



Exploration of Novel Industrial Enzymes from Extremophilic Communities for Biotechnological Applications

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ABSTRACT

Extremophilic organisms, which thrive in extreme environments such as geothermal hot springs, polar ice caps, deep-sea hydrothermal vents, and saline lakes, have emerged as a promising source of industrial enzymes. These enzymes are highly valued for their exceptional stability and catalytic activity under harsh conditions, making them indispensable in various industrial sectors, including biofuel production, food processing, textiles, and pharmaceuticals. Key enzymes these organisms produce, such as cellulases, xylanases, lipases, proteases, and amylases, are crucial for lignocellulosic biomass degradation, fat hydrolysis, and protein breakdown. Recent advancements in enzyme isolation, characterization, and optimization have provided significant insights into the molecular mechanisms that enable extremophilic enzymes to withstand extreme pH, temperature, and salinity variations. This review explores the enzymatic potential of extremophilic organisms and the challenges and opportunities associated with scaling up enzyme production, particularly through fermentation techniques like submerged and solid-state fermentation.

Additionally, we examine the ecological roles of these organisms in their native habitats, highlighting the untapped potential for discovering novel enzymes by exploring underexplored ecosystems. Given their remarkable stability, broad substrate specificity, and resilience to extreme conditions, extremophilic enzymes hold great promise as robust biocatalysts in sustainable and eco-friendly industrial processes. Ongoing research into extremophilic communities and their enzymes offers exciting opportunities to unlock new, economically viable, and environmentally sustainable applications in biotechnology.

Keywords: Extremophilic community, Industrial enzymes, Biocatalysts, Enzyme optimization, Sustainable processes.

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INTRODUCTION

Biotechnology profoundly impacts various aspects of daily life, many of which go unnoticed by the general public. Common applications include biofuels, lactose-free milk, bio-insecticides, industrial products such as "stone-washed" jeans, lipase- and protease-containing detergents and medicines that help maintain human health (Coker & Brenchley, 2006). Many industrial processes rely on mesophilic enzymes, which may not always suit extreme conditions like high or low temperatures, varying pressures, salinity, or pH. Modifications are often made through

genetic or chemical means to improve enzyme efficiency, with immobilization strategies used to enhance stability and performance (Rubio & Moreno, 2015). However, these modifications can be costly and time-consuming. The synergistic degradation of Azure B and sulfanilamide antibiotics by *Trametes versicolor* using an activated lignolytic enzyme system enhances the removal of these hazardous materials (Zhang et al., 2023). Nature offers a solution in the form of extremophiles—organisms that thrive in extreme conditions. These organisms produce enzymes, known as extremozymes, which are naturally adapted to survive in harsh environments (Miettinen &

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Suominen, 2002). Ecological factors, such as climate, habitat availability and resource distribution, play crucial roles in shaping organisms' environments and influencing their survival, reproduction and interactions. These factors define ecosystem structures and dynamics, affecting biodiversity and biological communities' stability. Research into *Pyrus* species' pollen morphology and fertility in the Greater Caucasus compares these traits under natural and controlled conditions. This study provides insights into the reproductive characteristics of these species, which are vital for conservation and breeding programs (Jafarzadeh & Iskender, 2024). Additionally, extremophiles contribute to diverse applications such as lactose-free milk production, antibiotic development, and electricity generation through microbial electron leaching. Extremozymes, including glycosyl hydrolases, lipases, and proteases, are particularly significant in biotechnology, showcasing their medicinal and industrial potential (Joseph et al., 2008). Furthermore, the study highlights the fungal pathogens affecting *Pyrus* species in the Greater Caucasus, focusing on their role as biotic stressors in plant health. Identifying these pathogens helps manage the disease and improve the resilience of these species in the region (Jafarzadeh & Iskender, 2024). The relationship between lignin peroxidase and manganese peroxidase production capacities and the cultivation periods of mushrooms highlights key factors affecting enzyme production (Xu et al., 2013). Extremophiles also offer valuable applications in medicine, particularly in the development of bioplastics (Joshi & Satyanarayana, 2023). Some extremophilic species, such as halophilic archaea, are renowned for producing polyhydroxyalkanoates (PHAs), a versatile group of polyesters (Charlesworth & Burns, 2015). PHAs serve as carbon storage in microbial cells. They are used in creating bioplastics known for their biocompatibility, water resistance, and biodegradability, making them a sustainable alternative to conventional petroleum-based plastics (DasSarma et al., 2009). The study also explores fungal communities in soils contaminated by human activities, emphasizing their ecological roles and potential for bioremediation. In medical and agricultural fields, enzymes produced by *Trichoderma viride* are noted for their anticancer and antifungal properties, demonstrating their potential as biocontrol agents and therapeutic compounds (Abu-Tahon & Isaac, 2020). This enzyme is also effective in starch hydrolysis, making it valuable in industrial applications in the food and biofuel sectors (Apostolidi et al., 2020). Laccase production by *Trametes versicolor* in solid-state fermentation using tea residues as a substrate demonstrates its potential application in dye decolorization (Xu et al., 2020). Additionally, the research into a chitinase enzyme isolated from the marine fungus *Penicillium chrysogenum* MH745129 revealed its antifungal properties, suggesting its potential in controlling postharvest pathogens in citrus fruits (Atalla et al., 2020). Extremophilic fungi are increasingly studied for their bioremediation potential, particularly their ability to degrade environmental pollutants under extreme conditions. These fungi's ecological adaptability and enzymatic diversity make them ideal candidates for sustainable environmental cleanup (Bhapkar et al., 2022). Moreover, the purification,

characterization, and optimization of a protease enzyme produced by *Aspergillus brasiliensis* strain BCW2 demonstrate its relevance in industries such as waste management, textiles, and food processing due to its stability and effectiveness in various conditions (Chimbekujwo et al., 2020). Research into thermophilic fungi, which thrive in high-temperature environments, reveals their adaptations to heat and their potential for biotechnological applications requiring thermostable enzymes (Chaturverdi & Sarethy, 2022). The catalytic properties and industrial applications of extremophilic enzymes, particularly in the pharmaceutical, food, and biofuel industries, are discussed. These enzymes improve the stability and efficiency of eco-friendly industrial practices (Choudhary et al., 2022). Lastly, converting paper waste into bioethanol using a novel cellulose-degrading fungal isolate contributes to more sustainable biofuel production (Darwesh et al., 2020). In microbial biotechnology for sustainable agriculture and biomedicine, microbial application diversity and functional perspectives are emphasized (Rastegari et al., 2020). Similarly, green polygalacturonase production by *Aspergillus awamori* NRC-F18 under solid-state fermentation for potential pharmaceutical applications (Roshdy et al., 2020). Lignin-modifying enzymes are essential in developing environmentally responsive technologies for degrading organic compounds, particularly in bioremediation and waste management. These break down complex lignin structures, contributing to sustainable environmental cleanup (Da Silva Vilar et al., 2021). A recent study identified a novel lignin-degrading strain that enhances biomass conversion efficiency for biofuels and value-added products, further exploring its biochemical properties and industrial applications (Zhang & Liu, 2022). White-rot fungi are particularly significant in bioremediation, as they degrade xenobiotic compounds such as pesticides and industrial pollutants through lignin-degrading enzymes, providing substantial ecological benefits in contaminated environments (Kathiravan & Gnanadoss, 2021). These fungi also show potential in biodegrading plastics, offering a promising solution to the global plastic pollution crisis through their enzymatic mechanisms (Bautista-Zamudio et al., 2023). Research on the effects of climate change on environmental pollution indicates that extreme weather events may alter the behavior and distribution of contaminants, emphasizing the need for adaptive management strategies to address these challenges (Bolan et al., 2024). Laccases, versatile enzymes produced by various organisms, are highly effective in reducing environmental pollution, particularly in the degradation of industrial waste and pesticides, offering both environmental and economic benefits (Paraschiv et al., 2022). Furthermore, the fungus *Cerrena unicolor* GC.U01 demonstrates significant promise in efficiently treating crop straws, facilitating the conversion of agricultural waste into biofuels, and supporting sustainable agricultural practices (Ying et al., 2024). The potential of white-rot fungi in biodegrading plastics highlights the mechanisms behind their ability to break down various plastic polymers (Bautista-Zamudio et al., 2023). The effects of climate change on contaminants, particularly how extreme weather events alter the fate of

environmental pollutants. Their findings underscore the need for a better understanding and management of contaminant mobility in the face of increasing climate instability (Bolan et al., 2024). The species composition of fungal biota in ecosystems impacted by human activities, highlighting shifts in biodiversity. The findings emphasize the resilience of certain fungal species in altered environments and their role in ecological balance (Safaralieva et al., 2020). An overview of fungal species in saline soils offers valuable insights into fungi adaptation mechanisms to saline conditions. It underscores the ecological importance of these species in maintaining soil health in saline ecosystems (Yunusov et al., 2021). The antimicrobial and enzymatic properties of fungi are isolated from diverse ecological environments. It demonstrates the potential of these fungi for biotechnological applications, particularly in the field of natural product development (Omar et al., 2023).

Solid-State Fermentation

Solid-state fermentation (SSF) utilizes solid substrates such as bran, bagasse and paper pulp as mediums for microbial growth. However, SSF is unsuitable for organisms requiring high water activity (aw), like bacteria, which prefer moist, liquid environments. Due to its lower moisture content, SSF provides a more controlled and stable environment, making it ideal for producing specific bioactive compounds or enzymes, particularly from extremophilic fungi and other slow-growing microorganisms (Babu & Satyanarayana, 1996). For example, the production of laccases by white-rot fungi under SSF conditions has been explored for its industrial applications in environmental cleanup and bioremediation. This method is cost-effective and environmentally friendly, with various factors influencing enzyme yield and activity during fermentation (Chmelová et al., 2022). A pilot-scale study on the solid-state fermentation of soybean residues for bioflocculant production demonstrates its potential in a bioreactor system (Zulkeflee & Sánchez, 2014). A review of

SSF in the circular bioeconomy emphasizes its potential to convert waste into bio-based products while minimizing environmental impact. The review also addresses the technological and economic barriers to fully integrating this process into sustainable industrial practices (Antoni Sánchez et al., 2024). Additionally, the enzymatic one-pot hydrolysis of sugar beet press pulp using an engineered *Aspergillus niger* strain demonstrates an effective conversion of agricultural waste into fermentable sugars, thereby enhancing biomass conversion efficiency for biofuel production (Knesebeck et al., 2023).

Table 1 summarizes various processes used to purify bioproducts obtained from solid-state fermentation. Sophorolipids, a type of biosurfactant, are extracted using ethyl acetate via solvent extraction (Rodríguez et al., 2021). For biopesticides, Bt-crystal protein is typically extracted from enriched compost (Ballardo et al., 2020; Shahid et al., 2023; Adilkhankyzy et al., 2025). Polyhydroxyalkanoates (PHA), a type of bioplastic, are purified using solvent extraction methods (Szacherska et al., 2021). 2-phenyl-ethanol, a valuable aroma compound, is extracted using methanol and filtration (Martínez-Avila et al., 2021). Antioxidants like phenolic compounds are extracted using microwave-assisted extraction with either water or ethanol (Rodríguez et al., 2021). Finally, other bioproducts, such as 6-pentyl-a-pyrone, are extracted using Soxhlet extraction with hexane, while flocculants are purified with water (Carboué et al., 2020; Zulkeflee & Sánchez, 2014). Improving solid properties is a common technique used in animal feed production to enhance its quality (Costa-Silva et al., 2022).

Recent studies have underscored the potential of fungal enzymes in the bioremediation of industrial pollutants, particularly dyes (Table 2). *Trametes flavida* WTFP2, which produces laccase, achieved an impressive 99.48% removal of Congo Red dye at a 100 mg/L concentration after 16 hours of incubation at 30°C. Similarly, *Trametes versicolor* WH21 demonstrated high efficacy in degrading Azure B dye and Sulfacetamide (SCT), with removal efficiencies of 86.5 and 96.2%, respectively, under

Table 1: Summary of some processes used to purify bioproducts obtained from solid-state fermentation

Category	Bioproducts	Extraction Methods	Details	References
Biosurfactant	Sophorolipids	Solvent extraction	Ethyl acetate	Rodríguez et al. (2021)
Biopesticides	Bt-crystal protein	Enriched compost		Ballardo et al. (2020)
Bioplastics	PHA	Solvent extraction		Carboué et al. (2020)
Aromas	2-phenyl-ethanol	Methanol	Filtration	Szacherska et al. (2021)
Antioxidants	Phenolic compounds	Microwave	Water or ethanol	Rodríguez et al. (2021)
Other Bioproducts	6-Pentyl-a-pyrone	Soxhlet extraction	Hexane	Martínez-Avila et al. (2021)
	Bioflocculant	Water		Zulkeflee & Sánchez (2014)
Animal Feed	Animal Feed	Improvement of solid properties		Costa-Silva et al. (2022)

Table 2: Some WRF and/or their associated liquid fermenters (LEs) in dye biodegradation

Enzyme-producing Strain	Involved Enzymes	Types of Pollutants	Optimum Pollutant Conc. (mg/L)	Optimum pH & Temp. (°C)	Incubation Time (hrs)	Removal Efficiency (%)	Reference
<i>Trametes flavida</i> WTFP2	Laccase	Congo Red	100	NR & 30	16	99.48	Sharma et al. (2023)
<i>Trametes versicolor</i> WH21	MnP and Laccase	Azure B dye and Sulfacetamide (SCT)	300, 30	NR & 28	168	86.5 (Azure B) and 96.2 (SCT)	Zhang et al. (2023)
<i>Trametes hirsuta</i> D7	Laccase	Reactive Black 5, Acid Blue 113, Acid Orange 7	100	NR & 30	118, 96, 120	92, 97, 30	Alam et al. (2023)
<i>Cyathus bulleri</i> (Brodie 195062)	MnP and Laccase	Reactive Orange (RO)	16	50	4 & 28	96	Afreen & Mishra (2023)
<i>Phanerochaete chrysosporium</i> CDBB 686	LiP and MnP	Congo Red, Poly R-478, Methyl Green	50 ppm	NR & 30	30	41.84, 56.86, 69.79	Sosa-Martínez et al. (2020)
<i>Trametes versicolor</i> Vault-encapsulated	Laccase	Reactive Blue 19, Acid Orange 7	50	5 & 27	24	72, 80	Gao et al. (2022)
<i>Emmilia latemargina</i> (MAP03)	VP, MnP, and LiP	Remazol Brilliant Blue R	150	NR & 28	576	100	Juárez-Hernández et al. (2021)

optimal conditions. *Trametes hirsuta* D7 effectively removed multiple dyes, including Reactive Black 5 and Acid Blue 113, with removal efficiencies ranging from 92 to 97%. The *Cyathus bulleri* strain showcased the potential of MnP (manganese peroxidase) and laccase in degrading Reactive Orange, achieving a 96% removal at a 16mg/L concentration after 28 hours of incubation. *Phanerochaete chrysosporium* CDBB 686 can degrade Congo Red and other pollutants, with removal efficiencies ranging from 41.84 to 69.79%. *Trametes versicolor* Vault-encapsulated laccase achieved 72 to 80% removal of Reactive Blue 19 and Acid Orange 7 under mild temperature conditions.

Emmia latemargina (MAP03), producing VP (veratryl peroxidase), MnP, and LiP (lignin peroxidase), wholly removed Remazol Brilliant Blue R after 576 hours. These findings demonstrate the broad potential of fungal laccases, MnP, and LiP in degrading various pollutants. By optimizing these enzymatic processes, an eco-friendly and efficient alternative for industrial waste treatment can be realized, offering a sustainable solution for the remediation of hazardous waste (Tadele et al., 2024).

High-value oxidative enzymes from *Cyathus bulleri* using agricultural and agri-food waste, aiming to apply these enzymes in the textile industry. Their study emphasizes the sustainable conversion of waste into valuable enzymes, providing an environmentally friendly approach to textile processing (Afreen & Mishra, 2023).

Fig. 1 illustrates the wide range of environments where extremophiles can be found, with the central focus being "Extremophiles." Surrounding this term are six primary categories of extreme habitats (Gallo & Aulitto, 2024). *High temperatures characterize Hot Springs and Geothermal Areas*, while *Deep-Sea Hydrothermal Vents and Sediments* are environments where high pressure and temperatures prevail (Rampelotto, 2024). *Polar Regions* represent areas with extreme cold, and *Radiation-Contaminated Sites* highlight areas exposed to high radiation levels. *Salt Flats and Hypersaline Environments* feature regions with elevated salt concentrations, while *Acidic and Alkaline Environments* encompass habitats with extreme pH levels. These varied conditions exemplify the extraordinary adaptability of extremophiles, who survive and thrive under harsh environmental stressors.

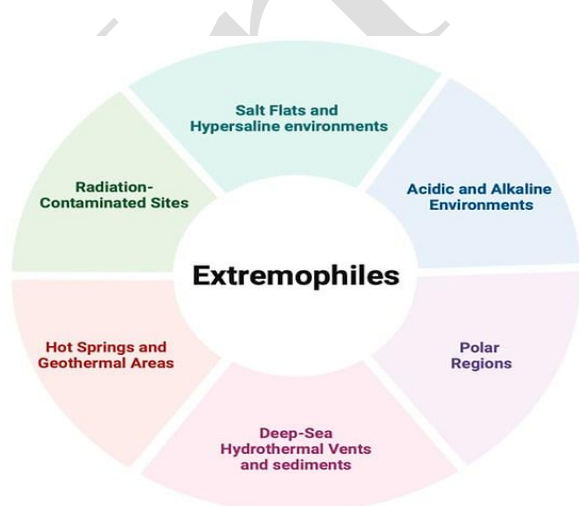


Fig. 1: A schematic overview illustrating the primary environments in which extremophilic microorganisms are found (Gallo & Aulitto, 2024).

Submerged Fermentation/Liquid Fermentation

Submerged Fermentation (SmF) or Liquid Fermentation (LF) involves using free-flowing liquid substrates like molasses, broths, and other nutrient-rich solutions. This method is especially effective for microorganisms that thrive in high-moisture environments, such as bacteria and yeast. Compared to Solid-State Fermentation (SSF), substrates in SmF are consumed more rapidly, often requiring constant replenishment to ensure nutrient availability (Subramaniam & Vimala, 2012). A key advantage of SmF is the ease with which bioactive compounds secreted into the fermentation broth can be collected and purified. Since SmF operates in a liquid medium, it is ideal for producing secondary metabolites that are either used in liquid form or for industrial applications where liquid extraction is more efficient (Dhillon et al., 2012). Additionally, SmF provides optimal conditions for microorganism growth, as it allows for controlled aeration and agitation, making it highly suitable for organisms that require a stable and controlled environment for efficient fermentation. SmF is widely employed in the pharmaceutical, food and biotechnology industries, particularly for the production of enzymes, antibiotics and other valuable metabolites (Dias et al., 2018).

Comparison of SSF and SmF

SSF (Solid-State Fermentation) is typically more energy-efficient due to its lower moisture requirements and slower fermentation rate. This makes it ideal for applications such as enzyme production and fungal growth, where less water and energy input is beneficial.

SmF (Submerged Fermentation) is more versatile for producing liquid-based bioactive compounds. It supports rapid microbial growth and offers easier downstream processing, making it a preferred method for requiring liquid products. Both techniques offer distinct advantages depending on the type of microorganism, product, and desired fermentation conditions. Biotechnology has revolutionized numerous industries, including chemicals, food and feed production, environmental management, energy generation, and healthcare. These advancements are driven by both social and environmental demands alongside economic considerations. Industrial enzymes have evolved to perform remarkably efficiently, providing precise, controlled mechanisms for cellular processes. This enables organisms to survive and adapt to diverse and often extreme environmental conditions. Enzymes play a crucial role across virtually all industries, from food production to healthcare, due to their natural efficiency, high specificity, and ability to catalyze reactions with precision and minimal environmental impact.

The Industrial Applications of Enzymes can be Categorized into Several Areas:

1. Enzymes are final products that are directly produced for commercial sale and use.
2. Enzymes as processing aids – Enzymes are used to facilitate or enhance other processes in production.
3. Enzymes are used in food and beverage production to improve the quality, flavor and nutritional value of food products.

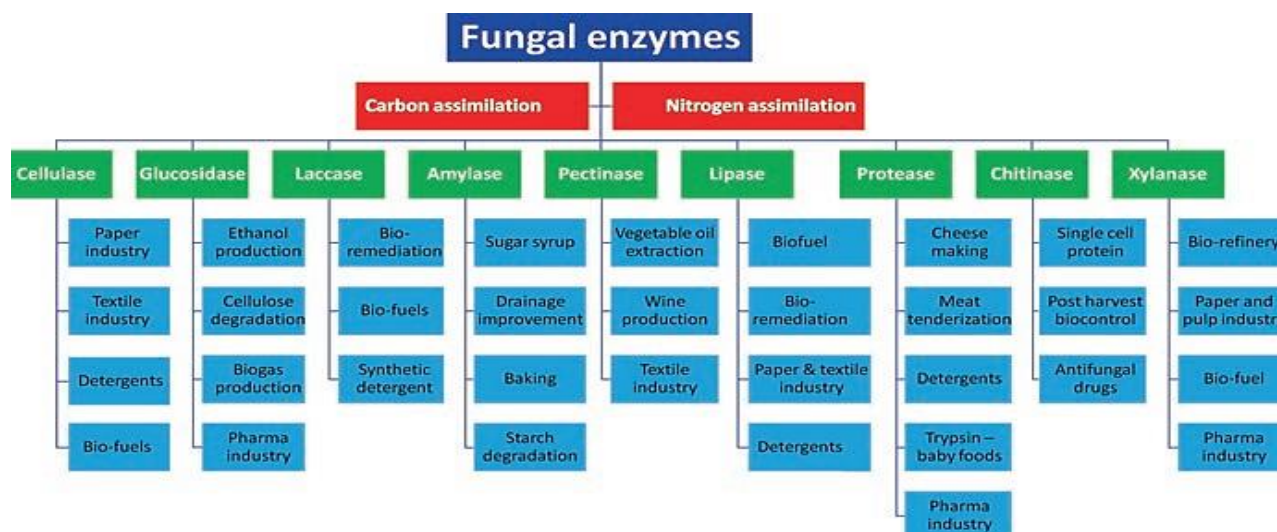


Fig. 2: Industrial important fungal enzymes and their potential applications (Dhevgai et al., 2022).

4. Enzymes as industrial biocatalysts – Enzymes are employed in various chemical reactions as a green alternative to traditional catalysts in manufacturing.

5. Enzymes in genetic engineering—Enzymes play a crucial role in modifying genetic material to develop new products or organisms.

Enzyme Properties for Harsh Industrial Environments

Extremophilic fungal enzymes (Fig. 2) used in these industries must exhibit specific properties that allow them to function effectively in harsh industrial environments. These properties include:

Thermal Stability: Many industrial processes operate at high temperatures, so proteases must maintain their activity at elevated temperatures without denaturing.

pH Stability: Proteases used in industries like textile and dairy must perform optimally across a wide range of pH levels, from acidic environments in cheese production to alkaline conditions in detergent formulations.

Solvent Tolerance: In some industries, such as biofuels and waste management, proteases are exposed to organic solvents. Enzymes with solvent tolerance remain stable and functional in these environments.

Specificity and Efficiency: Proteases must be particular in their action to target particular proteins or compounds, improving the efficiency of the process and reducing unwanted side reactions.

Resistance to Inhibitors: Industrial processes often involve inhibitors or harsh chemicals that can degrade enzymes. Proteases used in such conditions must resist inactivation by these substances.

Types of Industrial Enzymes Produced by Extremophilic Fungi

Extremophilic fungal enzymes are increasingly valued in biofuel production, waste management, and textiles due to their versatility. In biofuel production, proteases break down organic materials, making sugars more accessible for fermentation into biofuels like ethanol (Niehaus et al., 1999; Duarte et al., 2018; Teixeira et al., 2024; Ashaolu et al., 2024). In waste management, they help degrade the protein-rich waste, converting it into manageable, non-toxic by-

products. In the textile industry, proteases remove stains, soften fabrics and improve appearance by biopolishing. They also aid in eco-friendly leather processing, replacing harmful chemicals with enzymatic treatments.

Proteases

Protease enzymes, essential for breaking down proteins, have diverse industrial applications in dairy, beverages, detergents, baking, leather, and pharmaceuticals. Fungal sources, including *Aspergillus* species (*A. fumigatus*, *A. oryzae*, *A. niger*, etc), are commonly used for protease production (Yadav et al., 2020; Pócsi et al., 2024). In the food industry, fungal proteases assist in processes like beer clarification, cheese coagulation, and meat tenderization. They also hydrolyze proteins in juices, soy, whey, and gelatin. Milk-clotting proteases, especially those from *Aspergillus* species, are popular rennet substitutes for cheese production due to their stability and activity under acidic conditions (Kumra et al., 2017; Mamo et al., 2020; Gaonkar et al., 2023). A review of protease enzymes has focused on their current status and prospects in the industrial sector. Proteases, vital in numerous biochemical processes, are in high demand due to their broad applications in food, detergents, pharmaceuticals, and leather processing industries. The review highlights different proteases, including serine, cysteine, and metalloproteases, and discusses their specific industrial uses and production methods. It also addresses the challenges of optimizing protease production, including cost-effective enzyme production, stability, and substrate specificity. Furthermore, the article explores emerging trends in biotechnology, such as genetic engineering and fermentation technology, aimed at enhancing protease production and performance. The authors emphasize the potential for continued advancements in protease enzyme applications, particularly in eco-friendly and sustainable industrial processes (Ash & Mishra, 2023). Investigated the valorization of low-cost agro-waste residues for the maximum production of protease and lipase haloextremozymes by *Haloferax lucentensis* GUBF-2, highlighting the potential of agro-wastes for enzyme production (Gaonkar & Furtado, 2021).

Amylase

Amylases have been widely used in various industries such as food, textiles, detergents, paper, and pharmaceuticals since the 19th century, owing to their ability to hydrolyze starch into simple sugars like dextrans and oligosaccharides. Fungal sources like *Aspergillus* species (*A. oryzae*, *A. niger*, *A. terreus*, *A. fumigatus*), *Thermomyces lanuginosus*, and *Rhizopus oryzae* are commonly used for amylase production (Dumorné et al., 2017; Samanta, 2020). Amylases, including α -amylases, β -amylases, and γ -amylases, target different glycosidic bonds in amylose and amylopectin, facilitating processes like fermentation, sugar syrup production, and starch liquefaction. Similarly, cold-active amylases from *Penicillium chrysogenum* have many applications (Rafiq et al., 2020). The researchers investigated the catalytic and thermodynamic properties of an acidic α -amylase produced by the fungus *Paecilomyces* variety ATHUM 8891, providing insights into its potential industrial applications (Apostolidi et al., 2020). Amylases like those from *Paecilomyces variotii* offer stability and catalytic activity under varying temperatures, enhancing starch industry applications. In environmental applications, amylase from *Pleurotus florida* aids in starch degradation in potato and cotton waste (Devi et al., 2020). Digestive medicines containing α -amylase from *A. oryzae* are used for indigestion (Samanta, 2020). In detergents, α -amylases help remove starch-based stains due to their alkalophilic and resistant nature. Amylase production by *Neurospora intermedia*, an edible fungus, has potential applications in protein-rich biomass and feed industries. A comprehensive review of amylase enzymes, discussing their types, production methods, and diverse industrial applications, including their role in food, detergent, and biofuel sectors. The article also highlights recent advancements in amylase production, optimization, and biotechnological potential in various industries (Dhwani & Andhare, 2021). A thermophilic amylase from *Rhizomucor miehei* expressed in *Pichia pastoris* exhibits excellent properties for improving bread quality and antistaling effects (Wang et al., 2020). Amylase is usually an extracellular enzyme. Three types of microbial amylases exist: α -amylase, β -amylase, and γ -amylase. They each act differently on starch to obtain simple glucose monomers. The industrial production of amylase is carried out using two methods: Submerged Fermentation (SmF) and Solid-State Fermentation (SSF) (Kohli et al., 2020). The important factors that affect the fermentation process include pH, temperature, carbon and nitrogen sources, and metal ions. The research focused on isolating and characterizing this enzyme, highlighting its potential for industrial applications in starch processing. The study also emphasized the enzyme's stability and efficiency under various conditions, making it a valuable biocatalyst in biotechnology.

Cellulase

Cellulases are essential enzymes for breaking down cellulosic polysaccharides in biomass and are widely used in industries such as pulp and paper, textiles, detergents, food processing, agriculture, and bioethanol production. Fungal species like *Aspergillus fumigatus*, *Aspergillus niger*, *Trichoderma reesei*, and *Rhizopus oryzae* are key cellulase

producers (Kupski et al., 2014). In the pulp and paper industry, cellulases help modify fiber properties, reduce pulp viscosity, and enhance paper quality. In agriculture, cellulases control plant diseases and accelerate the breakdown of crop residues, improving soil fertility. In detergents, cellulases help remove dirt and maintain fabric quality. In textiles, cellulases are used in biopolishing and biostoning processes for cellulose-based fabrics, enhancing softness. In the bioethanol industry, fungi like *Penicillium funiculosum* and *Fusarium verticillioides* aid in converting agricultural wastes into biofuels (Vázquez-Montoya et al., 2020). The potential of extremophilic cellulases, enzymes produced by microorganisms that thrive in extreme environments. It highlights their industrial relevance, particularly in the bioconversion of plant biomass and waste materials. The article also discusses the biotechnological applications of extremophilic cellulases in various sectors, including biofuel production, paper, and textile industries. Additionally, it emphasizes the need for further research to improve the stability and efficiency of these enzymes under harsh conditions (Sharma et al., 2023). Highly alkali-stable and cellulase-free xylanases from *Fusarium sp.* 21 demonstrate their effectiveness in clarifying orange juice (Li et al., 2020)—a comprehensive review of extremophilic cellulases, focusing on their unique properties and potential applications in biotechnology. The article highlights the role of these enzymes in industrial processes and the challenges in optimizing their stability and efficiency under extreme conditions (Mohanta et al., 2023).

Xylanases

Xylanases are enzymes that break down the hemicellulose component, specifically beta-1,4-xylan, of lignocellulosic biomass into xylose (Vogel, 2018). Fungal species such as *Aspergillus* spp. (*A. tubingenisis*, *A. terreus*, *A. niger*), *Rhizopus oryzae*, *Mucor* spp., and *Trichoderma viride* are well-known for producing xylanases. *Neurospora intermedia* is also a promising candidate for large-scale xylanase production (Shahryari et al., 2019). In the textile industry, xylanases process plant fibers, particularly for linen and hessian fabrics. In baking, xylanases break down wheat hemicelluloses, improving dough softness, volume, and bread quality (Yadav et al., 2020). In the juice and wine industries, xylanases aid fruit pulp stabilization, juice clarification, and viscosity reduction (Li et al., 2020). Xylan, the dominant component of hemicelluloses, is one of Earth's most abundant organic substances and has significant applications in the pulp and paper industry (Pawan & Sharma, 2021). The wood used for pulp production is treated at high temperatures and basic pH levels, which means that enzymatic procedures require proteins exhibiting high thermostability and activity across a broad pH range. Treatment with xylanase at elevated temperatures disrupts the cell wall structure, which, in turn, facilitates lignin removal during various stages of bleaching (Yadav et al., 2020). Optimization studies on cellulase and xylanase production by *Rhizopus oryzae* UC 2 using raw oil palm leaves as a substrate under solid-state fermentation demonstrate agricultural waste's potential for enzyme production (Ezeilo et al., 2020).

Lipases

Lipases are enzymes that hydrolyze insoluble triacylglycerols and catalyze reactions such as esterification, alcoholysis, and acidolysis, demonstrating high specificity for substrates (Javed et al., 2018). Familiar fungal lipase producers include *Aspergillus*, *Fusarium*, *Mucor*, *Geotrichum*, *Penicillium*, and *Rhizopus* species. *Penicillium simplicissimum* and *Penicillium chrysogenum* HTF24, a psychrotrophic fungus, have attracted attention for their lipase production, with broad applications across industrial and environmental sectors. Lipases are used in textiles, detergents, pharmaceuticals, pulp and paper, and biofuels (Borowiecki et al., 2017). In the food industry, lipases like those from *Penicillium roquefortii* synthesize methyl ketones, enhancing the flavor profile of blue cheese. A study explored the expression of a novel acidic lipase from *Micrococcus luteus* in *Pichia pastoris*, emphasizing its potential for biodiesel production through transesterification (Adina et al., 2021). Another investigation focused on a thermoalkaliphilic lipase from *Geobacillus stearothermophilus* FMR12, demonstrating its stability under high-temperature and alkaline conditions, making it suitable for detergent formulations and bioremediation (Abol-Fotouh et al., 2021). Research on a psychrophilic fungus demonstrated its biomass as an efficient biocatalyst for esterification reactions at low temperatures, offering a sustainable alternative for bio-based chemical production (Kutyla et al., 2022). A study on *Haloferax lucentensis* GUBF-2 highlighted the valorization of agro-waste residues for producing haloextremozymes, particularly useful in high-salt environments (Gaonkar et al., 2021). Further research focused on optimizing a halotolerant lipase from *Halomonas* sp. C2SS100, showcasing its potential for detergent applications (Khmaissa et al., 2021). Enhancing thermostability in a lipase from *Pseudomonas alcaligenes* through the CREATE strategy improved its stability, expanding its applicability in industrial processes such as l-menthol production (Yu et al., 2022). Producing a halotolerant lipase from *Halomonas* sp. strain C2SS100 using response surface methodology demonstrates its potential application in detergent formulations (Khmaissa et al., 2021).

Ligninases

Ligninase is a heme-protein enzyme that oxidizes phenolic, non-phenolic, and aromatic compounds using hydrogen peroxide (H_2O_2), playing a critical role in lignin degradation (Tang et al., 2024). Lignin peroxidase (LiP), produced by white-rot fungi such as *Phanerochaete chrysosporium*, *Trametes versicolor*, *Trichoderma viride*, and *Aspergillus niger*, is one of the primary enzymes involved in this process. Additionally, manganese peroxidase (MnP), produced by fungi like *Pleurotus nebrodeusis*, *T. versicolor*, and *Grifola frondosa*, contributes significantly to lignin degradation (Xu et al., 2013; Xu et al., 2023). Fungal ligninases are widely used in biopulping and biobleaching, improving the digestibility of pulp and removing lignin and hemicelluloses, resulting in higher yield and softer products (Colonia et al., 2019). LiP from *P. chrysosporium* has also been shown to effectively decolorize various polymeric dyes, such as triphenylmethane, anthraquinone, and azo

dyes, through oxidation with a mediator like veratryl alcohol (Singh et al., 2015). The complexity and recalcitrance of the lignin structure present a significant challenge to its efficient utilization in the commercial production of high-value products. The biodegradation of synthetic dyes using fungal ligninolytic enzymes, optimizing the process, evaluating metabolites, and assessing the toxicity of the degradation products (Sosa-Martinez et al., 2020). The role of ligninolytic enzymes in sustainable agriculture, focusing on their applications and the challenges involved. Their study highlights how these enzymes contribute to eco-friendly agricultural practices, improving soil health and reducing waste while also addressing the difficulties in scaling up these biotechnological processes (Gałazka et al., 2025). Recent advances in microbial "biofunneling" transformation processes offer new opportunities for lignin conversion, particularly in integrated biorefineries. This mini-review introduces recent developments in lignin depolymerization by bacterial strains and discusses the application of microbial lignin degradation in lipid production. The research highlights innovative strategies for integrating lignin into biorefineries, enhancing sustainability and economic feasibility. The study emphasizes the potential of lignin valorization to reduce waste and create value-added products for industrial applications (Liu et al., 2021). The use of deep eutectic solvent extraction liquor of lignin to culture *Rhodotorula glutinis* enhances microbial lipid production (Zhang et al., 2021), while authors explored *Trichosporon cutaneum*'s tolerance to lignin-derived phenolic aldehydes (Zhang & Bao, 2022), promoting cell growth and lipid accumulation. In a similar study, authors isolated and evaluated a novel lignin-degrading strain for its performance in lignin degradation (Zhang & Liu, 2022).

Fig. 3 illustrates the potential applications of ligninolytic enzymes in promoting sustainable agriculture. As the agricultural sector shifts toward more eco-friendly practices, incorporating ligninolytic enzymes could play a vital role in maintaining ecological balance while addressing global food security challenges. In conclusion, utilizing ligninolytic enzymes in farming tackles pressing environmental issues and supports the transition to a more sustainable agricultural future.

Conclusion and Future Perspectives

Microbial enzymes, particularly those derived from fungi, are highly valued for their ease of production, stability, and superior efficiency in breaking down complex substrates. Fungal enzymes are indispensable across various industries, including food and beverage production, textile processing, bioremediation, biofuel production, paper manufacturing, wastewater treatment, detergents, dairy, leather, and pharmaceuticals. Their versatility allows for developing more sustainable and cost-effective processes in these industries. In addition to their industrial uses, fungal enzymes play an essential role in healthcare, particularly as supplements for individuals with enzyme deficiencies. For instance, lactase from fungi is widely used to aid lactose-intolerant individuals in digesting dairy products. These enzymes are also integral in producing critical pharmaceuticals, including antibiotics like penicillin and insulin and in treatments for conditions such as cancer and

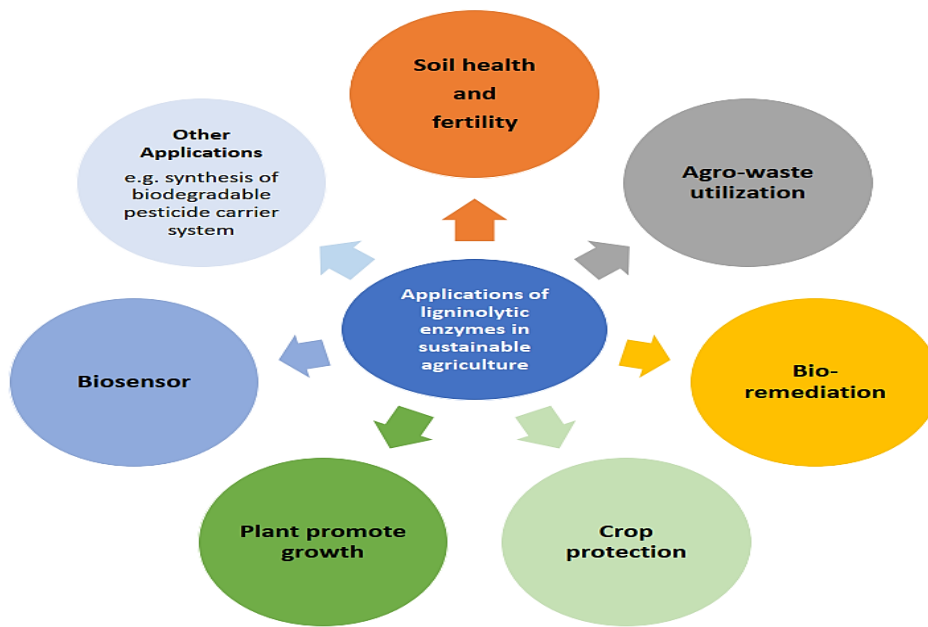


Fig. 3: Potential uses of ligninolytic enzymes in promoting sustainable agriculture (Gałazka et al., 2025).

autoimmune diseases. Looking ahead, the future of fungal enzymes appears promising. With advances in genomics, protein engineering, and synthetic biology, the production of fungal enzymes is expected to become even more efficient, cost-effective, and sustainable. As the demand for environmentally friendly solutions continues to grow, the potential for fungal enzymes in areas like biofuels, bioremediation, and green chemistry is immense. Additionally, exploring extremophilic fungi and their unique enzymatic properties may lead to the discovery of novel enzymes with exceptional capabilities for industrial and therapeutic applications. In the coming years, further research into the genetic manipulation of fungi and the discovery of new fungal strains with specialized enzyme profiles could enhance enzyme production yields, reduce costs, and open doors to innovative applications across various sectors. Furthermore, integrating artificial intelligence and machine learning into enzyme design can revolutionize enzyme optimization, leading to tailored enzymes for specific industrial and medical needs.

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formal analysis, data curation. E.L.T. contributed to writing – review & editing, visualization, methodology, formal analysis. S.J. (Sabina Jafarzadeh) contributed as the main author, with substantial contributions to conceptualization, writing – review & editing, and final draft preparation. K.B. (Konul Bakhshsaliyeva) contributed to writing – review & editing and formal analysis. E.I. (Elman Iskandar) contributed to data curation and formal analysis. P.M. (Panah Muradov) provided invaluable guidance and support throughout the work.

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