Pectinases of acidic nature are preferred for clarification of fruit juices, maceration of vegetables in the manufacturing of pastes and purees, and winemaking. Alkaline pectinases are often used in the retting of natural textile fibres, treatment of pectic-rich wastewater, fermentation of tea, extraction of vegetable oil, and treatment of paper and pulp (Kohli and Gupta 2015; Patidar et al. 2018; Thakur et al. 2021).

The literature available on microbial pectinases has established the importance of the catalyst in industrial sectors. The present review is solely inclined towards fungal pectinolytic interventions in enzyme biotechnology. The status of fungal pectinases and their cost-effective production strategies, the factors affecting production, the large-scale bioreactor-based productions and the purification of the enzyme have been highlighted in this review. Further, emphasis has also been made to include the recent innovations like immobilisation, directed evolution and omics-based approaches targeted in fungal pectinases.

Pectin

Pectin is an abundant natural product predominately observed in dicotyledonous plants. It is secreted by Golgi bodies into the apoplast of cells that are richly methyl-esterified (Sinclair et al. 2018). The committee of the American Society in 1944 accepted definitions of pectic substances, which include pectin acids, pectic acids, and protopectin within the complex class of these macromolecules. The pectinic acids are colloids of galacturonic acids methyl ester and pectic acids without methyl ester (Harholt et al. 2010). Protopectin is considered the parent molecule of a pectic substance and together with pectin and pectic acids was then summarised as "pectin" (Mohen 2008, Anderson 2019).

The solubility behaviour of pectins is categorised as (i) pectins soluble in water or diluted solutions, (ii) pectins soluble in chelators like EDTA, and (iii) protopectin soluble in alkaline or hot solutions based on this observation. The water-soluble and chelator-soluble pectins are derived from the middle lamella of the plant cell wall. These are composed of galacturonic acid residues with a tenth of neutral sugars and barely 2% rhamnose (Voragen et al. 2009; Patidar et al. 2018). The distribution of sugars attached with free carboxyl groups gives the classes their nature of water and chelator solubility. Pectin of alkaline solubility are embedded in part of the cell walls. Alkali-soluble pectins are structured with arabinose and galactose sugars. Typically, softening during ripening or heating is accompanied by a decrease in the proportion of protopectin and an increase in water-soluble pectin (Yapo 2011).

Apart from solubility, pectin has variable percentages of esterification as (i) High-methoxyl pectins, having esterification levels between 40 and 50%, and (ii) Low-methoxyl pectins with esterification levels below 40%. The esterification level can be controlled by acid, alkali, or enzyme treatment of high-methoxyl pectins. This imparts pectin its unique characteristics and helps form gels under specific conditions. The pectin polysaccharide is made up of distinct categories of sugars representing unique structures (Voragen et al. 2009; Wusigale et al. 2020). There are 17 different

monosaccharides linked with approximately more than 20 different linkages. These together give pectin a macro-complex structure (Yang and Anderson 2020; Gutierrez-Alvarado et al. 2022). These sugars govern the role of pectin in cell adhesion and separation, expansions and regulation of plant cell walls, and the development of organs and plants.

The complex nature of pectin structure includes components like homogalacturonan (HG), xylogalacturonan (XGA), homogalacturonan, rhamnogalacturonan I (RGI), and rhamnogalacturonan II (RGII) (Yang and Anderson 2020). The key constituent of the spine is α-1,4-linked galacturonic acid (GalA) residues. These residues undergo esterification at six carboxyl carbon and acylation at the third or second oxygen of the chain. This base is alternatively lined by rhamnose sugar and galacturonic acid residues having a structurally similar side chain of arabinose and galactose sugars. Homogalacturonan accounting for 60% of the total pectin structure forms the smooth region of sugar residues. The neutral sugars together are ramified to form a hairy sugar region. Rhamnogalacturonan II (RGII) within HG constitutes twelve different types of sugar resides, including 3-deoxy-lyxo-2-heptulosaric acid (DHA), 3-deoxy-manno-2-octulosonic acid (KDO), apiose and acetic acid. The reproductive tissues, fruits, and seeds store the xylogalacturonan. It forms a single side chain of units of b-D-Xylp-(1 → 3) which is commutated with HG molecules (Zdunek et al. 2021; Shin et al. 2021; Gutierrez-Alvarado et al. 2022).

Pectinases family: an overview

Pectinases act on pectic substances. They possess negative charge, high molecular weight glycosidic bond-linked macromolecules with substrate specificities on pectin (Anderson 2019). Pectinases are classified in respect of the type of modifications of the backbone chain as protopectin, pectic acid, pectin acid, and pectin. Pectinases amalgamate together lyases, hydrolases, and esterases classes of enzymes to act on pectin (Yadav et al. 2009b, Pedrolli et al. 2009). These can work endogenously by cleaving glycosidic bonds to release residues from the inside or in an exogenous manner to cleave residues from the ends. These can be produced through extracellular or intracellular modes. Though intracellular secretion is more costly in comparison to extracellular production. The classification of pectinases or pectinolytic enzymes based on the existence of different pectic substances, reaction mechanisms, and degradation of the hairy and smooth regions has been reported (Kashyap et al. 2001; Jayani et al. 2005; Favela-Torres et al. 2006).

A discrete collection of two hundred and sixty-nine enzymatic families that are similar on grounds of amino acid sequence are called the Carbohydrate-modifying enzymes. This family is broadly distributed under four classes: glycoside hydrolases (GHs), glycosyltransferases (GTs), polysaccharide lyases (PLs), and carbohydrate esterases (CEs). These classes have subgroups of structurally and catalytically related families. This has been listed in the carbohydrate-active enzyme (CAZy) database (www.cazy.org) (Cantarel et al. 2009). Pectinases share a diverse group of enzymes that distinctively occupy their positions in the GH, PL, and CE families (Drula et al. 2022).

Glycoside hydrolases (GH)

Family GH28 is commonly referred to as polygalacturonases, which are glycosidases acting on homogalacturonan and rhamnogalacturonan components of pectin. This includes enzymes with hydrolysis mechanisms. They are capable of hydrolysing glycosidic linkage between carbohydrates -carbohydrates and a non-carbohydrate moiety. GH28 enzymes are also categorized into three distinct categories acting on homogalacturonan, rhamnogalacturonan and xylogalacturonan (Sprockett et al. 2011; Villarreal et al. 2022). It hydrolyses polygalacturonic acid on α-1,4-glycosidic linkages producing D-galacturonate. Fungal polygalacturonase can produce monomeric galacturonic acids on its depolymerization. Mode of action distributes them as Endo-PG (EC 3.2.1.15) which liberates saturated oligogalacturonides and Exo-PG (EC 3.2.1.67) releases saturated galacturonic acid residue. The residue is obtained from the non-reducing end of homogalacturonan by hydrolytic catalysis (Yang et al. 2018; Anand et al. 2020; Christensen 2020). Xylogalacturonans (XG) are enzymes responsible for cleaving glycosidic linkages in the xylose-substituted rhamnogalacturonan chain and the end products are xylose-galacturonate dimers. Rhamnogalacturonan is hydrolytically cleaved by RG galalcturonohydrolase. Its non-reducing end produces monogalacturonate (Villarreal et al. 2022).

Polysaccharide lyases (PL)

These enzymes cleave uronic acid-containing polysaccharide chains. They use the β-elimination mechanism to generate an unsaturated (hexen)uronic acid residue and a new reducing end. PLs, can cleave alginate, heparin, hyaluronan, pectin, xanthan, and several exopolysaccharides (cazy.org/Polysaccharide-Lyases; Yadav et al. 2009c, Chakraborty et al. 2017). PL family 1, 2, and 9 share distributions of lyases degrading pectin. Pectate lyase (PL) results in forming an unsaturated product (α-4,5-D-galacturonate) through a trans-elimination reaction on polygalacturonase acids. Endo-PL (EC 4.2.2.9), acts on a nonreducing end. Pectin lyase (PNL) (EC 4.2.2.10) results in the formation of 4,5- unsaturated oligo-galacturonate. PNL performs a β-elimination mechanism without affecting the ester content of the polymer chain. This ester content is responsible for the specific

aroma of fruits. Toxic methanol production is limited by enzymatic degradation. Henceforth, these are preferred in fruit juice clarification industries. Rhamnogalacturonan lyases degrade rhamnogalacturonan I and are distributed in families 4 and 11 (Zheng et al. 2021).

Carbohydrate esterases (CE)

These enzymes catalyse acylation at the oxygen or nitrogen end. The members of this family remove esterified modifications from mono-, oligo- and polysaccharides. The acylation provides easy access to glycoside hydrolase (cazy.org/Carbohydrate-Esterases; Wardman et al. 2022). Pectin methyl esterases are grouped in CE 8 family and act preferentially on a methyl ester group of galacturonate to produce methanol and pectic acid. The action of PMEs forms pectate gel from homogalacturonan. The action of esterases can hinder the action of polygalacturonases (Benen et al. 2002). Rhamnogalacturonan acetyl esterase is responsible for cleaving acetyl groups of the rhamnogalacturonan chain that constitutes the major part of the hairy portion of pectin and belongs to the family CE12. Pectin acetyl esterase belongs to CE13 and hydrolyses the acetyl ester of pectin. They help the formation of pectic acid and acetate and acylation affects the age and differentiation of plant tissues. It even acts as protection from different enzymatic interactions. The esterases assist actively in biomass saccharification and have diverse biological and biotechnological applications (Benen et al. 2002; Bonnin and Pelloux 2020). The diversity of pectinases and their potential for industrial application is depicted in Fig. 1.

Fungal pectinases

Microorganisms have been in the environment from the beginning of time on this planet. In the scientific world, the study of the structural, functional, and ecological attributes of microorganisms is significant (Prasad et al. 2021). Microbial enzymes particularly from fungi are preferred over other sources because: (i) Their content is more predictable. (ii) They have a wide range of enzymes; (iii) Bulk production generally resin with low costs and reliable raw materials. (iv) Their productivity rate is high and they contain a greater amount of active ingredients. (v) Fungi can be easily managed to take the desired enzymes, and they can be made in large quantities rapidly and inexpensively through existing fermentation techniques and sophisticated instrumentation. (vi) Enzyme production may be programmable in various environments. and (vii) more potentially hazardous components like phenolic compounds, endogenous enzyme inhibitors, and proteases are found in plant and animal tissues than in microorganisms (Sharma et al. 2013; Singh et al. 2019).

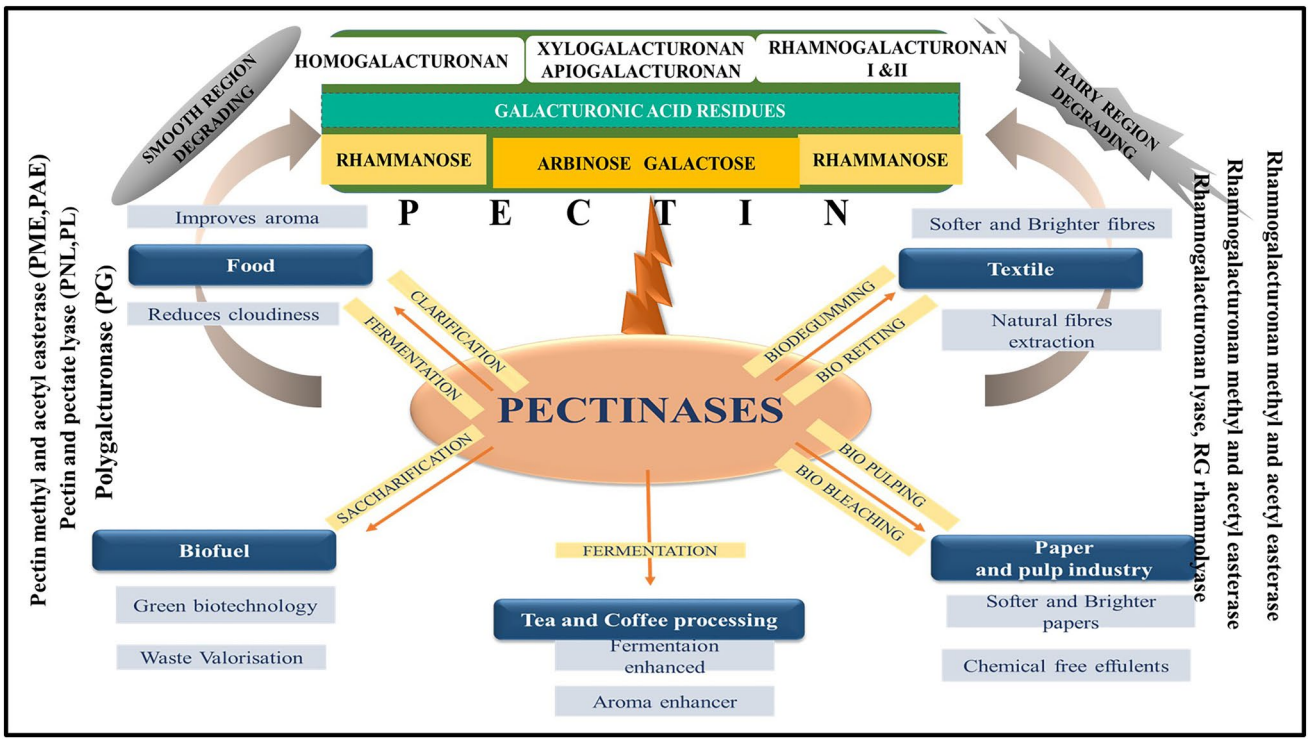

Fig. 1 Pectinases: classification and role as industrial catalyst

Fungal microbiota cover about 50% of microbial enzyme production. Around 35% of the production shared is held by bacteria and only 15% is produced from higher organisms (Wösten 2019). The fungal system is a popular source of enzymes because they provide a cost-effective technology with reduced resource consumption and minimal emissions, as opposed to animal and plant sources. Fungi and yeast alone are a producer of half of the globally used enzymes (Lübeck and Lübeck 2022). The secretion of pectinases by fungi assists in the breakdown of the middle lamella in plants (Prasad et al. 2021). Soil is a diverse and dynamic environment that is home to a diverse range of microorganisms, especially fungi. The traditional laboratory culture techniques have made the greatest contribution to gaining access to microbial diversity. Despite its familiarity and use, it is one of the world's least explored environments. Soil microorganisms play a crucial role in plant development and carbon and nutrient cycling. The bulk of soil microorganisms, on the other hand, have yet to be isolated, and their roles are mostly unknown. These microbial communities are exploited as a sustainable source for microbial enzymatic production systems (Baldrian 2019; Selvasekaran and Chidambaram 2020).

Fungi generate a plethora of extracellular enzymes capable of degrading organic materials, one of which is pectinolytic enzymes. Commercial enzymes have been produced using filamentous fungi for more than 50 years (Haile and Ayele 2022). Pectinolytic enzymes are one of the extracellular enzymes that fungi produce that can break down organic molecules. One of the most potent sources of pectinases is filamentous fungi, which can be extensively exploited in the production of SSF at a low cost. Many different fungal species have been reported to produce pectinases. *Aspergillus niger* is the most typical fungus used in the production of pectinolytic enzymes for industrial use (Gutiérrez-Correa et al. 2012). *A. oryzae, A. fumigatus, A. terreus, A. sojoe, A. awamori,* and *other Aspergillus* species are also known to produce pectinase. *A. giganteus* was the first species whose production of endo-PGL was noted. Additionally, species of *Penicillium, Fusarium, Mucor, Neurospora crass, Sclerotinia sclerotium*, and others play a part in the manufacture of pectinase (Sharma et al. 2013; Haile and Ayele 2022). Fungal pectinases play a part in the phytopathological process. They interact in plant–microbe symbiosis, and the decomposition of dead plant material, thereby, contributing to the natural carbon cycle. In the context of mining fungal pectinolytic sources, soil samples have been indefinitely explored for the isolation of novel fungal strains as listed in Table 1.

Production strategies

Fermentation-based production of microbial pectinases is facilitated by solid-state fermentation and submerged fermentation industrially and at a small scale. The advantages of fermentation-based production of enzymes include low costs, low energy consumption, and low waste-water generation, and it can be exploited to repurpose organic wastes into value-added products. Fermentation-based microbial enzyme mass production uses either solid-state fermentation (SSF) or submerged fermentation (SmF). SmF technology is often used to produce microbial enzymes, especially from bacterial sources and the major advantage is easy to control the process as compared to SSF (Sharma et al. 2013).

Solid State Fermentation uses a solid substrate that acts as a natural habitat for fungi to attach. The fermentation requires lower to no moisture content occurring in the absence or near absence of free water. The sturdy foundation offers support, or occasionally both support and sustenance. The main benefits of SSF include low capital expenditure, reduced levels of catabolite repression and end-product inhibition, low wastewater output, improved productivity, higher enzyme yields, and better product recovery. SSF has been used predominantly as it triggers the production of various enzymes directly from raw materials rich in lignocellulose (Kumar and Verma 2020). SSF is highly favourable for fungal microflora as it is like their natural habitat. Some of the limitations of the SSF include the need for proper aeration and humidity control and a time-consuming scale-up process. Pectinases of fungal origin have been extensively reported by using the solid-state fermentation method (Soccol et al. 2017; Lizardi-Jiménez and Hernández-Martínez 2017). The production of fungal pectinases by SSF requires optimization of several parameters which can directly affect the enzyme production.

Factors influencing the production of pectinases by SSF

The process of fermentation is dependent on biological and physio-chemical parameters that greatly affect the kinetics of the microbial enzymes. To improve the efficiency of the enzymes, these parameters need to be optimised and microbes, the size of the inoculum, and substrates are some of the important biological parameters. Further, incubation temperatures, pH specificities, moisture content, aerations, rotations, and heat transfer affect the performance of the enzymes (Soccol et al. 2017).

Fungal spores can directly be added as inocula and have a very fast production rate. These can grow over a range of temperature conditions between 24 and 30 °C. Thermophilic fungi can also grow optimally in this range. The pH range

Table 1 Fungal strains isolated from different soil samples with potential for pectinase production using fermentation methods

S. no.	Fungal strains	Soil samples	Pectinase type	Mode of production	References
1.	*Penicillium*	Pectin industry waste soil	PG	SSF	Patil and Chaudhari (2010)
2.	*Penicillium chrysogenum*	Municipal solid waste soil	PG	SmF	Banu et al. (2010)
3.	*Saccharomyces* sp.	Cold soils of fruit yards	PG	SmF	Naga Padma et al. (2011)
4.	*Aspergillus awamori*	Pectin-rich wastes and waste dump yard soils	PG	SmF	Padma et al. (2012)
5.	*Aspergillus niger, A. flavus, A. japonicus, and Chaetomium globosum*	Agricultural and non-agricultural soils	Pectinase	SmF	Reddy and Sreeramulu (2012)
6.	*Paecilomyces variotii*	Pectin industry waste soil	Exo-PG	SmF	Patil et al. (2012)
7.	*Aspergillus niger, A. terrus, A. stellatus, A. flavus, A. fumigatus*	Simipal Bioreserve Forest soil	Pectinase	SSF	Panda et al. (2012)
8.	*Penicillium atrovenetum, Aspergillus flavus and Aspergillus oryzae*	Decaying orange peels and soil sample	PG	SSF	Adeleke et al. (2012)
9.	*Aspergillus, Fusarium, Penicillium, Rhizopus, Syncephalastium*	Soil of composts, organic fertilizers and agro-industrial wastes	PG	SmF	Dhital et al. (2014)
10.	*Rhizomucor pusillus*	Fruit and vegetable markets	PG	SSF	Mohd et al. (2013)
11.	*Aspergillus niger*	Soil under fruit trees	pectinase	SSF	Islam et al. (2013)
12.	*Mortierella* sp., *Aspergillus fumigatus, Trichosporiella*	Organic soil sample	Exo-PG	SmF	Banakar and Thippeswamy (2014)
13.	*Penicillium chrysogenum*	Garden soil	PG	SmF	Sarkar (2014)
14.	*Aspergillus species*	Vegetative field soil	PG	SmF	Khan et al. (2014)
15.	*Species of Aspergillus, Penicillium, trichoderma*	Soil sample from manure fields	PNL	SmF	Usha et al. (2014)
16.	*Penicillium chrysogenum*	Garden soil samples	PG	SmF	Laha et al. (2014)
17.	*Thermomucor indicae-seudaticae*	Soil	PG	SSF	Martin et al. (2010)
18.	*Truncatella angustata*	Soil	PE	SSF	Singh et al. (2012a)
19.	*Aureobasidium pullulans*	Saharan soil of Algeria	PG	SSF	Garlapati (2015)
20.	*Rhizomucor pusillus*	Soil	Exo-PG	SmF	Trindade et al. (2016)
21.	*Cystofilobasidium infirmominiatum, Cryptococcus adeliensis and G. pullulans*	Soil from island	PG	SmF	Cavello et al. (2017)
22.	*Penicillium and Aspergillus*	Mangrove soil samples	PG	SSF	Mukunda et al. (2013)
23.	*Aspergillus Niger*	Soil samples collected from local fruit market waste	Pectinase		Bezawada and Raju (2018)
24.	*Aspergillus niger*	Soil sample	Pectinase	SmF	Abdullah et al. (2018b)
25.	*Aspergillus oryzae*	Mangrove soils	PG	SSF	Ketipally and Ram (2018)
26.	*Apergillus niger*	Samples of soil, fruits and vegetables were collected from agricultural fields	Pectinase	SSF	Abdullah et al. (2018a)
27.	*Apergillus*	Citrus dump waste soil	PG and PNL	SmF	Davanso et al. (2019)
28.	*Fusarium oxysporum*	Agriculture soil samples	Pectinase	SmF	Ibrahim et al. (2019), Ketipally et al. (2019)
29.	*Aspergillus nomius*	Mangrove soils	PG	SSF	Ketipally et al. (2019)
30.	*Aspergillus tubingensis*	Soil of vineyards	Pectinase	SmF	Huang et al. (2019)
31.	*Aspergillus* sp.	Soil of agro-industrial wastes, fruit pulp, composts, decaying leaves, spoiled fruits, and organic fertilizers	Pectinase	SmF	KC et al. (2020)
32.	*A. niger*	Soil from fruit processing sites, decaying matter, compost	PG	SSF	Patidar et al. (2020)
33.	*Aspergillus niger*	Botanical garden soil	Pectinase	SmF	Abd El-Rahim et al. (2020)

Table 1 (continued)

S. no.	Fungal strains	Soil samples	Pectinase type	Mode of production	References
34.	*Aspergillus fumigatus*	Agricultural fields	Pectinase	SSF	Mondal et al. (2020)
35.	*Aspergillus*	Crops soil	Pectinase	SSF	El-Ghomary et al. (2021)

PG polygalacturonases, *PNL* pectin lyases, *PL* pectate lyase, *Exo-PG* exo-polygalacturonases

may change according to the substrate used, however, for the best growth, fungi strains prefer an acidic to a neutral range (Prado Barragán et al. 2016). Optimizations of moisture content have resulted in more stress-resistant pectinase production. The rotation and agitation affect microbial growth and contamination. Production of fungal pectinase is severely constrained by bacterial contamination (Prado Barragán et al. 2016; Chen and Wang 2017).

The mesophilic and thermophilic fungal pectinase production during SSF is also affected by heat transfer during the process. The gases produced by the fungal inoculum and moisture vaporization regulate the heat of the system (Kumar et al. 2021; Chilakamarry et al. 2022).

Substrates used for the production of fungal pectinase

Higher fungi have well-tuned enzymes, spores, and metabolites for development on solid, moist substrates. For instance, fungus spores produced by SSF display greater stability, are more resistant to drying, and have higher germination rates for longer periods (Arun et al. 2020). The substrate acts as structural ed support rich in nitrogen and carbon for the growth of microorganisms. The nutritional composition and quality problems may affect the fermentation batches. This variation could lead to decreased production. The choice of substrate will determine how much heterogeneity is introduced during the process. The most often utilised substrates for SSF include agricultural and food processing wastes such as wheat bran, sawdust, apple pomace, cassava, sugar beetroot pulp, citrus waste, maize cob and banana waste. Innovations in the production of pectinases using different agro-wastes like peels and pulps of citrus, orange, coffee, grapefruit, and banana using both SSF and SmF have been reported recently (Bharathiraja et al. 2017; Chilakamarry et al. 2022).

Fruits and vegetable peels are rapidly utilized nowadays as they are environment-friendly and immensely nutritious for microbes. Peels of citrus fruits, bananas, sweet potatoes, and mango are being vigorously studied. The pomace of apple, kiwi, peach, and grapes are pectin-rich biomass for valorisation via fermentation. Other agro-industrial residues such as oil cakes of pumpkin, sesame, groundnut, and sunflower oil have also been used as substrates (Lopes and Ligabue-Braun 2021). Additionally, pectinolytic enzyme production has been reported by the use of sugarcane bagasse, corn cobs, soybean hulls, sugar beetroot pulp, barley husks and straws as sources of carbon. Tea extract serves as an important source of nitrogen. In addition to these, brewery waste, sewage wastewater, drainage effluents, tobacco stalks, molasses, and vegetable and fruit juices work excellently as liquid substrates for the fermentation of fungal pectinases (Sadh et al. 2018; Cano et al. 2020; Chukwuma et al. 2020).

Bioreactors for the production of fungal pectinases

For large-scale bulk production, bioreactors have been used. These bioreactors or fermenters are designed for processing biological products under a specifically controlled environment. Bioreactors for fungal pectinases have used lignocellulosic wastes, and agricultural wastes as substrates for industry efficient scaled production of enzymes (Cerda et al. 2019). Bioreactors prefer solid state-based fermentation methods for the production of fungal pectinases. In the light of fungal pectinases, *Aspergillus niger* has been extensively utilized for pectinases production by solid-state fermentation using the packed bed, and bench scale rotating-drum reactors (Finkler et al. 2017; Poletto et al. 2017; Reginatto et al. 2022). A 40 cm high packed bed bioreactor yielded productivity of 1840 U/g pectinases using *Aspergillus niger* (Pitol et al. 2016). Raimbault columns, packed-bed bioreactors, Erlenmeyer flasks, perforated trays, and other static bioreactors have been used to produce pectinases (Yang and Sha 2019). These bioreactors are chosen because of their usability and simplicity. *A. niger* on sugarcane bagasse and orange pomace has been utilized as solid-state substrates for production using a tray and rotating drum bioreactors (Mahmoodi et al. 2019). Agitated bioreactors utilise intermittent or continuous mixing to homogenise substrate using solid-state fermentation. It is possible to construct agitated bioreactors with or without a water jacket to regulate temperature (Mitchell and Krieger 2019). This type of reactor may be continuously or intermittently agitated. Shear problems

and damage to the fungal mycelium's structural integrity may occur, depending on the degree of agitation (Shanmugam et al. 2022). Large fermenters are commonly built of stainless steel in the food and beverage industries because of their ability to resist corrosion. A bioreactor's design incorporates numerous essential engineering elements that are regularly updated and modernised to increase the final product's productivity and quality (Kaur and Kaur 2019). Basal stirred tank fermenters utilised *A. foetidus* strain for optimization and evaluation of pH effect on microbial enzymes including pectinases (Li et al. 2018). Innovative forms of bioreactor-based fermentation largely depend on aeration techniques. These reactors have been modernised with the inclusion of steam traps, valves, mechanical foam breakers, pH temperature and pO_2 monitors, micro-spargers for self-cleaning, and other sampling ports. Connecting to computers is a crucial advancement for novel bioreactors since it speeds up data processing and calculation and facilitates operational optimisation (Mitchell et al. 2019; John et al. 2020; Leite et al. 2021).

Response surface methodology (RSM) utilisation for bioreactor-based production using shake flasks has been utilised recently to produce pectinases at a concentration of 380 U/ml by *A. sojoe* (Fratebianchi et al. 2017). Similarly, an indigenous *Aspergillus* sp. isolated from coffee waste was used in response surface methodology designed on an SSF-based tan ray bioreactor to yield 29.9 IU/g of pectinases (Núñez Pérez et al. 2022).

Purification of fungal pectinases

Enzyme purification can be achieved by using a variety of conventional and modern techniques. The choice of the best treatment stage is a prerequisite for the enzyme purification process to be successful. Depending on the intended usage of the enzyme, the degree of purification may vary. Purification of microbial pectinases has been attained by simple centrifugation, sedimentation, or precipitation (Holm et al. 2018). The removal of inorganic and organic impurities is highly feasible by salting out using ammonium sulphate salts. This method of purification or partial purification has yielded a stable protein with better activity. Solvent precipitation using acetone, ethanol, and methanol, based on the solubility of protein is a cost-effective method for the removal of organic and inorganic impurities. The salt-based precipitation has been preferred as other solvent methods for pectinase. This is generally followed by dialysis to yield salt unbound proteins which are dissolved in buffers for optimal activities. Purification using counter solvents like butanol or octanol or by ultrafiltration facilitates the generation of aqueous pectinase. This eliminates the need for precipitation with dialysis of salt-based methods (Patel et al. 2017; Raina et al. 2022).

Purification of pectin lyases produced from *Penicillium oxalicum, P. citrinum, Aspergillus flavus, A. ficuum, A. terricola, Fusarium decemcellulare,* and *F. lateritum* has been performed simply by using ammonium sulphate precipitation and column chromatography method (Yadav and Shastri 2007; Yadav et al. 2008, 2009a, c, 2013, 2014, 2017b). Exopolygalacturonase from *Aspergillus flavus* has been purified using solvent-based acetone purification, followed by cellulose column and gel filtration chromatography (Anand et al. 2017a).

Ion exchange, gel filtration, and affinity-based chromatographic methods are used to produce samples with a comparatively greater level of purity. The form, size, charge, hydrophobicity, or binding ability of the stationary phase are criteria used in chromatographic procedures to purify microbial pectinases. The molecular properties and interactions that underlie ion exchange, surface adsorption, partition, and size exclusion are also important considerations (Coskun 2016). Pectinolytic purification has been predominately accomplished by column chromatography (Smith 2005; Ullah 2012; Bassim Atta and Ruiz-Larrea 2022). Ion exchange or gel filtration, which gives rise to purer fractions of pectinases, along with a significant increase in its specific activity has also been reported. Anion exchange column-based purification for polygalacturonase from *Calonectria pteridis* utilized eucalyptus leaves in submerged fermentation (Ladeira Ázar et al. 2020). An indigenously isolated soil-borne *Aspergillus japonicus* yielded 2.9-fold purified polygalacturonase using two chromatographic techniques simultaneously (Cavalieri de Alencar Guimarães et al. 2022). A repertoire of purification strategies has been adopted for the purification of fungal pectinases from different fungal strains as shown in Table 2.

Innovations: diverse approaches

Immobilisation

The pectinolytic industrial intervention is disrupted due to their recovery rates, and low stability. Immobilization of enzymes enhances storage, reduces product contamination, and simplifies the separation of products, which in their free form is challenging. It improvises the catalytic properties of enzymes and enhances their functioning in adverse conditions (Bashir et al. 2020). Thereby, facilitating the recovery and reuse of enzymes in the medium and enhancing the economic feasibility of the enzymes. Suitable immobilization protocols and supportive environments are required for enzyme biocatalysts with high enzymatic activity (Patel et al. 2022). Pectinases have been immobilized

Table 2 Purification and biochemical characterization of Fungal Pectinases

S. no.	Enzyme	Fungal strains	Production methods	Substrate used	Purification methods	Kinetic properties	References
1.	Exo-PG	*Paecilomyces variotii*	SmF	Pectin	Ammonium sulphate followed by Sepahdex G-100 column with CMC anion exchange chromatography	Mol.wt = 39.4 kDa. specific activity = 98.49 U/mg protein	Patil et al. (2012)
2.	Pectinase	*Saccharomyces cerevisiae*	SmF	Pectin	Ammonium sulphate followed by Sephadex G-100 column	Specific activity = 21.69 U/mg	Poondla et al. (2015)
3.	Pectinase	*Aspergillus niger*	Liquid media	Pectin	Cold acetone followed by Sephadex G-75 gel filtration chromatography	Specific activity = 60 U/mg purification fold = 8.5	Khatri et al. (2015)
4.	Acidic endo-PG	*Penicillium oxalicum*	Spore culture	–	Ammonium sulphate followed by HiLoad 16/10 Phenyl Sepharose HP column (GE, Sweden)	Specific activity = 1.27 mg/ml and 5,504.6 U/mg	Cheng et al. (2016)
5.	Exo-PG	*Penicillium janthinellum*	SmF based bioreactor	–	Ammonium sulphate followed by DEAE-Sepharose FF column	The Km and Vmax for the enzyme = 1.74 mg/mL and 18.08 µmol/ (mL.min),	MA et al. (2016)
6.	Pectinase	*Aspergillus terreus*	SSF and liquid static surface fermentation (LSSF)	Peels of banana,	Ammonium sulphate followed by Sephadex G-100 column	Purification fold = 1.42, yield = 8.08%, specific activity = 634.73 Umg Mol.wt. = ~25 kDa − 1	Sethi et al. (2016)
7.	PG	*Aspergillus niger*	SSF	Banana peel	Ammonium sulphate followed by Sephadex G-100 column	Specific activity = 166.67U/mg, yield = 8.59% and purification fold = 42	Ire and Vinking (2016)
8.	PG	*Zygoascus hellenicus*	SmF	Orange peels	Ammonium sulphate precipitation, DEAE cellulose chromatography, and Sephadex G-100 gel filtration	Mol. Wt. = 75.28 kDa, purification fold = 16.89 with a recovery = 18.46% and specific activity = 2469.77 U/m	Lu et al. (2016)
9.	Pectinase	*Trichoderma viride*	SmF	Onion skins	Batch 50% ethanol-based solvent partial purification	Specific activity = 3.03 U/mg, purification fold = 1/5, yield = 74.91%	Ismail et al. (2016)
10.	Pectinase	*Aspergillus niger*	SmF	Orange peel waste	Ammonium sulphate followed by gel filtration chromatography	Purification fold = 5.59, specific activity = 97.2 U/mg % recovery = 12.96%	Ahmed et al. (2016)
11.	PG	*Aspergillus fumigatus*	SSF	Wheat bran + tea extract	Acetone precipitation and Sephadex G-100 column	Km and Kcat of the purified enzyme = 2.4 mg/ml and 44 s − 1,	Anand et al. (2017b)

Table 2 (continued)

S. no.	Enzyme	Fungal strains	Production methods	Substrate used	Purification methods	Kinetic properties	References
12.	PG	*Aspergillus niger*	SSF	Orange peel with papaya peel	Anion exchange chromatography on DEAE-cellulose and gel filtration chromatography using Sephadex G200	The Km and Vmax = 2.6 mg/l and 181.8 µmol/ml/min, respectively	Patidar et al. (2017)
13.	Exo-PG	*Penicillium notatum*	SSF	Wheat bran	Ammonium sulphate followed by anion exchange and gel filtration chromatography	Purification fold = 3.07, mol. Wt. of exo-PGI& PGII = 85 and 20 kDa	Amin et al. (2017)
14.	Pectinase	*Aspergillus fumigatus*	SSF	Plant peels	CM-Sephadex C-50 and Sephacryl S-200 column	Purification Fold = 4.45, yield = 26.16%, specific activity = 38.88 U/mg.Mol. wt = 31.6 kDa	Okonji et al. (2019)
15.	PG	*Aspergillus awamori,*	SSF	Orange peel	Acetone precipitation followed by Sephadex G100 column chromatography	Molecular weight, saturation constant, and maximum velocity for isolated polygalacturonase were 31.00–32.00 kDa, 55.55–90.91 U/mL, and 0.722–0.909 mg/mL, respectively	Adedeji and Ezekiel (2019)
16.	Pectinase	*Aspergillus pulverulentus*	SmF	Pectin	Solvent precipitation Acetone based	Specific activity = 2.265 U/ ml	Abd El-Rahim et al. (2020)
17.	Pectinase	*Mucor hemelis*	SSF	Brewery spent grains	Ammonium sulphate based partial purification	Specific Activity = 137 U/g,	Hassan et al. (2020a)
18.	Pectinase	*Aspergillus parvisclerotigenus*	Liquid static surface fermentation	Apple pomace	Ammonium sulphate followed by Sephadex G-100 column	Purification fold = 2.10, yield rate = 2.91%, specific activity = 1081.66 U/mg, mol. Wt. = 37.4 kda	Satapathy et al. (2021)
19.	Pectinase	*Aspergillus niger*	Spore culture	pomelo peels powder	Ammonium sulphate followed by anion exchange and Sephadex-100 column gel filtration chromatography	Specific enzyme activity = 11.41 U/mg, Purification fold = 14, yield = 86.51%	Mat Jalil and Ibrahim (2021)
20.	Pectinase	*Aspergillus terreus*	–	–	Precipitation, dialysis, ion-exchange chromatography, gel filtration chromatography	Purification fold = 20.85, Mol.wt. = 47 kDa, The Km and Vmax = 0.002 mM and 27.39 U/mL	Bhattacharyya et al. (2021)

Table 2 (continued)

S. no.	Enzyme	Fungal strains	Production methods	Substrate used	Purification methods	Kinetic properties	References
21.	Pectinase	*Penicillium oxalicum*	SmF	Sugar beet pulp	Ammonium sulphate followed by acetone to Sephahdex G 200 column	Km and Vmax = 0.67 mg/ml, purification fold = 28, yield = 57%	Almowallad et al. (2022)
22.	Pectinase	*Aspergillus niger*	Culture broth	Citrus pectin	Cold ethanol followed by sepahdex-50 column chromatography	Purification folds = 632, specific activity = 40 U/ml	Esawy et al. (2022)
23.	Exo-PG	*Aspergillus flavus*	–	–	Magnetic nano-particle-based affinity chromatography	Purification folds ~ tenfold, yield = 29%	Lodhi et al. (2022)

PG polygalacturonases, *PNL* pectin lyases, *PL* pectate lyase, *Exo-PG* exo-polygalacturonases, *Acidic endo-PG* acidic endo polygalacturonases

using diverse supports by membrane adsorption, covalent binding, and cross-linking mechanisms. A variety of supports, including beads, microspheres, pulp fibre, matrix, resins, capsules, nanoparticles pumice, and magnetic beads have been deployed (Martín et al. 2019; Karataş et al. 2021). The magnetic core of magnetic particles as beads makes it simple, rapid, and effective to separate the enzyme from the reaction mixture using an external magnetic field, making them suitable support for enzyme immobilization. Additionally, the size of the particle can be adjusted to give a large surface area and high enzyme activity (Soozanipour et al. 2019; Trindade Ximenes et al. 2021). Direct crosslinking of different enzyme preparations is the most typical technique for producing cross-linked enzyme aggregates (CLEAs). The advantages of this approach are highly concentrated enzyme activity, greater stability, and the absence of an extra carrier's associated production costs (Nouri and Khodaiyan 2020).

Adsorption, covalent binding, and entrapment are just a few of the methods utilised to keep enzymes inside the membrane. Enzymes are frequently attached to membranes by chemical bonds and adsorption. Pectinase is frequently bound to membranes using adsorption techniques. Chemical enzyme binders including glutaraldehyde, glycidyl methacrylate, and carbonyl diimidazole are used to adsorb membranes. It has been observed that membrane-bound enzyme exhibits enhanced thermal stability and temperature optima. Among the different methods of immobilising enzymes, covalent immobilisation is frequently preferred. This is so that it won't allow the enzyme to desorb from the support during the process (Nadar and Rathod 2019).

A scale bioreactor used in stainless steel bases matrix was immobilized to get a titre of 307.5 and 242.6 U/ml of exo and endo PG respectively from *Rhizopus oryzae* (Zheng et al. 2017). Beads of alginate-montmorillonite were used to immobilize pectinase from *A. aculeatus* recovering 53% of its initial activity (Mohammadi et al. 2019). Gel-based beads of alginate and agar facilitate the immobilization of pectinase from *A. awamori*. This retained initial activity even after 8 cycles of reaction (Abdel Wahab et al. 2018). An indigenously isolated pectinolytic yeast strain, *Geotrichum candidum* was immobilized retaining 70% of its initial activity using corn cob matrix (Ejaz et al. 2018). Similarly, beads of sodium alginate were used in different strains of *Geotrichum candidum* to immobilize pectinase enhancing its activity from 0.046 to 0.115 IU mL^{-1} (Ejaz et al. 2020). Pectinases have also been immobilized using magnetic chitosan particles by direct extraction from fruit juices without the intervention of microbes (Dal Magro et al. 2018, 2019; Soozanipour et al. 2019). Efforts on the immobilization of pectinases from fungal strains have been summarized in Table 3.

Table 3 Reports on immobilisation of Fungal Pectinases

S. no.	Fungal strains	Enzyme	Immobilisation method	Immobilised matrix	Functions altered	References
1.	*Aspergillus niger*	Pectinase	Entrapment	Polyvinyl alcohol (PVA) sponge	Reusability = 12 times Loss of activity = 9% of original	Esawy et al. (2013)
2.	*Rhizopus oryzae*	Exo-PG	Matrix immobilisation	Matrix of stainless-steel wire with cotton fibre	Enzyme activity 2.8 t times increased	Zheng et al. (2017)
3.	*Mucor hiemalis*	Pectinase	Covalent immobilization	Alginate beads	Enzyme recovery -80–83%	Hassan et al. (2020b)
4.	*Sporothrix schenckii*	Exo-PG	Adsorption	Silica yolk, shell spheres with magnetic property	The stability of the enzyme increased from 3 to 3.7 folds	Karataş et al. (2021)
5.	*Aspergillus niger*	PG	Microsphere entrapment	Calcium alginate beads	Retained 63% of the original activity	Deng et al. (2019)
6.	*Aspergillus niger*	Pectinase	Functionalized magnetic nanoparticles	Cyanuric chloride-functionalized chitosan grafted magnetic nanoparticles	Retained 60% of its initial activity and increased storage stability after 75 days	Soozanipour et al. (2019)
7.	*Aspergillus aculeatus*	Pectinase	Entrapment	Calcium alginate beads	Retained 80% of initial activity	De Oliveira et al. (2018)
8.	*Aspergillus niger*	Pectinase	Solid support based	Zeolite Socony Mobil–5 (ZSM-5)	activity 247% higher than free enzyme	Liu et al. (2021)
9.	*Aspergillus aculeatus*	Pectinase	Covalent binding	Amino-silane modified montmorillonite clay (MMC)	retaining 60% of its initial activity	Mohammadi et al. (2020)

PG polygalacturonases, *PNL* pectin lyases, *PL* pectate lyase, *Exo-PG* exo-polygalacturonases, *Acidic endo-PG* acidic endo polygalacturonases

Directed evolution

The state-of-the-art technology of directed evolution for the desired manipulation of enzymes for industrial application has been attempted for pectinases. Mutation using a UV range of 254 nm has been used for the enhancement of polygalacturonases production of *Aspergillus* and *Penicillium* species (Heerd et al. 2014; Kamalambigeswari et al. 2018; Nawaz et al. 2019). Mutated strains have also been used to study evolutionary relationships between PEL and PL subclasses of pectinases (Yang et al. 2020). Mutation of gaaX and gaaR allowed *A. niger* to express pectinases without an inducer (Alazi et al. 2019). The approach of directed evolution combined with computational technologies has been used to access different metabolic pathways of fungal pectinases (Wang et al. 2021). For fungal pectinases, artificial environments can be simulated through strain mutation, recombination, and gene overexpression. With this modification, the pectinolytic mechanism can be accelerated to catalyse chemical reactions in an entirely new environment employing a newer substrate, resulting in increased catalytic activity. Chromosomal mapping was used to analyse *S. bayanus* var. *uvarum* strains, and the results revealed three divergent genes, PGU1b, PGU2b, and PGU3b, which are situated on chromosomes X, I, and XIV, respectively. As a result, it was demonstrated that these yeasts' strong pectinolytic activity might be caused by the existence of many PGU polymeric genes in their genomes (Naumova et al. 2019). Heterologous expression of fungal pectinase targeting expression using microbes with a high capacity for protein production and enzyme secretion has been performed. It is a good alternative to the fermentation technique for the desired production of enzymes by targeting the relevant genes. The expression of pectinolytic genes has been summarized in Table 4.

Omics interventions

The omics-driven approach is the current trend in enzyme research which aims to analyse the potential of fungal species in terms of enzyme production by targeting the whole genome or proteome. Over 50% of the currently available eukaryotic genome sequences are from the kingdom of Fungi. Several fungal genome sequences have been targeted to decipher the diversity of pectinases. Recently using a shotgun proteomics approach two pectin lyase and one pectate lyase from *Saccharomyces cerevisiae* produced using passion fruit flour by solid-state fermentation has been reported (Takeyama et al. 2022). Two-dimensional electrophoresis-based proteomic analysis of *Aspergillus*

Table 4 List of pectinase gene studies

S. no.	Fungal strains	Pectinase type	Gene	Sequence-based/clone/recombinant	Host for expression	Accession no.	References
1.	*Aspergillus sojae*	PG	A*specA*	Cloned and expressed	*Aspergillus oryzae*	–	Yoshino-Yasuda et al. (2011)
2.	*Fusarium oxysporum*	Exo-PG	PGC2	Cloned and expressed	*Pichia pastoris*	GI:281372497	Dong and Wang (2011)
3.	*Fusarium oxysporum*	PG	Two PGC3	Cloned and expressed	*Pichia pastoris*	KP768396 and KP768397	Dong and Wang (2015)
4.	*Pseudothermotoga thermarum*	GH28 PG	TtGH28	Cloned and expressed	*Escherichia coli*	EH50492.1	Wagschal et al. (2016)
5.	*Aspergillus niger*	Endo-PG	pga-zj5a	Clone and expressed	*Pichia pastoris*	KU896780	Wang et al. (2017)
6.	*Penicillium oxalicum*	endo-PG	PoxaEnPG28A	Cloned and expressed	*Pichia pastoris*	KU366356	Cheng et al. (2017)
7.	*Aspergillus. aculeatus*	Endo-PG gene	endoPG recombinant = pPIC-PG1	Expressed and recombinant protein	*Pichia pastoris*	–	Abdulrachman et al. (2017)
8.	*Pectobacterium carotovorum subsp. carotovorum (Pcc)*	PG	Peh 28	Cloned and over-expressed	*Escherichia coli*	AA03624.1	Ibrahim et al. (2017)
9.	*Aspergillus niger*	Exo-PG	pgxB	Mutant	–	4980661	Liu et al. (2017a)
10.	*Aspergillus niger*	PNL	pel A-F	Clone and over-expressed	*Aspergillus. niger*	An14g04370, An03g00190, An11g04030, An19g00270 An15g07160,	He et al. (2018)
11.	*Rhizoctonia solani*	PG	RsPG3 RsPG4	Clone and expressed	*Pichia pastoris*	KP896520 KP896521	Chen et al. (2018)
12.	*Fomitopsis palustris*	Endo-PG	-	cDNA Clone, Insilico study and enzyme characterisation	–	–	Tanaka et al. (2019)
13.	*P. polymyxa*	PL	PL9	Cloned and expressed	*Escherichia coli*	–	Yuan et al. (2019)
14.	*Aspergillus luchuensis*	PG	PgaB	Clone and over-expressed	*Pichia pastoris*	BCWF01000021.1	Tan et al. (2020)
15.	*Penicillium oxalicum*	Rec.PoxaEnPG28B-Pp PoxaEnPG28B-Ec	Endo –PG	c- DNA cloning and expression	*Pichia pastoris GS115 and Escherichia coli BL21*	EPS29213	Cheng et al. (2020)
16.	*Aspergillus nidulans*	Endo-PG	AnEPG	Clone and expressed	*Pichia pastoris*	AN8327.2	Xu et al. (2020)
17.	*Fusarium oxyporum*		Pgc4			MT385837 and MT385838	Dong et al. (2020)
18.	*Aspergillus parasiticus*	PL	ApPel1	Cloned and expressed	*Pichia pastoris*	–	Yang et al. (2020)
19.	*A. oryzae*	PME	*Aopme1-5*	Cloned and expressed	*Escherichia coli*	BAE61126 BAE60873 BAE58553 BAE63101 BAE63594	Yamada et al. (2021)
20.	*Verticillium dahliae*	PG, PME	VdPG2 VdPME1	Cloned and expressed	*Pichia pastoris*	20,706,440 20,707,262	Safran et al. (2021)

Table 4 (continued)

S. no.	Fungal strains	Pectinase type	Gene	Sequence-based/clone/recombinant	Host for expression	Accession no.	References
21.	*Penicillium oxalium*	PG	Eno-PGase Recombinant = PoxaEn-PG28C	Cloned and expressed	*Pichia pastoris*	–	Lu et al. (2022)
22.	*F. virguliforme*	GH28 PGs	FpPG	Insilico based	–	–	Chang et al. (2016)
23.	*Clonostachys rosea*	exo-PL	Pel 1–17	Insilico based	–	BN869_T00008859 BN869_T00000002 BN869_T00000920 BN869_T00008472 BN869_T00010915 BN869_T00006080 BN869_T00010737 BN869_T00008735 BN869_T00007710 BN869_T00005779 BN869_T00006915 BN869_T00007653 BN869_T00008627 BN869_T00002081 BN869_T00010228 BN869_T00007566	Atanasova et al. (2018)

PG polygalacturonases, *PNL* pectin lyases, *PL* pectate lyase, *Exo-PG* exo-polygalacturonases, *endo-PG* endo polygalacturonases, *PME* Pectin Methyl esterases, *GH28 PG* glycoside hydrolase -28 Polygalacturonase

niger EIMU2 has been attempted. It revealed that the mutant EIMU2's multiple enzyme systems used for the degradation of pectin included the main-chain cleaving enzymes polygalacturonase, pectate lyase, and pectin esterase, as well as some accessory enzymes rhamnogalacturonan lyase (Lin et al. 2021). Studying the interaction of wood rotting fungi, pectinases proteomics profiling helped analysed other proteins secreted which might have a significant role in degrading wood (Presley et al. 2020). CRISPR/Cas9 system generated three chimeric GaaR-XlnR induces by D-galacturonic acid from *Aspergillus niger*. Their proteomics investigation verified that the gaaR mutants carrying the chimeric transcription factor produced several pectinolytic enzymes (Kun et al. 2021). The PL7 and PL8 enzymes required for the breakdown of laminarin, cellulose, lipids, and peptides, were found to be abundantly secreted by *Paradendryphiella salina* cultured on brown algae using proteomic analysis (Pilgaard et al. 2019). However, a significant issue with the existing fungal pectinases proteomics is to fully understand the expression, operation, and regulation of the entire set of fungus-genome-encoded proteins. Moreover, the sequencing of several fungal proteomes is in progress (Sudhakar et al. 2018).

Meta-omics approach collects total environmental DNA which is targeted for metagenomic studies. A metagenomic system can be any arbitrary environmental sample defining the collection of microbes. Soil, water, air, cow rumen, and

Table 5 Metagenomic intervention in search of novel Fungal pectinases

S. no.	Source	Methodology adopted	Sequence-based or function-based	Pectinase type	Salient features	References
1.	Soils from hot spring site	Use of pectinase Degenerate primer	Function-based	Pectinase	Recombinant protein expressed in E. coli M15	Singh et al. (2012b)
2.	Alkaline environment soils	Degenerate primer based	Function-based	Alkaline PL	Pel gene cloning and their purified protein characterization	Wang et al. (2014)
3.	Forest soil of Southern Western Ghats region	Metagenomic library	Function-based	GH-28	Nine pectinolytic clones	Sathya et al. (2014)
4.	Temperate soil especially black oak and white oak sited soil	GH28 primer amplification based	Sequence-based	GH-28	Ascomycota species showed dominant diversity in GH28 primers' results	Gacura et al. (2016)
5.	Microbial consortiums enhanced from compost ecosystems that are rice straw-adapted (RSA)	16S pyrotag metagenomic library of	Sequence-based	PNL	46.1% of CA Zyme genes representing cellobiohydrolase, esterase, β-glucosidase, arabinofuranosidase, acetyl xylan pectin lyase genes	Wang et al. (2016)
6.	Apple pomace-adapted compost (APAC) habitat	16 s sequencing	Sequence-based	Pectinase	Seventeen hundred fifty -six potential pectin-targeting genes were predicted	Zhou et al. (2017)
7.	Southern Brazil was the location of a 13-year field experiment comparing the effects of no-tillage (NT), conventional tillage (CT), crop succession (CS, soybean/wheat), and crop rotation (CR, soybean/maize/wheat/lupine/oat)	Four shotgun metagenomes	Sequence-based	Pectinase	Five hundred thirty- two sequences were identified by The KEGG database. In the NCBI-Database, they found 627 sequences	Souza et al. (2018)
8.	Mangrove soil sediments	Two metagenome sequences. (Namely PZ AND VJH)	Sequence-based taxonomic profiling	PE, exo-PG, endo-PG, PNL, PL	All pectin-degrading enzyme sequences were reported	Priya et al. (2018)

PG polygalacturonases, *PNL* pectin lyases, *PL* pectate lyase, *Exo-PG* exo-polygalacturonases, *endo-PG* endo polygalacturonases, *PME* pectin methyl esterases, *GH28 PG* glycoside hydrolase -28 Polygalacturonase

composts are such systems, thus, opening doors for unculturable and novel sources for catalytic enzymes. metagenomic approach for pectinase enzyme mining from soil resulted in the isolation of thermostable pectinase (Singh et al. 2012a, b). This approach has been used for identifying novel fungal sources for pectinases (Tanveer et al. 2016; Pilgaard et al. 2019; Ahmad et al. 2021). The metagenomic studies exclusively for fungal pectinases are summarized in Table 5.

Industrial applications

Pectin in plant cells is degraded by pectinases. They were first used commercially in the 1930s, and since then, they govern 25% of industrial applications. Wide-ranging industrial uses for pectin-degrading enzymes include degumming and retting of plant fibres, oil extraction, fruit juice clarification, wine production, fermentation of tea and coffee, bioconversion of wastes, and protoplast fusion technology (Singhania et al. 2015). Since 40% of the dry weight of plant cambium cells is made up of pectin, pectinases are essential for digesting natural fibres. With the aid of pectinases, the bast fibres of jute, flax, hemp, ramie, banana, pineapple leaf, and bamboo can be successfully degummed, macerated, and retted because they break down the pectin in the middle lamella and primary cell walls. Their wide applicability in the textile industry makes their study essential. Microbial pectinases-based natural fibre retting and extraction is biodegradable, recyclable, cuts production costs and is energy sustainable (Kumari et al. 2021). The fibres produced are reported with higher strength, shinier, easy to obtain and light weighted. The increasing demands on enzyme applications are growing as replacements for traditional harsh chemical processes. Fungal pectinases are also used for degumming natural fibres, bio scouring, bio bleaching and in wastewater treatment of textile power plants (Sharma et al. 2017).

They are also used to produce effective viral preparation from plant tissues, in the treatment of wastewater and for the isolation of protoplasts. Protoplasts are isolated from the mycelia of *Pleurotuseous* and *Pleurotus flabellatus* using enzymes comprising commercial cellulases, crude pectinases, and crude chitinases (Eyini et al. 2006; Ruiz et al. 2017). Pectinases are also applied in animal feeds as it helps in the efficient absorption of nutrients by animals by degrading the fibres that entrap them. These groups of enzymes have been used for biofuel production like bioethanol. The rate of ethanol generation rises when pectinaceous structures in the feedstock are destroyed and hydrolyzed by pectinases. Biomass enzymatic hydrolysis is a cost-effective and efficient treatment method that produces no hazardous waste (Samanta 2019). Sugar becomes more accessible and sensitive to hydrolytic enzymes after being treated with liquid hot water. Alkaline pectinases both from fungal and bacterial sources are also applied in the fermentation of coffee and tea. Degrading pectin, pectinase increases the pace of tea fermentation and reduces the foaming ability of instant tea granules (Tatta et al. 2022).

The fruit and food processing industries have wide applicability of pectinases. Fruits have a complicated pectin structure, making it challenging to extract juice from this very viscous, jellified pulp (Pagnonceli et al. 2019). The pectinase enzyme acts on the pectin of fruit peels and dissolves the glycosidic linkages between the galacturonic acid monomers, reducing the amount of water that may be held by pectin enzymatic treatment is the most frequently used method for juice extraction and clarity (Anand et al. 2017b). The enzymatic hydrolysis of cell walls enhances the extraction yield, soluble dry matter content, galacturonic acid content, and titratable acidity of the products. The amount of waste pomace decreased and the resulting pulp had a lower viscosity. The biomaterial is enzymatically degraded depending on the type of enzyme, incubation period, temperature, concentration, agitation, pH, and the use of various enzyme combinations. The wine industry chooses pectinases as they increase wine quality, and facilitate extraction, filtering, and taste and colour intensification (Gunjal et al. 2020). Pectinases were also used in extracting essential oils from a variety of sources like olives, flaxseed oil, dates, and other fruits and vegetables (Nagpal et al. 2021). These enzymes help to enhance the fatty acids, peroxide value, and colour intensity as compared to chemical treatment. In the paper industry, pectinases along with xylanases are preferred as a biobleaching agent. Enzymatic intervention is eco-friendly, less abrasive, and effective in improving paper quality (Nagpal et al. 2020). Biological bleaching with pectinases and xylanases brightens the paper and improves its physical characteristics, as well as lowers the kappa number and permanganate number of the pulp. In comparison to those chemical alternative solutions, the substitution of pectinases contributes to a reduction in chlorine discharge into the environment (Nagpal et al. 2020; Tatta et al. 2022). The diverse industrial application of pectinases has been summarized in Table 6.

The bottom line and future prospects

Pectinases represent an important group of enzymes with immense potential for diverse industrial applications. Substantial efforts have been made to explore the possibility of diverse approaches for enhancing pectinases production, manipulation and elucidating industrial applications, exclusively from fungal sources. The cost-effective

Table 6 Potential industrial applications of Fungal pectinases

S. no.	Industry	Pectinase type	Fungal strain	Production mode	Substrate used	Application	References
1.	Beverage industry	Pectinase	*Aspergillus foetidus*	SSF	Mango peel	Clarification of mango juice	Kumar et al. (2012)
2.		PG (exo)	*Aspergillus niger*	SmF	–	Fruit juice clarification	Anand et al. (2017b)
3.		Endo-and exo pectinase	*Aspergillus niger*	SSF	Orange pomace	Clarification of apple juice	Mahmoodi et al. (2017)
4.		PNL	*Aspergillus niger*	SmF	–	Fruit juice clarification	Poturcu et al. (2017)
5.		PG PL PME	*Penicillium digitatum*	SSF	Lemon peel	Apple juice clarification	Siddiqa et al. (2018)
6.		PG	*Aspergillus awamori*	SSF	Orange peel	Mango juice clarification	Anuradha et al. (2016)
7.		PG	*Penicillium janthinellum*	SmF	passion fruit peel	Juice clarification of gala apple tommy mango and orange pear	Pagnonceli et al. (2019)
8.		PG	*Aspergillus niger*	SSF	Carica Papaya peel	Pomegranate juice clarification	Patidar et al. (2020)
9.		Pectinase	*Geotrichum candidum*	Cell-free culture supernatant (CFCS)	–	Juice clarification of orange juice	Ahmed and Sohail (2020)
10.		Exo-PG	*Penicillium janczewskii*	SSF	Wheat bran	Juice clarification of apple, mango, and peach	Amin et al. (2020)
11.		PG	*Zygoascus hellenicus*	SmF	Orange peel	Juice clarification of tangerine, orange, grapefruit, and apple	Munir et al. (2020)
12.		PG	*Aspergillus tamarii*	SmF	–	Clarification of apple juice and enhancing poultry feeds	Belda et al. (2016)
13.		Pectinase	*Metschnikowia pulcherrima*	Semi-industrial fermentation	–	Wine fermentation	Rollero et al. (2018)
14.		PG	*Kluyveromyces marxianus*	–	–	Wine fermentation and aroma improvement	Jaramillo et al. (2015)
15.		Pectinase	*Aspergillus oryzae*	SmF	Passion fruit peel	Fruit juice processing and Bio scouring of raw knitted cotton fabrics	Aggarwal et al. (2020)

Table 6 (continued)

S. no.	Industry	Pectinase type	Fungal strain	Production mode	Substrate used	Application	References
16.	Textile industry	Pectinase	*Candida*	SSF	Wheat bran and orange peel	Bio-scouring of cotton	Shanmugavel et al. (2018)
17.		Exo & Endo PG, PNL, PE	*Aspergillus tamarii*	SSF	Peel banana Wheat bran, lemon peel, coffee pulp, and orange peel with sugarcane bagasse	Bio scouring of cotton	Ghosh et al. (2015)
18.		PL, PG	*Penicillium oxalicum*	SmF		Degumming of jute	Yadav et al. (2017a)
19.		PNL	*Fusarium oxysporum*	SSF	Wheat bran	Retting of fibres	Liu et al. (2017b)
20.		PG	*Phlebia radiata*	SmF	–	Retting of hemp fibres	Wong et al. (2017)
21.		PG	*Aspergillus fumigatus*	SSF	Rice bran	Retting of kenaf fibres	Wulandari et al. (2021)
22.		PG	*Rhizopus sp*	SmF	–	Bio degumming of ramie fibre	Azzaz et al. (2019)
23.		Pectinase	*Aspergillus niger*	SSF	Sugar beet pulp	Degradation of banana fibres	Jagajanantha et al. (2022)
24.		Pectinase	*Aspergillus sp*	SSF	The pseudo stem of banana, hulls of cottonseed and cottonseed meal	Bio-scouring of cotton	Sharma et al. (2011)
25.		Pectinase	*Pseudozyma sp.*	SSF	Citrus waste	Degumming of flax fibres	Wang et al. (2019)
26.	Biofuelproduct ion	Pectinase	*Aspergillus niger*	SSF	Wheat straw	Saccharification of agave biomass	Monjed et al. (2021)
27.		Pectinase	*A. fumigatus*	Mycelium culture	–	Saccharification of Chlorella vulgaris For ethanol production	Bader et al. (2020)
28.		Pectinase	*Trichoderma harzianum*	SSF	Wheat bran	Saccharification of Chlamydomonas *reinhardtii* for ethanol production	Monjed et al. (2021)
29.		Pectinase	*Aspergillus niger and Trametes hirsuta*	SSF	wheat bran, sugarcane bagasse and orange peel	Accessed butanol production	Mondal et al. (2022)
30.		Pectinase	*Trichoderma strains with Aspergillus niger or Pleurotus ostreatus*	SSF	Pineapple crown	Saccharification of pineapple crown for ethanol	Teixeira et al. (2021)
31.		Pectinase	*Doratomyces nanus*	Mycelium culture	–	Saccharification of *Cholera vulgarise*	Monjed et al. (2020)
32.	Oil industry	(Endo-PG), PGase	*Aspergillus giganteus*	SSF	Wheat bran and orange peel	Olive oil extraction	Ortiz et al. (2017)
33.		Pectinase	*Aspergillus niger*	Submerged	Pineapple peel	Coconut Oil Extraction	Ajayi et al. (2021)

Table 6 (continued)

S. no.	Industry	Pectinase type	Fungal strain	Production mode	Substrate used	Application	References
34.	Others		*Schizophyllum commune*	SSF	Mausami peels	Compatibility of alkaline enzyme with different locally available detergents, clarification of apple juice	Mehmood et al. (2019)
35.		Pectinase	*Aspergillus fumigatus*	SSF	Wheat bran + sugar-cane + orange peel	Proficient saccharification of plant bioresources	Mondal et al. (2020)
36.		Pectinase	*Penicillium chrysogenum*	SSF	–	Feed product of buffalo	Azzaz et al. (2019)
37.		PG	*Trichoderma virens*	Flax fibre		Bio-bleaching of the linen fabrics	Szabo et al. (2015)
38.		PNL PG	*Thermomyceslanugi-nosus*	SSF	Sugar-cane bagasse (SCB)	Biofertilizer for *Zea mays*	Makky and Yusoff (2014)
39.		Pectinase	*Aspergillus niger*	SSF	Soyabean hull	Processing of soy	Li et al. (2020)

PG polygalacturonases, *PNL* pectin lyases, *PL* pectate lyase, *Exo-PG* exo-polygalacturonases, *endo-PG* endo polygalacturonases, *PME* Pectin Methyl esterases, *GH28 PG* glycoside hydrolase -28 Polygalacturonase

production of fungal pectinases using agro-wastes is an eco-friendly approach that has immense potential for converting waste biomass. It also results in the production of different value-added products. This is also added to the saccharification potential of pectinases. Efforts have been made to optimize growth conditions as a precursor to enhanced fungal bioproduct production. Utilising waste valorisation techniques, it is possible to take advantage of the diversity of fungi by using contaminated items as a source of fungi. The fungus system offers many advantages and benefits, but it also poses a hazard due to its pathogenicity and ability to mitigate spoilage and damage. Recombinant and mutagenic approaches can be used to change the pathogenicity of native fungus hosts. According to industrial needs, the fusion of traditional and modern state-of-the-art technology has enormous potential.

Over the years, several fungal genera have been targeted for the production of pectinases and efforts have been made to enhance the catalytic activity, specificity, and applicability for industrial applications. Dual culture inoculums for fermentation-based manufacturing have been employed to increase enzyme productivity. These involve using more than one fungal species for the production of the same biocatalyst. But they strictly demand more comprehension of how various hosts interact with one another. The metagenomics approach has resulted in the deciphering of novel microbes with enhanced pectinase activity, thereby giving the world new industrially potent species. Despite metagenomics inclination in microbial studies, fungal metagenomic library construction and diversity studies are minimal. Though purity of metagenomic DNA from humic acid contamination and the easy extraction of prokaryotic diversity in metagenomics DNA limits the studies of pectinases of fungal metagenomic origin from s potential. The directed evolution approach for altered pectinases activity and specificity has resulted in diverse industrial applications predominately in the textile and food industries. Omics-driven approaches including genomics, proteomics, and metabolomics have been used for understanding the production and expression of pectinase genes. Sequencing of fungal strains, genome-wide mining of pectinases using a bioinformatics approach, and expression of the identified pectinases are intensely investigated areas of research in fungal pectinases. Immobilisation of fungal pectinases using novel approaches for enhancing stability and reuse for industrial application has also been attempted.

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of the article. Dr AT and Dr SY reviewed and revised it critically for important intellectual content, and Prof. DY approved the concept and the version to be published. The authors agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

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Declarations

Competing interests The authors declare no competing interests.

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