Comparative Insights into Fungal and Bacterial Cellulases: Efficiency and Applications

Vidya A. S[1]., Chandrakant S. Karigar[1], Sunil. S. More[2*]

[1]Department of Biochemistry, Jnana Bharathi Campus, Bangalore University, Bengaluru.

[2]School of Basic and Applied Science, Dayananda Sagar University, Bengaluru

***Corresponding Author**

DOI: https://doi.org/10.51584/IJRIAS.2026.110400138

Received: 16 April 2026; Accepted: 21 April 2026; Published: 14 May 2026

ABSTRACT

Cellulases are pivotal enzymes in the bioconversion of lignocellulosic biomass, finding applications across waste management, biofuel production, and industrial processes. Among microbial sources, fungi and bacteria represent two dominant and distinct producers of cellulases, each with unique enzyme systems, biochemical properties, and operational advantages. This review presents a comparative analysis of fungal and bacterial cellulases, focusing on their structural differences, catalytic efficiency, environmental stability, and industrial relevance. The synergistic use of both microbial types is also explored as an emerging strategy to enhance cellulose degradation. This synthesis aims to guide future research and practical applications by evaluating the strengths, limitations, and evolving potential of fungal and bacterial cellulases in sustainable waste valorisation and bioeconomic systems.

Keywords: Cellulase, Lignocellulosic biomass, Waste management, Bioeconomy.

INTRODUCTION

Cellulose represents the most abundant and renewable component of plant biomass (1), serving as a primary photosynthetic product and a cornerstone of the global bioresource economy (2). It exists either in pure form or intimately associated with hemicellulose and lignin, typically arranged in microfibrils ranging from 2–20 nm in diameter and 100–40,000 nm in length. These cellulose microfibrils constitute a highly ordered, load-bearing network that reinforces the structural integrity of plant cell walls. The global biosphere generates an estimated 100 billion dry tons of cellulosic biomass annually, underscoring its vast potential (3).

Due to its abundance, renewability, and structural properties, cellulose is recognized as a critical feedstock for the sustainable production of biofuels—particularly methane and bioethanol. Beyond energy applications, cellulose exhibits broad industrial utility across sectors such as food and beverage, animal nutrition, detergents, agriculture, textiles, and the pulp and paper industry. Its low-cost and renewable nature continues to draw scientific and industrial interest, particularly in the enzymatic production of high-value biocatalysts including cellulase, xylanase, and α-amylase at both laboratory and commercial scales. The strategic valorisation of cellulose thus contributes not only to the circular bioeconomy but also to national energy resilience and economic growth (4).

Cellulose is a linear polysaccharide composed of glucose monomers linked via β-1,4-glycosidic bonds. These monomeric units, primarily consisting of small chains of cellobiose and glucose (5), are liberated from the insoluble cellulose matrix through enzymatic hydrolysis mediated by cellulases.

Cellulase, the key enzyme responsible for cellulose degradation, is inducible and produced by a wide array of microorganisms—either as extracellular or cell-bound enzymes—when cultured on cellulosic substrates (6). The biological degradation of cellulose, or cellulolysis, is driven by a concerted enzymatic system comprising three major classes: 1,4-β-endoglucanase, 1,4-β-exoglucanase, and β-glucosidase (also known as β-D-glucoside glucohydrolase or cellobiase). Endoglucanases randomly cleave internal β-1,4-glycosidic bonds along the cellulose chain, while exoglucanases act on the non-reducing ends, liberating cellobiose units and separating elementary fibrils from crystalline cellulose. β-glucosidases catalyze the hydrolysis of cellobiose and water-soluble cellodextrins, yielding glucose as the final saccharification product [7,8]. Only the synergistic action of all three enzymes enables the complete hydrolysis of cellulose into glucose [9–11], or full mineralization into CO_2 and H_2O.

A broad diversity of microorganisms, especially fungi and bacteria, are naturally equipped to produce cellulolytic enzymes. Cellulose-degrading populations span aerobic and anaerobic mesophilic bacteria, thermophiles, alkaliphiles, actinomycetes, filamentous fungi, and select protozoa (12). Fungal cellulases—particularly from *Trichoderma* and *Aspergillus* species—are notable for their high productivity and efficiency under acidic conditions. Their performance in solid-state fermentation and compatibility with industrial-scale operations have led to their widespread use in textile, pulp and paper, and biofuel industries (13).

In contrast, bacterial cellulases often exhibit exceptional thermostability and tolerance to alkaline pH, making them valuable in high-temperature industrial environments such as detergents, waste treatment, specific food processing applications and paper (14). Their rapid growth rates and adaptive metabolism further enhance their industrial appeal.

Cellulase is a cornerstone enzyme in both biotechnology and waste valorization, enabling the conversion of one of Earth’s most abundant organic polymers—cellulose—into accessible and valuable products (15).

Microbial Sources and Enzyme Systems

A wide range of microorganisms—including bacteria, fungi, and actinomycetes—are capable of synthesizing cellulases during their growth on cellulosic substrates (16). *Trichoderma reesei* is among the most extensively studied cellulolytic fungi, known for its ability to convert both native and modified cellulose into glucose. Other fungal species with significant cellulolytic activity include *Humicola*, *Penicillium*, *Aspergillus*, and additional strains of *Trichoderma* (17). Commercially relevant cellulolytic strains include recombinant *Aspergillus niger*, *Trichoderma reesei*, *Humicola insolens*, *Thermobifida fusca*, and selected *Bacillus* species (18). Bacterial genera exhibiting cellulase production include *Pseudomonas*, *Bacillus*, *Streptomyces*, *Actinomucor*, *Actinomycetes*, and *Cellulomonas*. Aerobic bacterial species such as *Cytophaga*, *Cellulomonas*, and *Cellvibrio* are capable of degrading cellulose in pure culture (19) (Table 1).

Classification of Cellulase Systems

Cellulase systems are broadly categorized into two types—non-complexed and complexed—depending on the aerobic or anaerobic nature of the producing organism (19).

Non-complexed Systems

In non-complexed cellulase systems, the enzymes are secreted individually and function independently, making them easily recoverable from the culture supernatant. These systems are predominantly found in aerobic cellulose-degrading microorganisms, including both bacteria and fungi.

For example, *Bacillus* species secrete extracellular cellulases that frequently possess carbohydrate-binding modules (CBMs), which enhance attachment to insoluble cellulose and improve catalytic efficiency. Similarly, aerobic bacteria such as *Cellulomonas fimi* and *Thermobifida fusca* produce modular cellulases composed of a catalytic domain (CD) and a CBM, facilitating adhesion and degradation of cellulose in the surrounding environment.

Fungal cellulases, whether from aerobic or anaerobic sources, generally consist of two distinct domains: a CBM and a catalytic domain connected via a serine- and threonine-rich polylinker region at the N-terminus. This domain architecture allows for strong binding to cellulose and enhances enzymatic performance in free-enzyme systems.

Complexed Systems

Anaerobic cellulose-degrading bacteria such as *Clostridium thermocellum*, *Clostridium cellulolyticum*, *Clostridium cellulovorans*, and *Clostridium josui* employ a highly organized complexed cellulase system known as the cellulosome (20). This multi-enzyme complex is scaffolded by cohesin-containing proteins and populated with dockerin-tagged enzymes. The dockerin–CBM interactions facilitate targeted binding of the entire complex to the cellulose substrate, enabling efficient hydrolysis of cellulosic biomass.

Biochemical Properties of Cellulases

Optimal pH and Temperature

Fungal cellulases—especially from *Trichoderma reesei* and *Aspergillus niger*—are most effective in acidic environments (pH 4.0–6.0) and moderate temperature ranges of 40 °C to 60 °C (21). In contrast, Bacterial cellulases, particularly those derived from thermophilic species such as *Bacillus* and *Clostridium*, exhibit optimal activity under neutral to alkaline conditions (pH 6.5–9.0) and elevated temperatures ranging from 50 °C to 80 °C (22).

Stability Under Industrial Conditions

Thermostability: Bacterial cellulases, especially from thermophiles, demonstrate remarkable stability at elevated temperatures (50–80 °C), making them highly suitable for heat-intensive industrial applications such as biofuel production and detergent formulation (23).

Alkaline Tolerance: These enzymes also retain activity in alkaline conditions (pH 7–10), which is advantageous for their use in the textile and laundering sectors.

Acidic pH Preference: Fungal cellulases are typically more stable and active under acidic pH conditions (pH 4–6), aligning well with requirements in food processing, pulp, and paper industries.

Enzyme Kinetics and Substrate Specificity

Enzyme Kinetics

Bacterial cellulases, particularly from thermophiles like *Clostridium thermocellum* and *Bacillus subtilis*, are characterized by high turnover rates (kcat) and notable thermostability. These features enable their effective use under harsh industrial conditions, such as elevated temperatures and alkaline pH, especially in biofuel synthesis (24).

Fungal cellulases, primarily from *Trichoderma reesei* and *Aspergillus niger*, typically exhibit lower kcat values but higher substrate affinity (reflected by lower Km values), particularly under acidic conditions. These properties make them well-suited for fine-tuned applications such as textile modification and clarification processes in the food industry.

Substrate Specificity

Bacterial cellulases display broad substrate specificity, capable of degrading crystalline cellulose, hemicellulose, and complex lignocellulosic biomass. Some strains also act efficiently on soluble cellulose derivatives such as carboxymethyl cellulose (CMC) and phosphoric acid-swollen cellulose (PASC) (25–26).

Fungal cellulases generally exhibit more selective substrate preferences, showing high catalytic efficiency toward amorphous cellulose and CMC. However, their activity on crystalline cellulose is often limited unless enhanced by pretreatment processes or synergistic accessory enzymes (27).

Industrial Applications of Cellulase

Bacterial Cellulases

Bacterial cellulases are indispensable biocatalysts in diverse industrial sectors, owing to their robustness, substrate versatility, and adaptability to extreme operational conditions. Their major applications include:

Biofuel Production

Bacterial cellulases facilitate the hydrolysis of lignocellulosic biomass into fermentable sugars—an essential step in the production of second-generation bioethanol. Thermostable enzymes from *Clostridium thermocellum* and *Bacillus* species are especially suited for high-temperature bioreactors (28).

Textile Industry

Certain *Bacillus* strains are employed in biopolishing and stone-washing processes to enhance fabric softness and surface finish, eliminating the need for harsh chemical treatments. Their alkaline tolerance makes them particularly effective in denim processing and cotton softening (29).

Detergent Formulations

Cellulases from *Bacillus* species are incorporated into laundry detergents to remove microfibrils from cotton fabrics, thus preventing fabric dullness and preserving textile brightness. Their resilience in alkaline and oxidative environments enhances detergent performance.

Pulp and Paper Industry

Bacterial cellulases contribute to the deinking of recycled paper, fiber refinement, and biobleaching processes. These applications reduce dependence on chlorine-based chemicals and promote cleaner, more sustainable paper production.

Animal Feed

In livestock and poultry nutrition, *Bacillus*-derived cellulases improve feed efficiency by degrading plant cell walls, thereby enhancing nutrient availability and absorption.

Food and Beverage Industry

Bacterial cellulases assist in juice clarification, coffee bean processing, and the extraction of bioactive compounds from plant materials, contributing to improved product clarity and yield.

Waste Management

In composting and bioremediation, cellulases from organisms like *Cellulomonas fimi* and *Paenibacillus polymyxa* accelerate the breakdown of agricultural and municipal waste, supporting the development of sustainable waste-to-energy systems.

Fungal Cellulases

Fungal cellulases are widely recognized for their high secretion levels, efficient activity under mild conditions, and specificity toward cellulose substrates. Their primary industrial applications include:

Biofuel Production

Species such as *Trichoderma reesei*, *Aspergillus niger*, *Penicillium funiculosum*, and *Penicillium oxalicum* are utilized to convert lignocellulosic biomass into fermentable sugars, facilitating large-scale bioethanol production through the efficient hydrolysis of amorphous and pretreated cellulose.

Food and Beverage Industry

Aspergillus niger-derived cellulases are extensively employed in juice clarification and other food processing operations to enhance extraction and clarity.

Detergents

Although less commonly used than bacterial counterparts, thermostable cellulases from thermophilic fungi like *Humicola insolens* are valuable in detergents and textile treatments, particularly under high-temperature conditions.

Synergistic Potential of Cellulase Systems

The synergistic interplay between different cellulases significantly enhances the efficiency of cellulose degradation, offering improved hydrolysis yields and reduced enzyme input compared to individual enzyme use. Key examples include:

Food and Beverage Industry

In juice manufacturing from apple, grape, and citrus fruits, cellulases are used in tandem with pectinases and hemicellulases to maximize extraction efficiency and clarity (30).

Pulp and Paper Industry

Combined application of cellulases and xylanases facilitates biobleaching and deinking, thereby reducing chemical load, energy consumption, and improving fiber quality while minimizing environmental impacts (31).

Biofuel Production

Enzyme cocktails rich in endoglucanases (EGs) and cellobiohydrolases (CBHs) from *T. reesei* are often complemented with *A. niger* β-glucosidase to ensure complete cellulose saccharification. This synergy boosts sugar yields and reduces overall enzyme dosage requirements.

Waste Management

Combinatorial use of cellulase with xylanase and laccase enhances degradation of paper- and cotton-based waste, aiding deinking and valorization processes (32).

Table 1. The comparative analysis of bacterial and fungal cellulases.

Feature	Bacterial Cellulase	Fungal Cellulase	Reference
Source Organisms	Bacillus, Clostridium, Cellulomonas, Paenibacillus	Trichoderma reesei, Aspergillus niger, Penicillium, Humicola	16-19
Optimal pH	Neutral to alkaline (pH 6.5–9.0)	Acidic (pH 4.0–6.0)	21-22
Optimal Temperature	Often thermophilic (50–80 °C)	Typically mesophilic (30–60 °C), some thermotolerant	21-22
Enzyme Stability	High thermostability and pH tolerance. Ex:Bacillus licheniformis PANG L optimally active at 60 °C and pH 5	Moderate stability; sensitive to extreme conditions Ex:Aspergillus niger IFO31125: optimum around 70 °C** and pH 6 (39).	23
Substrate Specificity	Broad — acts on crystalline cellulose, hemicellulose, CMC, PASC	Narrower — prefers amorphous cellulose and CMC	25-27
Secretion Efficiency	Lower extracellular secretion; often intracellular or membrane-bound	High extracellular secretion, especially in filamentous fungi	13

Enzyme Yield	Lower natural yield; often requires genetic enhancement	Naturally high yield; industrial strains optimized for secretion	36-37
Industrial Applications	Biofuels, detergents, animal feed, waste valorization	Textiles, food & beverage, pulp & paper, biofuels	28-29
Synergistic Potential	Often used in engineered consortia or with accessory enzymes	Naturally synergistic enzyme systems (e.g., EG + CBH + BG)	29
Cost of Production	Lower with agro-waste substrates, but may need optimization	Higher initial cost, but efficient in large-scale fermentation	30-32

Table 2. Comparison of Km and Vmax of bacterial and fungal cellulases.

Source	**K_m**	**V_{max}**	**Reference**
Trichoderma viride	68 µM	148 U/mL	40
Aspergillus niger	0.648 mM	12.953 mM/min	41
Aspergillus niger	0.975 mM	41.493 mM/min	41
Bacillus subtilis SU40	1.97 mg/mL	75.41 mg/mL/s	42
Bacillus vallismortis RG-07	1.923 mg/mL	769.230 µg/mL	42
Bacillus pumilus ND8	0.81 mM	14.2 µmol/min	43
Bacillus subtilis	0.996 mM	1.647 U/mL	44
Aspergillus niger	0.648 mM	12.953 mM/min	41
Aspergillus niger	0.975 mM	41.493 mM/min	41
Bacillus subtilis SU40	1.97 mg/mL	75.41 mg/mL/s	44

Recent Advances in Cellulase Engineering and Applications

Strategies for Cellulase Engineering

Contemporary protein engineering techniques—particularly rational design and directed evolution—have significantly advanced the functional optimization of individual cellulase components. Rational design, often aided by computational modeling, enables targeted modifications at the molecular level. Enhancements have been achieved through site-directed mutagenesis, promoter and transcription factor engineering, codon optimization, increased gene copy number, and the incorporation of molecular chaperones and leader peptides. Structural modifications such as improved glycosylation patterns and optimized enzyme folding have further led to the development of high-yield, robust cellulase-producing strains (33).

Utilization of Agro-Waste Substrates for Cost-Effective Production

The deployment of agricultural residues as fermentation substrates presents a sustainable and cost-efficient route for large-scale cellulase production. Agro-wastes like rice straw and distillery spent wash have proven particularly effective, yielding high levels of cellulase and xylanase when used in submerged fermentation with *Aspergillus heteromorphus* (34). This approach aligns with the principles of green chemistry and circular bioeconomy, reducing raw material costs while valorising agri-industrial waste. In contrast, bacterial systems are often more suitable for specialized industrial conditions than for bulk enzyme production, since their scale-up can require tighter process control and may not match the low-cost substrate advantage typically seen in fungal systems.

Enzyme Immobilization for Reuse and Process Efficiency

Immobilization of cellulases has emerged as a pivotal strategy to improve their operational stability, reusability, and overall cost-efficiency in industrial applications. Techniques such as covalent attachment onto magnetic nanoparticles have demonstrated enhanced enzyme activity and recyclability, particularly in biofuel production workflows (35). These innovations support continuous bioprocessing and reduce the need for enzyme replenishment.

CRISPR-based strain improvement

CRISPR-based strain improvement is transforming cellulase engineering by allowing precise, multiplex editing of fungal genomes to increase enzyme yield and improve regulatory control. In Trichoderma reesei, CRISPR systems such as tRNA-gRNA arrays and targeted gene disruption have been used to accelerate strain construction and relieve repression of cellulase expression, especially through regulators like *cre1* and *xyr1*. This approach offers a faster and more rational route to high-performance cellulase-producing strains than traditional mutagenesis (38).

Recent progress in AI and ML driven Cellulase engineering

Recent advances in AI and machine learning are accelerating cellulase stability engineering by enabling mutation screening, structure-function prediction, and thermostability-focused redesign; for example, computational analysis of Penicillium verruculosum Cel5A identified the C-terminus as a stabilizing target, while newer ML-based redesign workflows such as Pythia/ESM-2 and iCASE demonstrate improved thermostability and industrial robustness in glycoside hydrolases (45-47).

Challenges and Future Prospects

Microbial sources—particularly bacteria and fungi—continue to serve as the principal producers of cellulases due to their high enzymatic yields and amenability to genetic manipulation. Advancements in protein engineering, the development of synergistic enzyme cocktails, and the discovery of novel cellulolytic enzymes remain central to improving the efficiency and scalability of cellulase-driven processes.

The convergence of cellulase technology with emerging interdisciplinary fields—such as nanotechnology, bioinformatics, and synthetic biology—offers considerable promise. Nanotechnology has the potential to enhance enzyme stability, activity, and delivery. Bioinformatics and computational biology provide powerful platforms for in silico enzyme modeling, rational design, and kinetic optimization. Meanwhile, synthetic biology enables the construction of tailor-made biosystems and high-performance microbial cell factories for more efficient cellulase production.

Sustainable and environmentally conscious production strategies are increasingly vital to reducing the ecological footprint of cellulase technology. Leveraging renewable substrates, applying green chemistry principles, and optimizing process lifecycles are pivotal in driving eco-friendly innovation. Moreover, continued progress in bioreactor design and fermentation engineering—especially when integrated with other biotechnological workflows—can significantly enhance both the economic viability and environmental sustainability of cellulase-based applications.

Despite the strides made, several bottlenecks remain unresolved. Challenges such as enzyme instability under harsh industrial conditions, high production costs, and narrow substrate specificity still hinder broader implementation. Addressing these limitations will require sustained research, targeted innovation, and cross-sector collaboration.

The future of cellulase technology hinges on the development of robust, cost-effective enzyme systems. Their successful deployment will be instrumental in advancing key industrial sectors, including biofuels, textiles, pulp and paper, food and beverage processing, and sustainable waste management.

CONCLUSION

The bacterial and fungal cellulases exhibit distinct biochemical and operational advantages that make them well-suited for specific industrial applications. Bacterial cellulases are generally more thermostable, tolerant to alkaline conditions, and possess broad substrate specificity. These traits render them highly effective in rigorous industrial environments, including biofuel production, waste valorisation, and detergent manufacturing. Fungal cellulases, by contrast, are characterized by efficient extracellular secretion, high enzyme yields, and optimal activity under acidic conditions. As a result, they are widely employed in textile processing, food and beverage manufacturing, and the pulp and paper industry, where gentler reaction conditions are preferred. Collectively, these innovations are propelling cellulolytic biotechnology toward greater sustainability, versatility, and economic feasibility—paving the way for its broader adoption in next-generation industrial bioprocessing.

REFERENCES

1. Srivastava N, Rawat R, Singh Oberoi H, Ramteke PW. A review on fuel ethanol production from lignocellulosic biomass. International Journal of Green Energy. 2015. 12:949-60.
2. Zhang YH, Lynd LR. Toward an aggregated understanding of enzymatic hydrolysis of cellulose: noncomplexed cellulase systems. Biotechnology and bioengineering. 2004 88:797-824.
3. Wang N, Ren K, Jia R, Chen W, Sun R. Expression of a fungal manganese peroxidase in Escherichia coli: a comparison between the soluble and refolded enzymes. BMC biotechnology. 2016. 16:1-5.
4. Sher H, Zeb N, Zeb S, Ali A, Aleem B, Iftikhar F, Rahman SU, Rashid MH. Microbial cellulases: a review on strain development, purification, characterization and their industrial applications. Journal of Bacteriology and Mycology. 2021.8:1180-1095.
5. Taherzadeh MJ, Karimi K. Enzymatic-based hydrolysis processes for ethanol from lignocellulosic materials: A review. BioResources. 2007. 2: 707-38.
6. Lee SM, Koo YM. Pilot-scale production of cellulase using *Trichoderma Reesei* rut C-30 fed-batch mode. Journal of Microbiology and Biotechnology. 2001. 11:229-233.
7. Shewale JG. β-Glucosidase: its role in cellulase synthesis and hydrolysis of cellulose. International Journal of Biochemistry. 1982. 14 435-443.
8. Woodward J, Wiseman A. Fungal and other β-d-glucosidases—their properties and applications. Enzyme and Microbial Technology. 1982. 4:73-79.
9. Ryu DD, Mandels M. Cellulases: biosynthesis and applications. Enzyme and Microbial Technology. 1980. 2 :91-102.
10. Samdhu DK, Bawa S. Improvement of cellulase activity in *Trichoderma.* Applied Biochemistry and Biotechnology. 1992. 34:175-183.
11. Wood TM, McCrae SI, Bhat KM. The mechanism of fungal cellulase action. Synergism between enzyme components of *Penicillium pinophilum* cellulase in solubilizing hydrogen bond-ordered cellulose. Biochemical Journal. 1989. 260:37-43.
12. Shah, Kamlesh & Sutaria, Devanshi, Microbiology and Biotechnology in Human Life, Chapter -3 Microbial Cellulase: Production, Purification and Application, JPS Scientific Publications, 2020, 50-75
13. Imran M, Anwar Z, Irshad M, Asad MJ, Ashfaq H. Cellulase production from species of fungi and bacteria from agricultural wastes and its utilization in industry: a review. Advances in Enzyme Research. 2016. 4 :44-55.
14. Sharada R, Venkateswarlu G, Venkateswar S, Rao MA. Applications of Cellulases-Review. International Journal of Pharmaceutical, Chemical & Biological Sciences. 2014. 4: 424-437.
15. Singh S, Chakravarty I, Khade SM, Srivastava J, Sinha R. Cellulase: a catalytic powerhouse for lignocellulosic waste valorisation. In Thermochemical and Catalytic Conversion Technologies for Future Biorefineries: 2022. 1:157-187. Springer Nature.
16. Kuhad RC, Gupta R, Singh A. Microbial cellulases and their industrial applications. Enzyme research. 2011:280696.
17. Hayashida S, Ohta K, Mo K. Cellulases of *Humicola insolens* and *Humicola grisea*. In Methods in Enzymology 1988. 160, pp. 323-332. Academic Press.
18. Ellouz Chaabouni S, Belguith H, Hassairi I, M'rad K, Ellouz R. Optimization of cellulase production by *Penicillium occitanis*. Applied microbiology and biotechnology. 1995. 43:267-9.
19. Lynd LR, Weimer PJ, Van Zyl WH, Pretorius IS. Microbial cellulose utilization: fundamentals and biotechnology. Microbiology and molecular biology reviews. 2002. 66:506-77.
20. Schwarz W. The cellulosome and cellulose degradation by anaerobic bacteria. Applied microbiology and biotechnology. 2001.56:634-49.
21. Kant S, Das S, Roy S, Tripathy S. Fungal cellulases: a comprehensive review. The Nucleus. 2024. 24:1-7.
22. Bala A, Singh B. Cellulolytic and xylanolytic enzymes of thermophiles for the production of renewable biofuels. Renewable Energy. 2019 136:1231-1244.

23. Kazeem MO. Enhanced cellulase production by a novel thermophilic *Bacillus licheniformis* 2D55: characterization and application in lignocellulosic saccharification. Bioresources 2016. 11:5404-5423.
24. Ajeje SB, Hu Y, Song G, Peter SB, Afful RG, Sun F, Asadollahi MA, Amiri H, Abdulkhani A, Sun H. Thermostable cellulases/xylanases from thermophilic and hyperthermophilic microorganisms: current perspective. Frontiers in Bioengineering and Biotechnology. 2021. 9: 794304.
25. Islam F, Roy N. Screening, purification and characterization of cellulase from cellulase producing bacteria in molasses. BMC research notes. 2018. 11:1-6.
26. Duan CJ, Huang MY, Pang H, Zhao J, Wu CX, Feng JX. Characterization of a novel theme C glycoside hydrolase family 9 cellulase and its CBM-chimeric enzymes. Applied microbiology and biotechnology. 2017. 101:5723-5737.
27. Ghosh S, Godoy L, Anchang KY, Achilonu CC, Gryzenhout M. Fungal cellulases: Current research and future challenges. Industrially Important Fungi for Sustainable Development: Volume 2: Bioprospecting for Biomolecules. 2021:263-98.
28. Bhardwaj N, Kumar B, Agrawal K, Verma P. Current perspective on production and applications of microbial cellulases: a review. Bioresources and Bioprocessing. 2021. 8:1-34.
29. Ejaz U, Sohail M, Ghanemi A. Cellulases: from bioactivity to a variety of industrial applications. Biomimetics. 2021. 6:44.
30. de Souza TS, Kawaguti HY. Cellulases, hemicellulases, and pectinases: Applications in the food and beverage industry. Food and Bioprocess Technology. 2021. 14 :1446-1477.
31. Budhraja AA, Roy R. Advancements in cellulase enzyme technology: applications, challenges, and future perspectives. International Research Journal of Modernization in Engineering Technology and Science. 2024. 6:3988-4002.
32. Rawat S, Singh A, Rajput VD, Ghazaryan K, Minkina T, Mohammad Said Al-Tawaha AR, Al-Tawaha AR, Adel Qotb M, Karnwal A. Microbial Enzymes for Eco-Friendly Recycling of Wastepaper by Deinking. In Microbial Applications for Environmental Sustainability 2024 pp. 165-176. Springer Nature.
33. Dadwal A, Sharma S, Satyanarayana T. Progress in ameliorating beneficial characteristics of microbial cellulases by genetic engineering approaches for cellulose saccharification. Frontiers in Microbiology. 2020. 11:1387.
34. Bajar S, Singh A, Bishnoi NR. Exploration of low-cost agro-industrial waste substrate for cellulase and xylanase production using *Aspergillus heteromorphus*. Applied Water Science. 2020.10:1-9.
35. Narisetty V, Tarafdar A, Bachan N, Madhavan A, Tiwari A, Chaturvedi P, Varjani S, Sirohi R, Kumar V, Awasthi MK, Binod P. An overview of cellulase immobilization strategies for biofuel production. BioEnergy Research. 2023. 16: 4-15.
36. Singhania RR, Patel AK, Sukumaran RK, Larroche C, Pandey A. Retracted: Role and significance of beta-glucosidases in the hydrolysis of cellulose for bioethanol production. Bioresource technology. 2013. 127:500-507.
37. Fonseca, L.M., Parreiras, L.S. & Murakami, M.T. Rational engineering of the *Trichoderma reesei* RUT-C30 strain into an industrially relevant platform for cellulase production. *Biotechnol Biofuels* 2020.13, 93.
38. Zhang J, Li K, Sun Y, Yao C, Liu W, Liu H, Zhong Y. An efficient CRISPR/Cas9 genome editing system based on a multiple sgRNA processing platform in Trichoderma reesei for strain improvement and enzyme production. Biotechnology for Biofuels and Bioproducts. 2024 Feb 11;17(1):22.
39. Sajith S, Priji P, Sreedevi S, Benjamin S. An overview on fungal cellulases with an industrial perspective.
40. Iqbal HM, Ahmed I, Zia MA, Irfan M. Purification and characterization of the kinetic parameters of cellulase produced from wheat straw by Trichoderma viride under SSF and its detergent compatibility. Advances in Bioscience and Biotechnology. 2011 Jun 1;2(3):149.
41. Fatima N, Ahmad IR, Shakir HA, Khan M, Franco MA, Irfan M. Production and characterization of cellulases from Aspergillus niger under static fermentation. Cellul. Chem. Technol. 2024 Jul 1;58:705-12.
42. Ugras S, Bicen HE, Emire Z. Determination of cellulase enzyme produced by Bacillus cereus DU-1 isolated from soil, and its effects on cotton fiber. Brazilian Archives of Biology and Technology. 2024 May 31;67:e24230391.

43. Dikbaş N, Al Dahluz WS, Alım Ş, Uçar S. Partial Purification and Biochemical Characterization of Cellulase from Bacillus pumilus ND8 Isolated from Garden Waste. Türk Doğa ve Fen Dergisi. 2024 Sep 9;13(3):62-6.
44. Malik WA, Javed S. Biochemical characterization of cellulase from Bacillus subtilis strain and its effect on digestibility and structural modifications of lignocellulose rich biomass. Frontiers in bioengineering and biotechnology. 2021 Dec 20; 9:800265.
45. Contreras Leiva F. *Cellulase protein engineering towards improved thermostability* (Doctoral dissertation, Dissertation, RWTH Aachen University, 2021).
46. Zheng N, Cai Y, Zhang Z, Zhou H, Deng Y, Du S, Tu M, Fang W, Xia X. Tailoring industrial enzymes for thermostability and activity evolution by the machine learning-based iCASE strategy. Nature Communications. 2025 Jan 11;16(1):604.
47. Zhang H, Zhu T, Zhai Q, Chen Q, Zhang X, Chen Y, He W, Li J, Fan J, Tao J, Hu X. Two-step computational redesign of Bacillus subtilis cellulase and β-glucanase for enhanced thermostability and activity. International Journal of Biological Macromolecules. 2025 Jan 1;285:138274.