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THE ROLE OF THE ENZYME CELLULASE AS AN ECOLOGICAL AGENT IN THE DEGRADATION OF CELLULOSE IN NATURE AND INDUSTRY

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Cellulase comprises a sophisticated synergistic complex of enzymes, primarily comprising three types: endo-glucanases, exo-glucanases and β-glucosidase. The interaction of these biocatalysts ensures the effective breakdown of the resilient structure of the natural polysaccharide cellulose into simple mono- and disaccharides, such as glucose and cellobiose. In nature this enzyme is synthesized by a diverse array of organisms - either independently or through symbiotic relationships – with species from the kingdom Fungi and Bacteria acting as primary degraders of plant biomass. This process of degradation of cellulose is fundamental to the global Carbon cycle, thereby sustaining life on our planet.

In industrial contexts, this enzyme is produced through solid-state or submerged fermentation. The efficiency of enzyme yield controlled by combination of factors: chemical (media composition, including Carbon and Nitrogen sources), physical (temperature, aeration and agitation), biological factors (microbial strain selection, mutagenesis and synergistic interaction). Utilizing agricultural waste as a substrate is a key strategy to enhance the economic viability of production.

Due to its versatility, cellulase finds widespread application across multiple economic sectors. This enzyme is critical in the food and beverage industry (winemaking, baking, juice clarification), pulp and paper manufacturing, textile production, detergent formulation, pharmaceutical industry. Furthermore, the enzyme plays important role in production of alternative biofuels, and in enzyme-assisted extraction of bioactive compounds from plant material.

The aim of this study is to search and systematize the information on the role of the enzyme cellulase in enzymatic hydrolysis, emphasizing it as a sustainable approach as a process refined by evolution in nature and successfully adapted for industrial «green» technologies.

Keywords: enzyme cellulase, cellulose degradation, ecological agent, industry, green technologies.

Introduction. Cellulose is a linear polysaccharide, consisting of thousands of β-D-glucopyranose residues linked by β-(1,4)- glycosidic and hydrogen bonds. These cellulose chains form reducing and non-reducing ends (Chatterjee et al., 2016). Yearly, plants generate nearly 10^{11} - 10^{12} tons of cellulose through photosynthesis as primary producers (Han et al., 2022; Foroughi et al., 2021).

This makes cellulose a sustainable, biodegradable and cost-effective source of carbohydrates with broad potential for application in industry. However, its main challenge lies in is insolubility in water and other solvents due to hydrogen bonds (Etale et al., 2023; Aldred, 2009). Several methods are used to break down cellulose, including physical, chemical and biological. The biological method employs the enzyme cellulase, which mimics natural hydrolysis of this polysaccharide. This enzymatic process is sustainable and aligns with some of UN sustainable development goals, such as Goal 7 (Affordable and clean energy) and Goal 12 (Responsible consumption and production), etc (The 17 Goals, 2026; Aziz et al., 2022).

1. Characteristics of enzyme cellulase

1.1. Classes of cellulase. Cellulase is a complex of induced enzymes that synergistically degrade the complex structure of cellulose. Cellulolytic enzymes consist of 3 main types: endo-glucanases or 1,4-β-D-glucan-4-glucanohydrolases; exo-glucanases (1,4-β-D-glucan glucanohydrolases (cellodextrinases) and 1,4-β-D-glucan cellobiohydrolases); β-glucosidases (glucohydrolases), which mode of action illustrated in fig. 1 (Biswas et al., 2020; PubChem).

1) Endo-1,4-D-glucanase (factor Cx, EC 3.2.1.4) acts on the nonamorphous section of phosphate-expanded cellulose, carboxymethyl cellulose, and amorphous cellulose with production of glucose, cellotriose, cellobiose, various dextrins, which have more reachable ends for other enzyme – cellobiohydrolase. Endo-glucanase has low substrate specificity and can hydrolyze cellulose with substituents.

2) Exo-β-1,4-glucanase one type is β-1,4-glucan cellobiohydrolase (EC 3.2.1.91, cellobiohydrolase, CDH, C_1 factor). This enzyme breaks down β-1,4-glucoside bonds from the non-reducing sugar end of cellulose with the facilitation of cellobiose. Studies

indicate that certain strains produce an alternative form of exoglucanase-1,4-glucan glucohydrolase (EXG, EC 3.2.1.74), which hydrolyzes to produce glucose (Chen, 2014; Bhardwaj et al., 2021; Jain and Agrawal, 2020).

3) β-glucosidase (cellobiase, EC 3.2.1.21) primarily hydrolyzed from non-reducing ends of dextrins, releasing cellobiose and glucose. The hydrolysis rate of β-glucosidase increases as size of the substrate decreases. In enzyme preparation, the protein content of β-glucosidase accounts for the least compared to other cellulase components, making up only about 1%. Advanced genetic engineering studies shows, that glucosidase keeping the β-structure of glucose and prevent inhibition of cellulolytic hydrolysis (Chen, 2014; Bhardwaj et al., 2021; Jain and Agrawal, 2020).

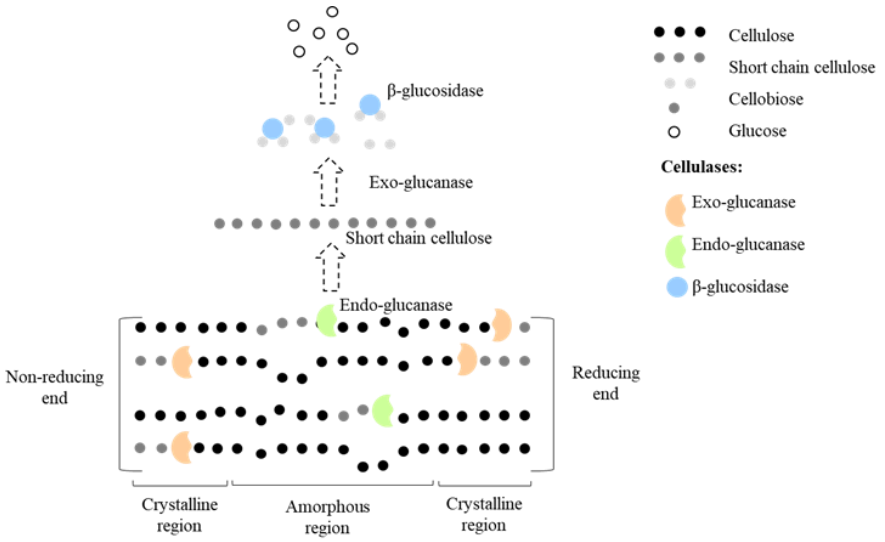

Fig. 1. Enzymatic hydrolysis of cellulose by cellulases (Adapted from Thorsen et al., 2021)

Additional compounds that also take part in cellulose degradation:

1) cellobiose dehydrogenase or cellobiose oxidase (EC 1.1.99.18; CBO) - heme flavoprotein with FAD as a prosthetic group of the enzyme. CBO is mostly produced by white-rot filamentous fungi and oxidizes to lactone cellobiose and celloligosaccharide substrates (Kracher and Lugdwig, 2016).

2) cellobiose quinone oxidoreductase (CBQ) - flavoprotein, which only includes FAD and has the same function as CDH, but CBQ doesn't reduce cytochrome C.

3) phosphorylase phosphate adds phosphate group to cellobiose and cellulose to increase the metabolism.

4) cellulosome (bacterial complex of cellulases) - a complex of cellulases that is used by bacteria (Chen, 2014; Bhardwaj et al, 2021).

CAZy classification categorized cellulases into different GH (glycoside hydrolase) families: endo- with exo-glucanases - GH5, GH6, GH7, GH9, GH48; only endo-glucanases - GH8, GH10, GH12, GH26, GH44, GH45, GH51, GH74, GH124 (Nguyen et al., 2018).

1.2. Molecular structure of cellulase. Cellulases are produced by fungi and aerobic bacteria as a free-form enzyme, which can be easily operated. In contrast, bacteria, rarely fungi, form the cellulosome that are cell-associated (Biswas et al., 2020; Sutaoney et al, 2024).

The structurally free cellulase molecule of model cellulolytic filamentous fungi *Trichoderma reesei* contains: a catalytic domain (CD) that can hydrolyze primarily soluble cellulose with a molecular weight of 56 kDa. The CD has low adsorption ability; the cellulose-binding or non-catalytic center (CBD) has a weight of 10 kDa and binds to the cellulose surface; the hinge region or peptide linker connects two domains of cellulase, which are rich in Pro, Thr, Ser amino acids.

Cellulase modification by the removal of the CBD only slightly changes the cellulolytic activity of the enzyme, but the adsorption and hydrolysis of crystalline cellulose become limited. Additionally, changes in the amino acid composition of the CBD, specifically aromatic amino acids, reduce binding activity (Ejaz et al, 2021; Goodsell, 2023).

The protein domain structure of the cellulase enzyme of *T. reesei* (main industrial strain used for cellulase synthesis) has different conformation: β-sheet, α/β-barrel, β-distorted sandwich. Information on key cellulases protein structures by CATH classification is described in table 1 and illustrated in fig. 2 (Cellulase - Worthington).

Table 1.

Structural conformation of the cellulase enzymes of Trichoderma reseei

Cellulases	Class	Protein structure
Endo-glucanase I	Mostly beta	Distorted sandwich
Endo-glucanase I I	Alfa Beta	α/β-barrel
β-1,4-glucanase	Mostly beta	Sandwich
Cellobiohydrolase I	Mostly beta	Distorted sandwich
β-glucosidase I and I I	Alfa Beta	α/β-barrel

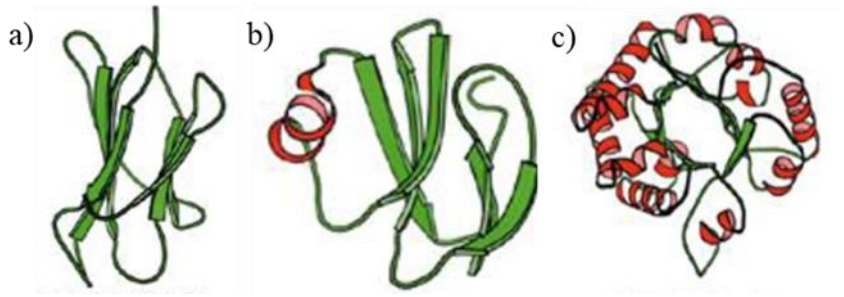

Fig. 2. Protein structures of the enzyme cellulase by CATH classification: a) sandwich; b) distorted sandwich; c) α/β-barrel (Goodsel, D., 2023)

Cellulosomes comprises two main elements: cohesin-bearing scaffoldins and non-catalytic proteins with different dockerin-bearing enzymes. The structure of cellulosomes can be diverse among the species of microorganisms and often depends on the substrate nature (Alves et al., 2020).

There are three types of cohesion-dockerin interaction: type I – connects to the scaffolding; type I I bound scaffolding to the cell surface; type I I I exhibits significant sequence divergence from the other categories. This classification is founded on bacterial coherins and dockerins; the structure of fungal cellulosomes has to be studied (Hsin et al., 2025).

1.3. Cellulase mechanism of hydrolysis. The theory of the C_1-C_x step-by-step hydrolysis of cellulose was presented by Reese et al in 1950 (fig. 3), where C_1 – exo-glucanase and C_x – endo-glucanase.

$$\text{Crystal cellulose} \xrightarrow{C_1} \text{Amorphous cellulose} \xrightarrow{C_x} \text{Cellulose} \xrightarrow{\beta\text{-glucosidase}} \text{Glucose}$$

Fig. 3. Pattern of cellulose hydrolysis by cellulase be C1-Cx- hypothesis (Chen, H., 2014)

The C_1-C_x hypothesis states, that C_1 modifies the crystalline cellulose to an amorphous structure, which C_x randomly catalyzes. Subsequently, β-glucosidase hydrolyzes cellobiose into glucose.

The synergistic model is a modern hypothesis that replaced historically important C_1-C_x hypothesis. This modern model of cellulose catalysis include the following mechanism: endo-glucanase (C_x) cleaves the chains of the cellulose molecule in the amorphous region for further exo-glucanase or cellobiohydrolase (C_1) hydrolysis of the appearing end group of crystalline cellulose. After this, the complex of enzyme CBH and EG facilitates the synthesis of cellobiose, which is subsequently converted into glucose by β-hydrolase.

Other synergic theory of endo- and exo-glucanase, applicable only to natural cellulose: exo-glucanase I breaks down the reducing end and exo-glucanase I I – non-reducing end of cellulose chain.

In the study, Gao et al. highlight a popular theory, where non-hydrolytic enzymes catalyze the structure of cellulose and then three united cellulase enzymes degrade cellulose to fiber dextrins and glucose (Chen, 2014).

The hydrolysis of the β-1,4- glycosidic bond can be achieved through two separate mechanisms with stereochemical modification: inverting and retaining (fig. 4). The inverting mechanism occurs without the formation of enzyme-substrate complex and hydrolysis is carried out by deprotonation. On other hand, the retaining involves the formation of an enzyme-substrate complex after attack on the Carbon, which act like a nucleophilic base, with breakage of glycosidic bonds of the oligomeric fraction (Barati et al., 2015; Bhati et al., 2020; Shrivastava, 2020).

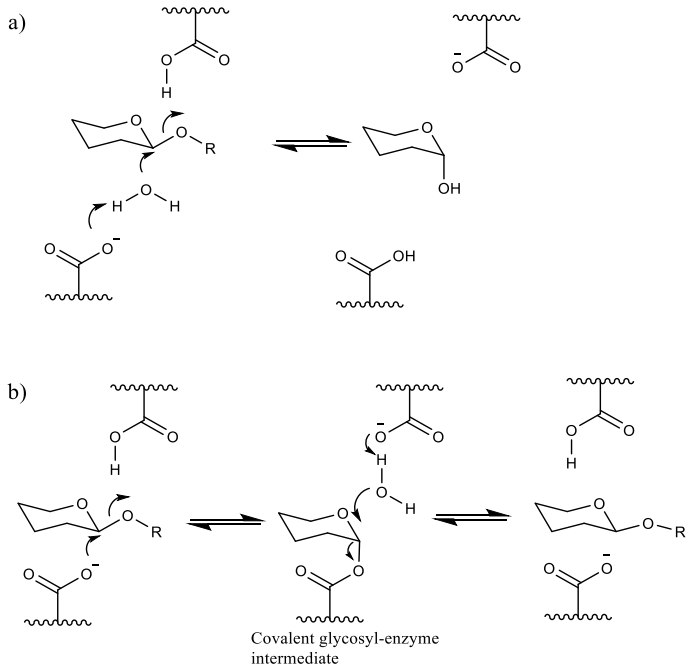

Fig. 4. Mechanisms of cellulose hydrolysis by cellulase: a) inverting; b) retaining (Barati et al., 2015)

1.4. Variety of cellulolytic organisms

1) Kingdom *Bacteria*

Bacteria that can degrade the cellulose structure belong to the four phyla *Actinobacteria, Firmicutes, Proteobacteria, Bacteriodetes*. Isolated bacterial enzyme cellulase has high specificity, but the activity of the enzyme can be increased by genetic modification of strains (Obeng et al., 2017).

Bacteria of the phyla *Firmicutes, Bacteriodetes* are widely distributed in various environments, mostly in the gut. Main classes of cellulolytic bacteria of this phyla are *Bacilli*, *Clostridia*. They produce different forms of enzyme: anaerobic *Clostridia*, such as *Clostridium thermocellum*, produce cellulosomes, but as an exception, anaerobic *Clostridium sterocorarium* synthesizes free cellulases like aerobic microorganisms. Some bacteria can secrete multi-modular cellulases, like *Caldicellulosiruptor sp*.

Bacteria of the phylum *Bacteriodetes* have adapted to various ecosystems, such as the digestive tract of animals, soil, ocean and freshwater environments. Some bacteria of this genus develop the capability of utilizing complex polysaccharide utilization loci (PUL) – a complex that bind and cleaves target polysaccharides at the cell surface and then imports the oligosaccharides into the periplasm, where degradation is completed.

However, bacteria of the genus *Fibrobacter* do not produce cellulosomes or free cellulases, but are attached to cellulose through a complex of tetratricopeptide repeat (TRP) domain protein, which is the basis for the assembly of various enzymes and fibro-slime proteins into a complex, where the fibro-slime proteins bind to the substrate and the outer membrane protein A (OmpA) serves to enhance the attachment of the complex to the peptidoglycan in the cell wall. The partially hydrolyzed cellulose chains are then transported across the outer membrane to the periplasm, where sequential cellulose degradation occurs (Obeng, et al., 2017; Seveso, et al., 2024).

2) Kingdom *Archaea*

Archaea as a distinct kingdom of microorganisms, which are distributed in the extreme ranges of temperature, pH, high salt concentration (Cabrera and Blamey, 2018). *Archaea* enzymes have few advantages: enzymatic catalysis at higher temperature has enhanced diffusion kinetics in the cultivation media and notably lower risk of contamination. In the last 30 years, a significant number of glucoside hydrolases were isolated from hyperthermophilies. Among the first GH described *Archaea* enzymes have been cellulase derived from *Pyrococcus furiosus*, which can demonstrate peak activity at 99 ℃ (Suleiman et al., 2020).

3) Kingdom *Plantae*

Fruit ripening is a complicated process involving a significant transformation, which including the hydrolysis and modification of cell walls by enzymes, such as β-1,4-glucanase, β-galactoxidase, xyloglucan endotransglycosylate, pectate lyase, etc. ripening (Zhang et al., 2020). Enzymes cellulase and pectinase are also included in leaves abscission in a response to stress, which also involves accumulation hydrogen peroxide,

decreasing of catalase, peroxidase (Li et al., 2023). Cellulolytic activity takes place in the growth of plants and reconstruction of cell walls: celulase can release cellulose, which is synthesized by cellulose synthase (Wilson, 2009).

4) Kingdom *Animalia*

Some insects (class *Insecta*), mollusks (snail, slugs, shipworm; phylum *Molusca*) produce their cellulases. Sometimes animals acquire cellulolytic enzymes in a symbiotic relation with microorganisms, for example, suborder *Ruminantia* and the clades described above (Zhang et al., 2020; New and Future Developments in Microbial Biotechnology and Bioengineering, 2019).

5) Kingdom *Fungi*

Fungi are recognized as highly effective lignocellulose degraders and the most extensively studied group of microorganisms, which are responsible for plant biomass hydrolysis. However, the significant variability of cellulose degradation is observed in the fungal phyla. Studies of the genomic data of 308 fungal genomes performed by Beimforde et al., 2014 showed that more than 98 % of cellulolytic fungi are referred to the subkingdom *Dikarya*, that consists of two phyla – *Ascomycota* and *Basidiomycota* (Juturu and Wu, 2014; Beimforde et al., 2014; Liu et al., 2021).

Phyla *Ascomycota* has a diverse morphology and is distributed in different ecological niches. This division mostly consists of soft rot fungi, like *Aspergillus niger*, *Trichoderma reesei*, *Penicilium chrysogenum*. Generally, soft rot fungi damage plant cell walls by forming erosion, caused by enzymes such as cellulases, hemicellulases, pectinases, laccases, but don't produce the peroxidase for lignin degradation (Shrikavand et al., 2015).

Over 90 % of the *Basidiomycota* phyla fungi are part of the white rot fungi. This group possesses the capability to degrade all structural polymers in the cell walls, but some species can hydrolyze lignin over cellulose, that leaves remaining bleached polysaccharides (cellulose and hemicellulose) (Tuomela and Hattkka, 2011; Makela et al., 2020).

On the other hand, brown rot fungi, which comprise only 7 % of *Basidiomycetes* class, decompose only cellulose and hemicellulose, resulting in residual brown lignin byproduct. This group utilizes the Fenton reaction with chelators, generating hydroxyl radicals, which through, an oxidation reaction, facilitate the breakdown of biomass (Daniel, 2016; Schilling et al., 2012).

The traditional classification of cellulolytic fungi described above includes soft, white, and brown rot fungi is based on microscopic characteristics and relative. Notably, genomic analysis revealed that species such as *Aspergillus niger*, *Trichoderma reesei* and *Postia placenta* have sequences associated with various mechanisms of lignocellulose decomposition. Further studies of fungi demonstrate the alternative mechanisms (Liu et al., 2021).

2. The role of the enzyme cellulase in the global carbon cycle. Soil is one of the biggest pools of organic Carbon on our planet, particularly in forest ecosystems, where the dead plant material is retained and accumulated. Researchers have pointed out that leaf litter consists of over 50 % of Carbon (Datta et al., 2024; Chen et al., 2023), with cellulose, a common polysaccharide, making up 20-30 % of this composition (Bautista-Cruz et al., 2024; Olatunji et al., 2021). This cellulose is gradually degraded by a complex of the cellulase enzymes, which are synthesized by soil bacteria and fungi (Sobucki et al., 2021).

Chinese scientists discovered and confirmed that field decayed plants step-by-step break down through action of litter cumulative microorganisms. After 1 year of decomposition, 50 % of cellulose was decomposed under condition similar to natural. After 2 years, this percentage increased to 80 % (Chen et al., 2019). A study supervised by Gao J. was conducted under controlled condition, shows the progressive decomposition of cellulose from *Eriobotrya japonica* litter by various, such as cellulase, laccase, lignin peroxidase, etc. The mass of cellulose reduced to nearly 60 % at 189 days after enzymatic hydrolysis. The dominant producers of lignocellulolytic enzymes were from phyla *Proteobacteria*, *Bacteroidota* and *Myxococcota* (Nie et al., 2023). Also, the release during hydrolysis of heat and carbon dioxide could have an important part in speeding up the decomposition process. Cooperation between investigators from Hemholtz-Centre for Environmental Research and Martin Luther University Halle-Wittenberg recorded a peak of heat at 6.2 days – nearly 30 μW/g and CO_2 at 4.7 days - nearly 2.7 μg/(g*hour) - in the experiment of commercial cellulose decomposition in soil by microbiota (Dehghani et al., 2025).

After monosaccharide glucose is released by β-glucosidase, it is utilized by the soil microbiota as an energy source for growth, including cellulolytic microorganisms (Sobucki et al., 2021; Lenhardt et al., 2023; Chen et al, 2023; De Oliveira Costa and Nahas, 2012). For instance, the denitrification activity was raised to more than 90 % by glucose addition (Huang et al., 2024). These microorganisms further transform Nitrogen, Phosphorus, Sulfur and other inorganic compound substrates into a form that is suitable for plants by enzymatic transformation (Jamir et al.,2019). Thus, cellulase takes place in a driving reaction within biogeochemical cycles of

Carbon and other cycles. Modern «green» chemistry applies natural-like processes, like enzymatic hydrolysis for cellulose and lignocellulose modification and points of industrial production and implementation are described subsequently.

3. Some aspects of industrial synthesis of cellulase. The enzyme cellulase demand can be confirmed by CAGR growth to 2032 by 6.9 % to approximately an estimation of market - $3153.1 million (in 2032) from $1621 million in 2022. This growth is connected to the biofuel industry development, where cellulase is the second most used enzyme after amylase. The top companies that produce cellulase: Novozymes (Denmark), Genencor (USA), DSM (Netherlands), AB Enzymes (Germany), Amano Enzyme (Japan). The only manufacturer of cellulase in the Ukrainian industry is «ENZIM» (Ilic et al., 2023; Biotech, E).

Industrially, cellulase can be produced by surface or submerged fermentation with downstream processing to obtain liquid concentrate or dried powder.

1) Solid-state fermentation (SSF) is accomplished on moist substrate, which is better for fungi cultivation. The advantages of this method are that isolated enzymes have higher activity, and this process is more economically viable, since it is not energy-consuming and inexpensive media are used in the process. However, SSF has an inefficient distribution of nutrients, oxygen, water. But the application of a drum bioreactor can solve this problem. The heat generated during fermentation is the main problem of the solid-state fermentation process, so only small reactors are used. Also, all processes must be done in highly labor-intensive.

2) Submerged fermentation (SmF) is carried out in aqueous media in which nutrients are dissolved. Fermentation in this mode can be automatically controlled, which allows scaling process. SmR has higher conversion, since the medium is agitated and is more aseptic, since bioreactor is sealed. Regardless, SmR has major energy consumption. For each strain, the process of fermentation needs to be optimized. Also, mixing and aeration can lead to foam formation, but it can be eliminated by antifoam. Submerged fermentation is often used for hyperproducers, like *Aspergillus niger* and *Trichoderma reesei* (New and Future Developments in Microbial Biotechnology and Bioengineering, 2019; Biotech, E (Cellulase); Hennessey-Ramos et al, 2021; Patel and Amaresan, 2022; Dodge, 2010).

The crude extract obtained after fermentation contains microorganism-producers, cellulase and residual nutrients. In this solution, the metabolite has a low concentration and is prone to degradation; thus, it needs to be concentrated. Industrial separation of biomass should be performed either continuously (centrifugation, flotation) or in batch processes (automatic filter press separation).

Then the excess water needs to be removed from the solution with an enzyme by ultrafiltration or evaporation, for highly purified enzymes chromatography or crystallization are used. The formulated cellulase can be contained in the liquid concentrate or be dried by using freeze-drying or spray-srying process (Dodge, 2010).

4. Influence of factors on the process of cellulase industrial production. The process of cellulase synthesis by microorganisms is a complex mechanism influenced by many factors, including substrate components, as well physical and biological factors (fig. 5).

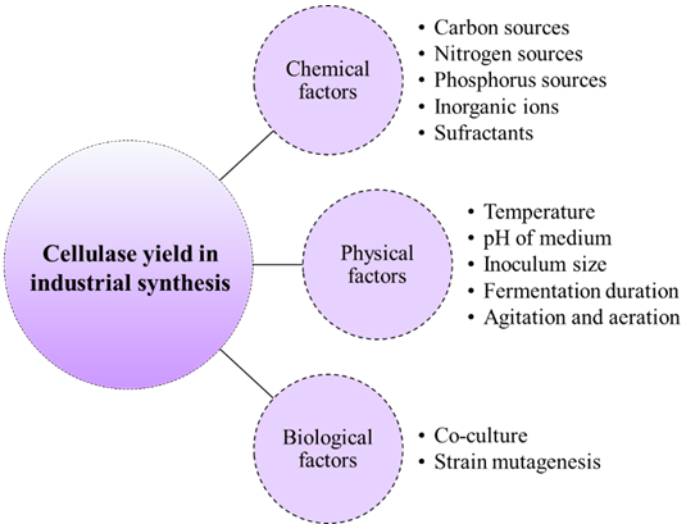

Fig. 5. Conceptual scheme of the main factors influencing the industrial synthesis of enzyme cellulase

I The impact of medium components. The cellulase enzyme is an inducible type, and its production depends on the source and concentration of cellulose and its derivatives in the fermentation medium. Obtaining an optimal nutrient medium consists of supplementing the substrate with nutrients: sources of C, N, P, S, macro- and microelements, inducers, etc.

1) Effect of Carbon source: the origin of Carbon plays a vital role in cellular metabolism, cellulase biosynthesis. Polysaccharides enhance enzyme production, thus being preferred when choosing a medium, in comparison to glucose, which improves growth of biomass, but inhibits synthesis of cellulase. (New and Future Developments in Microbial Biotechnology and Bioengineering, 2019). The results of the Georgian scientist confirmed this statement: the basidiomycete fungus *Irpex lacteus* produces more hydrolytic enzymes, such as β-glucosidase (cellulase), xylanase, on media with suplemented with Avicel (commercial pure cellulose) rather that glucose (Metreveli et al, 2021). Industry often utilizes waste material, for example from agriculture, which is rich in cellulose and carboxymethyl cellulose, to make fermentation media more cost-effective. Food industry waste is one of the most efficient materials for fermentation: researchers from the Indian Institute of Technology (India) revealed that the application of vegetable peel for cellulase production by two ascomycetes fungi has great potential (Verma and Kumar, 2020). As alternative sources of Carbon forage grasses can also be used. For example, gamba grass (*Andropogon gayanus*) was used by researchers from the Federal University of Visoca, Federal University of São Juan del Rey (Brazil) in various concentrations in the fermentation of the filamentous fungi *Fusarium verticillioides*; the highest endoglucanase activity was found when 4 % of gamba grass was added to a medium (De Almeida et al, 2019).

2) Effect of Nitrogen source: this element has a major role in the uptake of soluble carbohydrates during fermentation, which is supplement in an optimal ratio C:N, and protein synthesis (New and Future Developments in Microbial Biotechnology and Bioengineering, 2019). Scientists at the Dr. B. Lal Institute of Biotechnology (India) optimized cellulase synthesis by selecting a nitrogen source from the following option: ammonium sulfate, urea, yeast extract, peptone. The best nitrogen source for *Aspergillus niger* was the inorganic salt $(NH_4)_2SO_4$, while organic sources also increased the yield. The only exception was urea, which reduced enzyme synthesis (Sethi and Gupta, 2022). Therefore, a Korean researcher highlighted that yeast extract is the best nitrogen-based compound for cellulase synthesis by *Bacillus amyloliquefaciens* FW2, following tryptone, casein, skim milk, KNO_3, NH_4Cl (Pham et al., 2022).

3) Effect of Phosphorus source. Phosphorus takes part in the formation of cell membranes, as a part of phospholipid molecules and participates in the formation of nucleotides and numerous intermediate products, enzymes, coenzymes (Kumar et al., 2008). 0.2 % of K_2HPO_4 in fermentation media enhances secretion of the enzyme cellulase by isolated bacteria, especially by strain S-6 (*Nocardiopsis* sp.), which was discovered by scientists from the University of Sri Jayewardenepura (Sri Lanka) (Weerasinghe et al., 2021). Another inorganic salt - KH_2PO_4 improve cellulase biosynthesis by strains of *Aspergillus flavus* AT-2, *Aspergillus niger* AT-3, in experiments conducted by researchers from the Indian Institute of Technology Roorkee (India) (Dutt and Kumar, 2014).

4) Effect of inorganic ions: metal ions have diverse effects on the production of the enzyme cellulase. For example, Calcium induces enzyme synthesis by *Rhizopus*, *Trichoderma*, *Aspergillus*, *Penicillium* sp.; at the same time, Lead, Potassium, Copper, Manganese, Iron, Mercury ions inhibit (Onyia et al., 2022). Similarly, *Aspergillus flavus* cellulolytic activity was enhanced by Iron, but in optimal concentration – 1 mM of Fe^{2+} ions in media (Okonkwo et al., 2019).

5) Effect of surfactants (Tween 20 and 80, Triton X-100). The addition of surfactants minimizes the binding of the enzyme to the substrate, alleviates the tension from agitation and improves the absorption of substrate by microorganisms (New and Future Developments in Microbial Biotechnology and Bioengineering, 2019; Li et al, 2018). In the study of cellulolytic activity of *Paenibacillus elgii* TKU051, a Chinese scientist shows that commercial surfactants – anionic, such as SDS, improve cellulase synthesis, cationic (CTAB) – have moderate activity and non-anionic (Triton X-100, Tween 20) have a minor effect (Doan et al., 2024).

I I The impact of physical factors. Physical factors significantly affect the fermentation process, microorganism vital activity and synthesis of the enzyme cellulase by the producers.

1) Effect of temperature: temperature moderates the growth and metabolism of microorganisms. Low temperature can lead to the inhibition of the absorption of nutrients by cells and slow down producers activity. High temperature can break down formed enzymes activity, slowing the microorganism metabolism and potentially leading to their death (New and Future Developments in Microbial Biotechnology and Bioengineering, 2019). Studies shows that different producers and even strains exhibits distinct optimal temperature for cellulase production: *Bacillus* sp. – 35 ℃ (Islam et al., 2019); *Bacillus subtilis* M-11 – 42 ℃ (Yazici et al., 2020); 4 isolates from mangrove waters possessed maximum cellulolytic activity at 35 ℃, 27 ℃, 31 ℃, 31 ℃ (Alamsjah et al., 2024).; *Trichoderma reesei* RP698 at 60-65 ℃ (Silva et al., 2019).

2) pH of the medium: the starting pH of fermentation medium affects cell growth, membrane transport and enzyme synthesis, while acidic conditions can reduce the yield of the enzyme, basic – modify the substrate (New and Future Developments in Microbial Biotechnology and Bioengineering, 2019). *Talaromyces amestolkiae* CMIAT 055 demonstrated the greatest cellulolytic capacity at pH 5.0, when cultivated in the media containing banana pseudostem as cellulose source, (Faheina et al., 2022).

3) Effect of the amount of inoculum: an important step in the successful fermentation and synthesis of metabolite (cellulase) is the quantity of a «starter» culture. A smaller amount of inoculum will require a longer

period of biomass growth in the fermenter, which is insufficient for an industrial process (New and Future Developments in Microbial Biotechnology and Bioengineering, 2019). The effect of inoculum size factors was evaluated on *Aureobasidium pullulans* LB83 fungi by researchers from the University of São Paulo (Brazil). The concentration of 1.6*10-6 CFU (colony forming units) expressed the maximum secretion of enzyme, compared to 0.8*10-6 and 3.2*10-6 CFU (Viera et al., 2020).

4) Effect of fermentation time: an essential parameter of the industrial production of the cellulase enzyme is the incubation time, which is directly proportional to the amount of the formed metabolite (New and Future Developments in Microbial Biotechnology and Bioengineering, 2019). A comparative analysis of the synthesis of the cellulase enzyme by the filamentous fungi *Trichoderma reesei* UMK 004 and *Aspergillus awamori* UMK 002, carried out by scientists under the leadership of N.M. Zein, showed that during deep fermentation on rice straw as a substrate, *T. reesei* is the best producer. The optimal time for enzyme formation for both microorganisms is 5 days (Naher et al., 2021). In other studies, *T. reesei* Rut C30 was incubated for 4 days on spent mushroom waste (He et al., 2021); another strain of *A. avamori* DSM No. 63272 fermentation was lasted for 7 days (Martau et al., 2021).

5) Effect of agitation and aeration. Agitation maintains the homogeneity of the fermentation medium, disperses dissolved oxygen, which enhances microbial activity and substrate conversion for bacterial culture. Nonetheless, it leads to stress for the filamentous fungi culture, but it's essential, so for fungi, other types of agitators are used, such as Elephant Ear and Rushton turbines. These types of impellers provide less fragmentation on fungal clusters (New and Future Developments in Microbial Biotechnology and Bioengineering, 2019; Buffo et al., 2020; Buffo et al., 2016). Aeration is important for aerobic microorganisms. The oxygen level must be stable and supplied throughout the fermentation process New and Future Developments in Microbial Biotechnology and Bioengineering, 2019).

I I I The impact of biological factor.

1) Effect of co-culture. The synthesis of the cellulase enzymes endo- and exo-glucanase and β-glucosidase is heterogeneous. So, a combination of microorganisms will provide the desired mixture of cellulases (Kumar et al., 2008). Scientists from Prince of Songkla University (Thailand) studied the effect of synergistic fermentation of *Aspergillus tubigensis* TSIP9 and *Trichoderma reesei* Q9414 strains (at an inoculation ratio 1:1), resulting the highest yield of cellulase after submerged cultivation for 14 days – 103.7 U/g of RM (raw material) and β-glucosidase – 63.1 U/g RM (Intasit et al., 2021).

2) Mutagenesis of strains. Mutation and selection are widely used to improve cellulolytic strains (Kumar et al., 2008). Derivative strains of *Trichoderma reesei* SS-II, which were characterized by Chinese researchers as hypercellulolytic mutants and determined that these samples hydrolyze lignocellulose better than *Trichoderma reesei* RUT-C30 (a classic genetically modified strain that is an overproducer of cellulase): the hydrolysis activity of the derived strains is over 30 U/ml, compared to RUT-C30 – over 15 U/ml (Liu et al., 2019).

5. Application of the enzyme cellulase. Cellulases currently have a wide range of applications, from the pharmaceutical industry to biogas production, as described in this chapter.

1) Food and feed industry. The growing global population demands more nutritious food. Thus, the enzyme cellulase is used in various ways, like the extraction of olive oil, which not only improves the quality of the product, but also reduces waste and bitterness. For example, enzymatic extraction of olive oil from Jordanian cultivars increased from 48.8 % (classical extraction) to 79.0 % (Al-Rousan et al., 2021).

In the wine industry, cellulase breaks down cellulosic biomaterials for subsequent fermentation of sugars into alcohol. This enzyme enhances quality, improves stability and maceration, and reduces the viscosity of the must. β-glucosidase hydrolyzes glycosylated precursors into glucose and aglycones, enhancing the aroma of wines. Enzymatic hydrolysis with cellulase can increase the yield of natural dyes – carotenoids (Ejaz et al., 2021).

Furthermore, by converting cellulose polymers into monomeric glucose, cellulase increases the amount of sugars in baked goods. In an experiment conducted by scientists from Marwari University and Christ's College (India), it was found that the addition of heat-resistant cellulase from *Bacillus licheniformis* improves dough rise, aroma, density and friability of bread and reduces hardness (Ejaz et al., 2021; Chauhan et al., 2023).

To prevent fruit juices from clouding during storage, hydrolytic enzymes can be added. Immobilized enzymes are preferred, because they are stable and reusable (Ozyilmaz and Gunay, 2022).

Besides, the enzyme cellulase is used to increase the nutritional value of animal feed by hydrolyzing non-digestible oligosaccharides, β-glucans, pectins, lignins, inulins, dextrins, cellulose, arabinoxylans (Ejaz et al., 2021).

2) Light industry. Cellulase is used in the following sectors: pulp and paper, textile, detergent and washing products.

The manufacturing of paper and paper products is one of the largest industrial sectors in the world, utilizing nearly 40 % of all harvested wood. To reduce deforestation, the concept of recycling and reuse of paper and cellulose is being developed in this industry. Enzymatic hydrolysis is used to improve the process of modifying paper fibers and removing dyes from paper (Jayasekara and Ratnayake, 2019).

Cellulase is the third most used enzyme in the production and processing of fabrics, since enzymatic processing changes textile properties, such as softening the material or bleaching. In addition, this process is environmentally friendly and reduces the consumption of water, energy and chemical reagents (Jayasekara and Ratnayake, 2019; Korsa et al., 2023).

Cellulase detergents are mainly used for washing cotton fabrics, as they modify the fabric fibers, improving brightness, removing dirt, providing softness. To increase the efficiency of cellulase action, combinations of four

enzymes - lipase, cellulase, amylase and protease are used. These combinations are effective for cleaning endoscopic equipment and surgical instruments (Jayasekara and Ratnayake, 2019).

3) Agriculture. Cellulases are used in crop cultivation to improve growth (Jayasekara and Ratnayake, 2019). The cellulase enzyme synthesized by *Aspergillus niger* degrades the agricultural waste substrate (rice straw and sugar cane bagasse), enriching *Triticum aestivum* (wheat) with total soluble carbohydrate, Nitrogen and Phosphorus and enhances its growth, according to the studies of Egyptian scientists (Ismaiel et al., 2017). Lithuanian researcher obtained similar results: cellulase and other hydrolytic enzymes produced by *Trichoderma ghanense* and *Trichoderma tomentosum* improve development of *Secale cereale* L. (rye) (Bridziuviene et al., 2022).

Moreover, the enzyme can be used as agent for controlling plant diseases (Jayasekara and Ratnayake, 2019). For example, a *Talaromyces* sp. enzyme cellulase can inhibit the growth of plant pathogen *Pythium* sp. of cucumber and tomato as an environmentally friendly plant disease control agent (Kulakivska and Konechna, 2024).

4) Production of alternative energy sources. It has been estimated that the use of enzymatic treatment of lignocellulolytic raw materials before fermentation reduces the cost of the process by 40 %. The enzyme cellulase hydrolyzes biomass into pentoses, hexoses and monosaccharides as carbon sources. The thermophilic strain of the only one bacteria *Caldicellulosiruptor bescii*, can directly convert the raw material into bioethanol (Ejaz et al., 2021).

5) Medicine and pharmaceutical industry. An indirect application of cellulase for medical purposes is the use of this enzyme in combination with chitinase and lysozyme for the decomposition of chitosan in surgical threads, hemostatic bandages, etc.

Direct application is aimed at the decomposition of cell walls directly. For example, when the digestive system is impaired, residues of plant materials accumulate in the stomach, which can be hydrolyzed using a mixture of fungal cellulases.

Pharmacology uses only consumer-safe strains of *Trichoderma reesei* and *Bacillus licheniformis* (Jayasekara and Ratnayake, 2019).

6) Extraction of biologically active compounds from plant materials

Enzyme-assisted extraction (EAE) is an unconventional method of extraction that is based on the application of cellulase or other enzymes, or their combination, to hydrolyze the structures of plant cells, aiming to facilitate release of more phytocompounds.

Most plant metabolites are stored in the cell cytoplasm, but some are also found in vacuoles or plastids, and can also be associated with the polysaccharide-lignin structure and enzymes can break down these covalent bonds, releasing compounds.

EAE process efficacy depends on factors, such as temperature, pH, amount of enzyme used and duration of the process, type and size of crushed plant materials.

Enzymatic extraction has a number of advantages:

- environmentally friendly, since water and aqueous buffers are used as a solvent;
- the process is carried out at low temperatures, which does not require high heat consumption, preserving the molecules that are unstable at high temperatures;
- the process usually takes from 1 to 48 hours (Kulakivska and Konechna, 2024; Lubek-Nguyen et al., 2022).

A complex of the cellulase enzymes synergistically hydrolyzes β-1,4-glycosidic bonds and release long chains of cello-oligosaccharides, releasing glucose and cellobiose (Lubek-Nguyen et al., 2022).

Currently, researchers extract bioactive compounds from plant material using EAE, such as polyphenols and their derivatives, essential oils or other oils (fatty acid), polysaccharides.

Enzymatic hydrolysis using cellulase from *Aspergillus niger* during the ultrasound extraction of *Hibiscus sabdariffa* flowers shortened the process duration. This method is preferred for obtaining thermally unstable compounds such as tannins and flavonoids, as reported by scientists from the Lucian Blaga University in Sibiu (Romania) (Kulakivska and Konechna, 2024; Oancea and Perju, 2020).

Cocoa (*Theobroma cacao*) shells contain phytocompound that were found to be elevated after EAE using Viscozyme L as an enzyme. A group of researchers from the International University, Vietnam National University studied this. The extraction yield was increased compared to the control for theobromine (from 1.22 to 1.29 g/100g), catechin (from 0.51 to 0.54 g/100g), caffeine (from 0.23 to 0.235 g/100g), polyphenols (from 3.68 to 3.9 g gallic acid/100g), flavonoids (from 10.67 to 10.83 g rutin /100g) after 10 min of incubation (Kulakivska and Konechna, 2024; Oancea and Perju, 2020; Huynh et al., 2023).

A team of scientists supervised by L. Hennessey-Ramos investigated the extraction of pectins (polysaccharides) from cocoa bean shells using cellulase (Celluclast). Their study found that the optimal condition for EAE resulted the extraction recovery - 10.20 g of pectins from 100 g raw material, in comparison, chemical extraction has a yield of 8.08 g/100 g raw material (Hennessey-Ramos et al., 2021).

For the extraction of essential oils, microwave extraction combined with enzymatic extraction, which is based on the destruction of cell walls by enzymatic hydrolysis and vibrations of polar molecules, increasing the pressure in the cells. Researchers from the College of Life Sciences, Jiangxi Normal University, School of Marine and Biological Engineering, Yangcheng University and Laboratory of Esophageal Cancer Prevention and Treatment (China) studied this method on *Cinnamomum burmannii* leaves. The combined extraction yield achieved 57.71 %, compared to microwave extraction alone - 50.73 % (Liu et al., 2021).

Carotenoids are compounds that color the plants, accumulating in plastids and binding to proteins, which limits their release from cells. Scientists from the National University of the Center of Peru (Peru) conducted research that confirmed a higher concentration of carotenoids extracted by EAE. They found a yield of

10037.21 mg/g raw material, in contrast to the maceration - 4160.61 mg/g raw material (Mendoza et al., 2020).

The results of the literature analysis data indicate that enzyme-assisted extraction can increase the release of a variety of biologically active substances, when the process is carried out under optimal conditions.

A systematized overview of the widespread application of cellulase across different economic sectors, highlighting its main function and the specific advantages of its implementation, in presented in table 2.

Table 2.

Systematization of the industrial application of the enzyme cellulase and its efficiency

Industry sector	Specific apllication	Main function of cellulase	Key advantages/efficiency
Food and feed industry	Olive oil extraction, winemaking, baking, juice clarification, animal feed	Breaks down cell walls and glycosylated precursors; converts cellulose polymers to simple sugars	Increases extraction yield (e.g. olive oil up to 79%); enhances aroma and dough properties; improves nutritional value of feed
Light industry	Pulp and paper recycling, textile processing, detergent formulation	Modifies cellulose fibers, removes dyes and facilitates dirt removal	Eco-friendly alternative to harsh chemicals; significantly reduces water, energy and reagent consumption
Agriculture	Crop cultivation, plant disease control	Degrades agricultural waste to release nutrients (Nitrogen, Phosphorus); acts as an antagonist to plant patogens	Promotes plant growth naturally; serves as a safe, eco-friendly biocontrol agent
Alternative energy	Bioethanol and biogas production	Hydrolyses lignocellulosic biomass into fermentable pentoses and hexoses	Reduces pretreatment costs by up to 40%; allows direct conversion of agricultural waste into biofuel
Medicine and pharmaceuticals	Digestive aids, decomposition of surgical material	Hydrolyzes undigested plant residues in the stomach; assists in chitosan decomposition	Provides safe, targeted degradation of specific biopolymers using consumers-safe microbial strains
Extraction of bioactive compounds (EAE)	Recovery of polyphenols, essential oils, carotenoids and pectins from plant tissues	Destroys plant cell walls and break covalent bonds associated with polysaccharide-lignin matrix	Significantly increases extraction yield; uses eco-friendly solvents; preserves thermally unstable compounds due to low temperatures

As demonstrated, the integration of cellulase across these sectors provides significant economic and ecological benefits.

Conclusion. Cellulase is a group of cellulolytic enzymes, which are produced by *Bacteria*, *Archaea*, plants, animals, Fungi. This enzyme leads to gradual hydrolysis of polysaccharide cellulose and involves the binding of the enzyme to polysaccharide followed by the catalytic action of the 3 main and 4 additional enzymes to hydrolyse the β-1,4-glycosidic bonds. In nature, cellulase takes place in the biogeochemical cycle and decomposes mostly litter of dead plant cellulose, thus sustaining life of soil microbiota and life. The enzymatic process of decomposition of cellulose that was developed by evolution operates without high pressure, toxic chemicals or excessive energy input, thus it is successfully applied in diverse industries from biogas production to the pharmaceptical industry.

Conflict of interest*. the authors declare that the research was conducted without any commercial or financial relationships that could be constructed as a potential conflict of interest.*

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РОЛЬ ФЕРМЕНТУ ЦЕЛЮЛАЗИ ЯК ЕКОЛОГІЧНОГО АГЕНТУ У РОЗКЛАДАННІ ЦЕЛЮЛОЗИ У ПРИРОДІ ТА ПРОМИСЛОВОСТІ

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Целюлаза являє собою складний синергетичний комплекс ферментів, що складається переважно з трьох типів: ендоглюканаз, екзоглюканаз та β-глюкозидаз. Взаємодія цих біокаталізаторів забезпечує ефективне розщеплення складної структури природного полісахариду целюлози на прості моно- та дисахариди, такі як глюкоза та целобіоза. В природі цей ензим синтизується широкою різномантністю мікроорганізмів – незалежно або через симбіотичні стосунки – при чому представики типів Fungi та Bacteria виступають як основні деградатори рослинної біомаси. Цей процес деградації целюлози є фундаментальним для глобального циклу вуглецю, тим самим підтримуючи життя на нашій планеті.

В промисловому контексті, цей фермент вироблять твердофазною та глибинною ферментацією Ефективність виходу ферменту контролюється комбінацією факторів: хімічних (склад середовища, включаючи джерела Карбону та Нітрогену), фізичних (температура, аерація, перемішування), біологічних (вибір штамів мікроорганізмів, мутагенез, синергетична взаємодія). Використання сільськогосподарських відходів як субстрату є ключовою стратегією підвищення економічної доцільності виробництва. Завдяки своїй універсальності целюлаза знаходить широке застосування в багатьох секторах економіки. Фермент є важливим для харчової промисловості та виробництва напоїв (виноробство, хлібопекарство, освітлення соків), целюлозно-паперовому виробництві, текстильному виробництві, складу мийних засобів, фармацевтичної промисловості. Крім того, фермент відіграє важливу роль у виробництві альтернативного палива та в екстракції за участі ферменту біологічно активних сполук з рослинної сировини.

Метою цього дослідження є пошук та систематизація інформації про роль ферменту целюлази в ферментативному гідролізі, підкреслюючи його стійкий підхід як процес відточений еволюцією та успішно адаптований для промислових «зелених технологій.

Ключові слова: фермент целюлаза, розкладання целюлози, екологічний агент, промисловість, зелені технології.

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