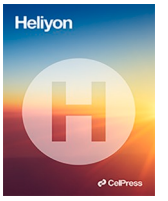
Heliyon 10 (2024) e24022

Contents lists available at ScienceDirect

Heliyon

journal homepage: www.cell.com/heliyon



Research article

# Enzymatic degradation of cellulose in soil: A review

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ARTICLE INFO

*Keywords:*
Lignocellulose
Biofuel
Cellulose degradation
Cellulases

ABSTRACT

Cellulose degradation is a critical process in soil ecosystems, playing a vital role in nutrient cycling and organic matter decomposition. Enzymatic degradation of cellulosic biomass is the most sustainable and green method of producing liquid biofuel. It has gained intensive research interest with future perspective as the majority of terrestrial lignocellulose biomass has a great potential to be used as a source of bioenergy. However, the recalcitrant nature of lignocellulose limits its use as a source of energy. Noteworthy enough, enzymatic conversion of cellulose biomass could be a leading future technology. Fungal enzymes play a central role in cellulose degradation. Our understanding of fungal cellulases has substantially redirected in the past few years with the discovery of a new class of enzymes and Cellulosome. Efforts have been made from time to time to develop an economically viable method of cellulose degradation. This review provides insights into the current state of knowledge regarding cellulose degradation in soil and identifies areas where further research is needed.

## 1. Introduction

Cellulose is the most widespread biopolymer on earth. It is widely present in eukaryotic, prokaryotic, and microorganisms like bacteria, and amoeba [1]. Cellulose, a major part of the cell wall, comprises 60 % of the lignocellulosic biomass. Lignocellulosic complex contains 40–60 % cellulose and 20–40 % hemicellulose, and 10–25 % lignin. Apart from plant origin, cellulose is also secreted extracellularly in the form of a continuous film by some bacteria, e.g., *Acetobacter, Sarcina ventriculi,* and *Agrobacterium* [2]. Cellulose secreted from bacteria has different physicochemical properties, although they have the same structure Bacterial cellulose is more porous, crystalline, and ribbon-like small microfibrils (Fig. 1a and b) in contrast to the plant cellulose (Fig. 1c,d). Fig. 1a and b, adapted from Wen [3]. and Fig. 1b and c, adapted from Ref. [4].

Cellulose in the soil may be either of plant origin or lignocellulosic waste from the food industry [4,5]. Soil organic matter contains up to 25 % cellulose, hemicellulose, and soluble sugar [6]. A large percentage of cellulose is present as ligno-cellulosic complex (LCC) in the soil. LCC is an intricate arrangement of polysaccharides, lignin, and protein. LCC is recalcitrant and difficult to degrade by itself. In terms of energy, cellulose it is the most abundant source of clean, renewable energy [7].The enzymatic degradation of lignocellulosic biomass is the center of attraction for many kinds of research because it could be a source of economically viable biofuel [8].

Cellulose degradation is mainly based on the biotic process, aerobic process, and co-metabolic process. Cellulases secreted by specific aerobic-anaerobic bacteria and fungi [9,10] can break down various biopolymers. Although chemical homogenous, cellulose exists in crystalline and amorphous topologies and, thus, requires multiple enzymes to hydrolyze the cellulose [11,12]. Microorganisms usually secrete a group of enzymes that act as synergism to degrade the recalcitrant polymer. Fig. 2 demonstrates the difference between aerobic and anaerobic fermentation of the products generated by cellulose degradation (Fig. 2.). An anaerobic

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https://doi.org/10.1016/j.heliyon.2024.e24022
Received 11 October 2022; Received in revised form 13 December 2023; Accepted 2 January 2024
Available online 3 January 2024

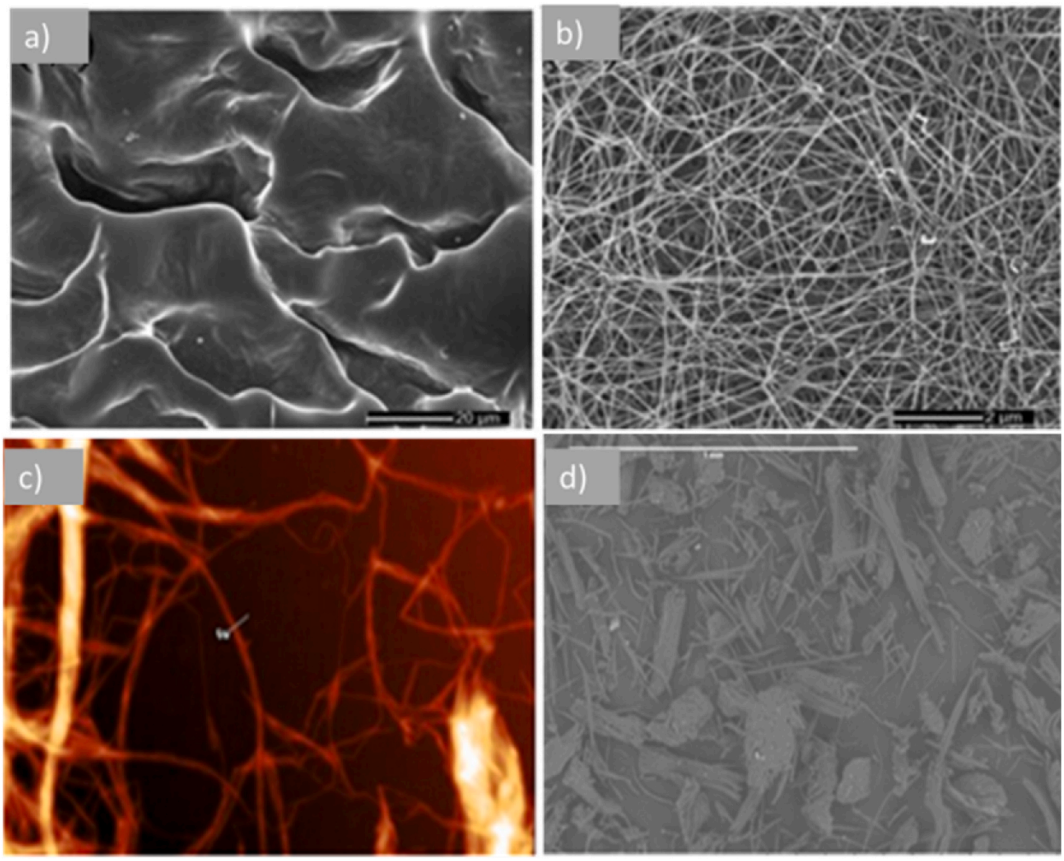


**Fig. 1.** Bacterial origin cellulose a) SEM image (2000 × ) [3] b) SEM image (20,000 × ); Plant origin cellulose (Brewer's Spent Grain) [3] c)AFM image d) SEM image [4].

environment initiates the formation of Cellulosome, where different enzymes work in a group. However, aerobic microorganisms secrete different cellulolytic enzymes that work independently.

Cellulose degradation is a subject of major research for decades. Our understanding of cellulose degradation shows that enzymes from soil microorganisms have a dominant role in these processes [13,14]. The purpose of this review is to describe different enzymes required for the degradation of cellulose molecules, a recent advancement, a new type of enzyme, and a classification of these enzymes considering recent relevant reports. In this review, I have described the structural biodiversity of the cellulose molecule, its distribution, and biodegradation by various groups of microorganisms. The new enzyme system, its sequence-based classification, and its role in the cellulose degradation has been discussed. In this article degradation of cellulose in soil has been my focus.

## 2. Cellulose structure and its biosynthesis

Cellulose is a linear homopolysaccharide polymer of thousands of glucosyl units linked together by β-1,4 glycosidic linkage (Fig. 3a and b). Each glucosyl unit contains one primary hydroxy group ($C_6$–OH) and two secondary hydroxy groups ($C_2$–OH&$C_3$–OH) to form an insoluble crystalline microfibril structure (Fig. 3c). Such microfibril structures are resistant to the actions of the hydrolytic enzymes [15]. Several microfibril bunches form a macrofibre. Cellulose microfibrils are embedded in the pectin of the cell wall of single cell. The hydrogen bond formed between the cellulose chain provides extra strength to the structure. Many single cells (Fig. 3d) combine to form a cell bundle (Fig. 3e) and cell bundle further unite to form tendril helix (Fig. 3f). The molecular arrangement and bonding nature of cellulose in the plant cell wall has been presented by Habibi et al. (2010) [16].

The typical structure of cellulose molecule is shown in (Fig. 4) detailed explanation of the structure is above the scope of this review.

The biosynthesis of cellulose is still not much clear; it starts with simple glucose molecules. The only substrate for cellulose synthesis is uridine diphosphate (UDP) glucose to form the homopolymer p-1,4-*d*-glucan. The biosynthesis starts in the cell from simple glucose molecule (Fig. 5).

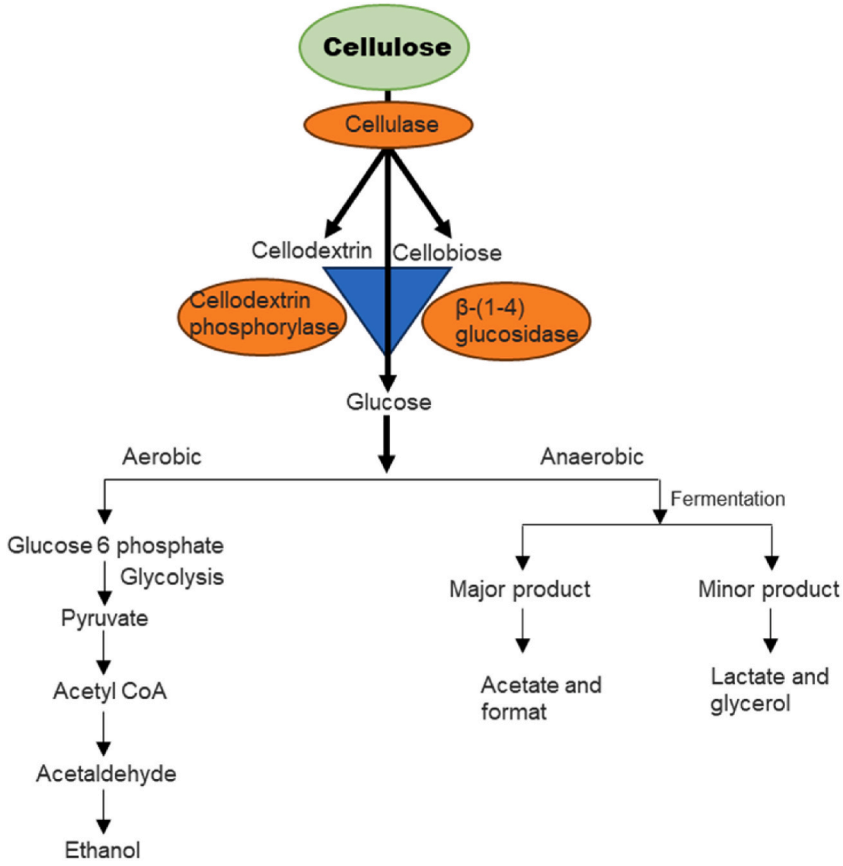


**Fig. 2.** Aerobic and Anaerobic pathways of cellulose degradation.

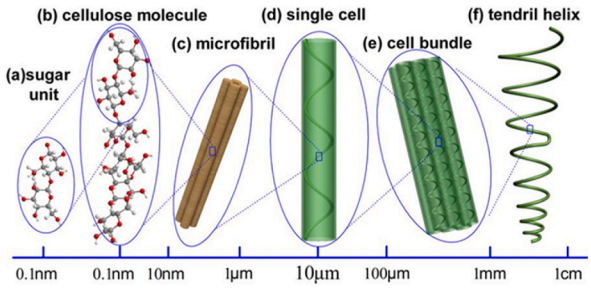


**Fig. 3.** Hierarchy of chirality in a tendril helix: (a) sugar unit, (b) cellulose molecule, (c) microfibril consisting of cellulose molecules, (d) single cell containing a cellulose helix, (e) cell bundle, and (f) tendril helix [17]. (Creative Commons Attribution International License (CC BY)) (https://creativecommons.org/licenses/by-nc-sa/3.0/).

## 3. Cellulose degradation

Cellulose degradation is a complex process requiring a group of enzymes that synergize [19]. Degradation can be done chemically or biochemically. Biochemical degradation has an advantage over the thermochemical degradation as it leads to the destruction of carbohydrates, whereas in biochemical degradation, the original carbohydrate moiety is preserved [20]. Enzymes secreted from bacteria and fungi are involved in the degradation process of cellulose and are classified under the category of cellulase (3.2.1.4) [21]. New enzyme and enzyme modulators have been discovered that increase the efficiency of classical cellulase [22].

The classical cellulose degradation scheme requires three different enzyme systems that convert the polymeric substrate into its monomeric glucose. Endo-β-1,4-glucanases (endocellulases, EC 3.2.1.9.1), cellobiohydrolases (exocellulases, EC 3.2.1.91) and β-1,4-glucosidases (cellobiases, EC3.2.1.21) (Fig. 6) [13]. The alliance of these enzyme activities only enables them to interrupt the structure at the solid-liquid interface making the individual fiber available for hydrolysis [11]. All three enzymes are hydrolases and cleave

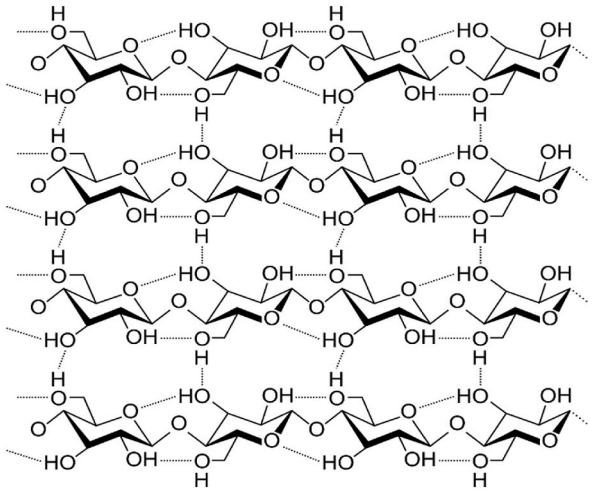

**Fig. 4.** 3D structure of cellulose (a), Chemical structure of cellulose (b).

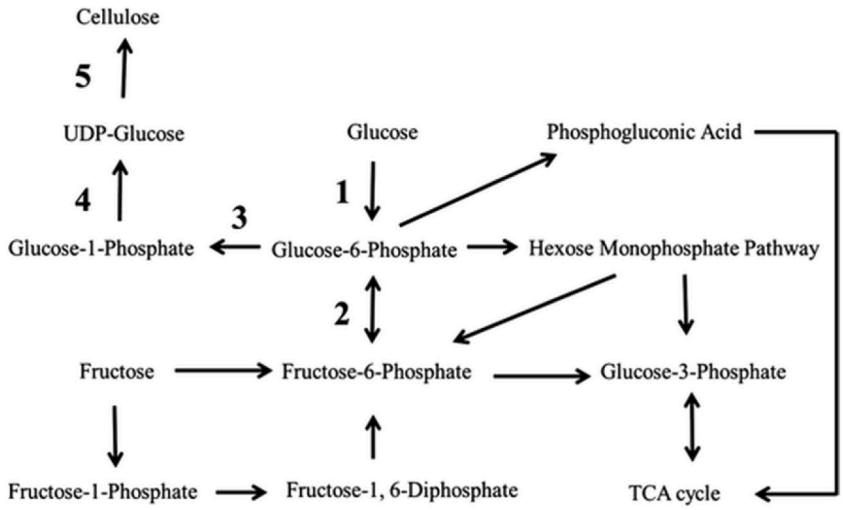


**Fig. 5.** Pathway of cellulose synthesis from glucose in Acetobacter xylinum. 1. glucokinase, 2. isomerase, 3. phosphoglucomutase, 4. UDPG-pyrophosphorylase, 5. cellulose synthase [18].

glycosidic bonds by the addition of water molecules [23].

Endo-1,4-β-glucanase randomly cleave the cellulose molecule and attack the amorphous part of the cellulose molecule. Endo-glucanase may be processive or non-processive in nature [24,25]. The action of endo-hydrolases creates a new reducing and non-reducing chain end. Reducing and non-reducing end of cellulose polymer is prone to exo-1,4-β-glucanase action. β-glucosidases act on the product released by the action of exo-1,4-β-glucanase and endo-1,4-β-glucanase. These are not called true cellulases as they do not directly act on cellulose, but their presence is as crucial as the other enzymes [26,27]. Table 1 shows the group enzyme involved in cellulose degradation.

Endo and exoglucanases enzymes are responsible for the degradation of cellulose in the solid phase, whereas glucosidases enzymes carry out degradation in the liquid phase. Cellulose degrading enzymes are a cluster of enzymes that hydrolyze glycosidic bond either by inversion or retention of anomeric configuration at the point of cleavage [11,28]. In inversion, the removal of leaving group takes place along with the removal of the water molecule. In contrast, the retention mechanism involves double displacement with the formation of glycosyl-enzyme intermediate [29]. An efficient and extensive breakdown of cellulose architecture requires the synergistic action of different cellulose-degrading enzymes.

During synergism product formed by two or more enzymes acting together is greater than the sum of product formed by the action of each enzyme. Synergism could be enzyme-substrate cooperation or enzyme cooperation. Typical synergism in a cellulase system is: a) between exo- and endo-type cellulases. b) between two exocellulases from both reducing and non-reducing ends of the substrate. c) processive endocellulases, and synergism between b-glucosidases and other cellulase enzymes [30]. d) cellobiohydrolases, endoglucanases and β glucosidases [31,32]. Different combinations of cellulases enzymes have been investigated for their synergism action,

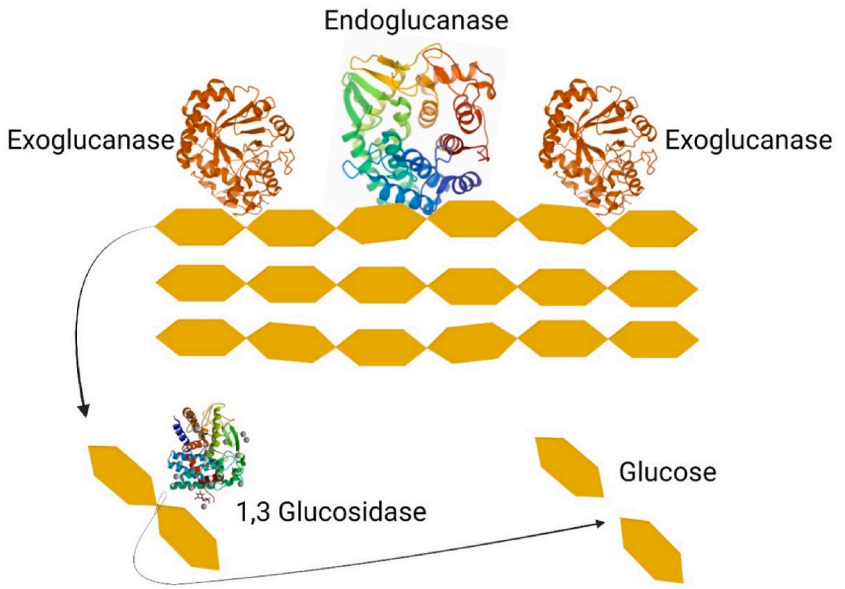


**Fig. 6.** Role of different enzymes in cellulose degradation. Endoglucanase releasing cellooligosaccharides by breakdown the long polymerase chains of cellulose fiber. Exoglucanases cleave chain ends and releases cellobiose which is then cutdown by β-glucosidase to release glucose.

**Table 1**
Cellulases types, their systemic name, and their mode of action.

| Enzyme | Enzyme Nature | EC Code | Class | Systematic name | Mode of Action |
|---|---|---|---|---|---|
| **Glucanohydrolase** | Endo-(1–4)-13-D- glucanase | 3.2.1.4 | Hydrolases; Glycosylases; Glycosidases | 4-beta-D-glucan 4-glucanohydrolase | acts on the amorphous region of the cellulose molecule. It cleaves internal beta-1,4-glucosidic bonds in cellulose. |
| **Cellobiohydrolase** | Exo-(1–4)-13-D-glucanase | 3.2.1.91 | Hydrolases; Glycosylases; Glycosidases | 4-beta-D-glucan cellobiohydrolase (non-reducing end) | acts on reducing or non-reducing ends of cellulose molecule by hydrolyzing 1,4-β-D-glycosidic bonds. It has a tunnel-like structure formed by two surface loops. The aspartic acid residue is present inside the tunnel act as catalytic residues. It is active against crystalline cellulose |
| **Cellodextrinase** | Exo-(1–4)-13-D-glucanase | 3.2.1.74 | Hydrolases; Glycosylases; Glycosidases | glucohydrolase | acts on cellooligosaccharides to remove cellobiose. It is active against the crystalline surface and inactive against crystalline and soluble forms of cellulose. |
| **β-glucosidase** | 13-Glucosidase | 3.2.1.21 | Hydrolases; Glycosylases; Glycosidases | gentiobiase | It hydrolyzes cellooligosaccharides and cellobiose to terminal non-reducing residues in beta-D-glucosides and oligosaccharides with the release of glucose molecules. Glucosidase is inactive against both crystalline and amorphous cellulose. |
| **Cellobiase** | cellobiose phosphorylase | 2.4.1.20 | Transferases; Glycosyltransferases; Hexosyltransferases | phosphate α-D-glucosyltransferase | catalyzes the reversible phosphorolytic cleavage of cellobiose to form α-D-glucopyranosyl phosphate. cellobiose + phosphate = α-D-glucose 1-phosphate + D-glucose |
| **Cellodextrin Phosphorylase** | Cellodextrin Phosphorylase | 2.4.1.49 | Transferases; Glycosyltransferases; Hexosyltransferases | phosphate alpha-D-glucosyltransferase. | It catalyzes the reversible phosphorolytic cleavage of cellodextrins (cellotriose to cellohexose) to glucose. (1,4-beta-D-glucosyl) n + phosphate = (1,4-beta-D-glucosyl)n-1 + alpha-D-glucose 1-phosphate |
| **Cellobiose Epimerase** | Cellobiose Epimerase | 5.1.3.11 | Isomerases; Racemases, epimerases; | cellobiose 2-epimerase | Interconversion ofD-glucose and D-mannose residues present at the reducing end of beta-1,4-linked disaccharides is catalyzed by enzyme epimerase by epimerizing the hydroxyl group at the C-2 position of the glucose moiety. |

**Table 2**
Microorganism secreting cellulase enzyme.

| Bacteria | Fungi | Actinomycetes |
|---|---|---|
| **Aerobic Bacteria** | **Micro fungi** | *Actinopolyspora halophila* |
| *Acetobacter oboediens* | *Aspergillus aculeatus* | *Cellulomonas biazotea* |
| *Bacillus circulans* | *Aspergillus candidus* | *Cellulomonas cartae* |
| *Bacillus flexus* | *Aspergillus flavus* | *Cellulomonas cellulans* |
| *Bacillus subtilis* | *Aspergillus heteromorphus* | *Cellulomonas flavigena* |
| *C. flavigena* | *Aspergillus oryzae* | *Cellulomonas gelida* |
| *Cellulomonas bioazotea* | *Penicillium decumbens* | *Cellulomonas subalbus* |
| *Cellvibrio gilvus* | *Penicillium funmiculosum* | *Cellulomonas uda* |
| *Citrobacter freundii* | *Penicillium oxalicum* | *Microbispora bispora* |
| *Cytophaga hutchinsonii* | *Acremonium cellulolyticus* | *Micromonospora chalcea* |
| *Escherichia coli* | *Bispora betulina* | *Micromonospora melanosporea* |
| *Geobacillus pallidus* | *Ceratocystis albida* | *Pseudonocardia thermophila* |
| *Halomonas caseinilytica* | *Xylogone sphaerospora* | *Streptomyces albogriseolus* |
| *Klebsiella pneumonia* | *Ceratocystis stenoceras* | *Streptomyces drozdowiczii* |
| *M. bispora* | *Chrysosporium pannorum* | *Streptomyces flavogriseus* |
| *Proteus vulgaris* | *Cylindrocarpon didymium* | *Streptomyces glomeratus* |
| *Pseudomonas aeruginosa* | **Macro fungi** | *Streptomyces lividans* |
| *Pseudomonas fluorescens* | *Schizophyllum commune* | *Streptomyces malachitofuscus* |
| **Anaerobic Bacteria** | *Phanerochaete chrysosporium* | *Streptomyces nitrosporeus* |
| *Butyrivibrio fibrisolvens* | *Pycnoporous sanguineus* | *Streptomyces stramineus* |
| *Clostridium acetobutylium* | *Pleurotus Djamor* | *Thermoactinomyces* spp. |
| *Clostridium cellulolyticum* | | *Thermomonospora curvata* |
| *C. Cellulolyticum* | | |
| *Clostridium papyrosolvens* | | |
| *Clostridium stercorarium* | | |
| *Fibrobacter succinogenes* | | |
| *Ruminococcus albus* | | |
| *Ruminococcus flavefaciens* | | |

**Table 3**
Some recent literature examples of cellulases production from fungi grown on different biomass residues in SSC.

| Fungal Strain | Carbon Source | CMC Activity (Ug-1) | Reference |
|---|---|---|---|
| *Penicillium* sp. | carboxymethyl cellulose | 18.82 | [48] |
| *Aspergillus niger* | pretreated bamboo-shoot shell | 5.5 | [49] |
| *Cerrena maxima* | Tree leaves | 57 | [50] |
| *Fomes fomentarius* | Mandarin peels | 45 | [51] |
| *Funalia trogii* | Wheat straw | 72 | [50] |
| *Penicillium funiculosum* | cellulignin bagasse | 11 | [52] |
| *P. oxalicum* | dignified corn cob residue | 24 | [53] |
| *Pleurotus ostreatus* | Wheat straw | 12 | [51] |
| *Pseudotremella gibbosa* | Wheat straw | 18 | [51] |
| *Trametes versicolor* | Apple peels | 135 | [50] |
| *Trichoderma harzianum* | cellulignin bagasse | 36 | [54] |
| *Trichoderma harzianum* | cellulignin bagasse | 27 | [55] |
| *T. reesei* | microcrystalline cellulose | 6 | [56] |

the surface structure of enzymes and substrate has been a significant issue to synergism. Various non-catalytic proteins are classified whose specificaction is still unknown, but they assist in cellulose degradation.

Although various organisms secrete cellulases, there is still a shortage of the significant amount of cellulase in the soil to efficiently degrade cellulose to fermentable products [33]. Most research focuses on cellulase from fungi compared to bacteria, although the bacterial cellulolytic enzyme is more stable due to their high natural diversity [34–36].

## 4. Intracellular and extracellular secretion of cellulase

In bacteria, cellulases are bound to the cell wall as an enzyme aggregate [37].These extracellular aggregates are known as cellulosomes [38,39]. Cellulosomes are regulated by the presence of hemicelluloses [13]. Fungal cellulases are secreted during the phase of the growth cycle, several biochemical changes occur at this time, and as a result, cellulase is secreted into the extracellular space. Extracellular cellulase help fungi to degrade organic matter surrounding the host plant and in penetration and colonization into host root cells [40]. Cellulase production rate is higher in fungi as compared to other microorganisms. Certain fungi can secrete a large number of extracellular cellulases; this makes such strain as most studied fungi. e.g., *Trichoderma* spp., *Pseudomonas* sp., *Aspergillus* spp., *and Actinomycetes.* [41–43]. Different research groups have already reported the list of microorganisms involved in cellulose degradation [44] (Table 2.).

## 5. Cultivation system of cellulases

### 5.1. Solid state cultivation (SSC)

Earlier fungal-based enzymes are mainly being produced by liquid-based submerged cultivation, but solid-state cultivation (SSC) is also gaining the attention from many researchers. SSC can be defined as the growth of microorganisms on moist, water-insoluble solid substrates at low or no water activity [45]. Most fungi require a solid surface for growth as they grow via elongation and penetration of hyphae through the substrate [46]. Besides the above benefits, SSC has several other benefits as it is less expensive, has low energy expenditure, low wastewater output, and potentially higher volumetric productivity. The moisture requirement is directly related to the lignocellulose substrate structure and fungal species [47]. SSC generally requires moisture levels below 60 %–80 %, and above this level, it is less favorable for cellulase production [47]. Some examples of SSC of cellulases are summarized in Table 3.

General Guidelines for FSSF methodologies have been given by Ref. [57] as follows.

1. Inoculum preparation - generally spores raised on the actual substrate
2. Substrate preparation including size reduction, nutrient addition, and pH adjustment
3. Autoclaving to sterilize/pasteurize and cook the medium for increased amenability to fungal growth
4. Inoculation of the moist solid medium
5. Incubation under near-optimal conditions in suitable reactor systems
6. Drying of the solids and extraction of the product(s).

## 6. Final steps involving filtration, concentration/purification

Solid-state cultivation has been used at the industrial level for fungal production of a wide variety of lignocellulolytic enzymes [46,51,58–60].

### 6.1. Submerged cultivation

Submerged culture is the system used to produce a variety of metabolites produced by filamentous fungi. Fungi colonies grow in a liquid medium that contains the required nutrients and the insoluble lignocellulosic substrates for cellulase production. In submerged culture, fungal growth can be predicted by the formation of pellets [61]. The culture medium can be ventilated through air-liquid interphase. An enzyme produced may be constitutive or inducible. It depends on the fungal strain and culture conditions. However, enzyme recovery from a liquid medium is relatively easy in submerged culture compared to a solid medium, but the enzyme gets diluted into the liquid cultivation medium. Therefore, enzyme concentration processes are required to get pure and concentrated enzymes.

## 7. Cellulose and its degradation in soil

Soils contain one of the largest pools of organic carbon compounds on the earth, and soil processes, thus, play a major part in the global C cycle [62] especially; forest soils are one of the most important terrestrial carbon sink sources. In forests, dead plant materials are not removed during harvesting but left on the forest floor for accumulation [62]. These dead plant biomasses mainly consist of variety of plant cell wall polymers such as cellulose, hemicellulose, and lignin. Among these polymers, cellulose is one of the most abundant polysaccharides in a terrestrial and typically add up to 20–30 % of the plant litter mass [63]. The cellulose content in the soil decreases as we go down into the soil from the O horizon, but aromatic carbon measured by solid-state 13C nuclear magnetic resonance (NMR) was reported to increase in some cases. A large portion of the soil microbial community implies carbon hydrolyzing activities [64] and the main producers of polysaccharide degrading enzymes. These enzyme production abilities make them the most important players in the plant biomass degradation [65]. Usually, it is presumed that soil fungi are the main decomposer of dead plant biomass. However, recent advanced studies showed that soil bacteria also play an imperative part in polysaccharide composition [66].

Cellulosic enzymes secreted from bacteria and fungi and root excaudate present in soil are actively involved in the degradation of different polysaccharide present in the soil. The orientation, adsorption, and diffusion of the such enzymes in the soil solid phase affect the cellulose degradation in soil [67,68]. A high inflow of aromatic organic matter into the soil makes cellulose a chief component in the soil organic matter. High stability and complex degradation of cellulose contribute to increasing humus formation. Identification of cellulolytic bacteria in the soil is carried out by morphological and biochemical characterization [69]. Techniques used for enzyme assay of isolated cellulases, e.g., Endo-β-1,4-glucanase activity assay by DNS method and purification is done by Ammonium sulfate precipitation, DEAE-cellulose column chromatography, CM-cellulose column chromatography, Protein estimation, and molecular weight determination. Cellulose undergoes oxidation in the presence of nitrogen dioxide and forms a Cellulosic acid. The presence of Cellulosic acid in soil reflects the extent of cellulose present in the soil. Oxidative, thermal, and hydrolytic degradation are the primary process involved in cellulose degradation. Cellulases play a critical role in improving the soil quality. The excessive dependence of farmers on mineral fertilizers can be reduced by incorporating straw in the soil. Past studies on the use of microbes, e.g., *Aspergillus, Chaetomiumand, Trichoderma, and actinomycetes,* to accelerate straw decomposition showed a promising result [70,71].

Fungi and bacteria play an important in the degradation of cellulose in soil. The degradation process involves a series of coordinated steps between these microorganisms. First, bacteria Spp. like Cellvibrio, or Fibrobacter produce cellulases, enzymes that break

down the cellulose polymer into smaller sugar units, such as cellobiose 1 2. Next, fungi, such as Trichoderma and Aspergillus takeup cellobiose and produce there own cellulases enzymes called cellobiohydrolases, which break down the cellobiose into glucose monomers 3 4. These fungi can also produce enzymes that break down other polysaccharides, such as hemicelluloses and pectins.

The glucose monomers are then taken up and metabolized by both fungi and bacteria. Bacteria, such as Bacillus and Pseudomonas, can utilize glucose as a carbon and energy source, while fungi, such as Neurospora or Actinobacteria, can use glucose to produce energy.

Throughout this process, both fungi and bacteria play important roles in providing each other with essential nutrients and creating favorable conditions for growth. For example, bacteria can produce organic acids that create a more acidic environment, which stimulates fungal growth. Fungi, in turn, can produce enzymes that break down bacterial cell walls, releasing nutrients for bacterial growth.

### *7.1. Factors affecting cellulose degradation in soil*

Cellulose degradation is a slow process in soil. Many factors directly or indirectly affect the cellulose degradation process, such as the addition of available nitrogen, temperature, aeration, moisture content, pH, lignin content, concentration location of cellulases, and their activities. Understanding how different factors affect or limit cellulose degradation is crucial for estimating global C flux and potential future changes.

#### *7.1.1. Nitrogen availability*

One of the well-established ecosystem ecological patterns is that litter decomposition rate is significantly correlated with an initial ratio of C (carbon):N (nitrogen), lignin: N, or lignin: cellulose in litter [72]. The addition of inorganic nitrogen increases cellulose degradation by alleviating the N limitation of C use by decomposers.

#### *7.1.2. Temperature*

Temperature is another critical factor that limits the cellulose degradation process. Temperature seasonality influences the photosynthetic activities that directly affect C input through the rhizodeposition process [73]. Additionally, temperature seasonality significantly alters soil microbial community and their functions. Changes in C input and microbial community and its functions directly or indirectly lead to soil organic matter decomposition and its stability [74,75]. Tang et al. (2018) reported that temperature plays a predominant role in affecting the rate of soil C mineralization, while soil substrate determines the mineralizable SOC under given conditions [76]. Further, the author reported that microbial communities only play a secondary role in driving SOC mineralization compared to climate and soil substrate, as soil microbial community is both affected and adapts to climatic factors and soil matrix.

#### *7.1.3. Moisture content*

Excessive soil moisture content leads to anaerobic condition and reduces the decomposition rate in the soil. The potential for metabolites and enzyme fluxes of microbes and their substrates is significantly controlled by the interplay of the soil moisture retention and pore network structure. which further regulate microbial access to organic matter and affect the gross C mineralization process in the soil [77–79]. Another study by Menhout et al. (2018) studied the indirect effect of the soil structure and moisture content on the plant polysaccharide decomposition by soil microbes using the X-ray method and reported that soil structure and moisture content significantly affect the soil N availability or content which further limit decomposition process in the soil [80].

#### *7.1.4. pH*

pH represents the most potent known predictor of microbial community composition and diversity in the surface soils, with an R2 value of 0.70 when phylotype diversity and pH were examined [81]. Further, soil pH significantly affects soil biochemical properties such as carbon and nutrient availability, fungal and bacterial biomass composition. Changes in microbial community composition and its function and other soil properties directly or indirectly control the cellulose degradation process in the soil.

#### *7.1.5. Lignin content*

Lignin content is one of the most limiting factors in the cellulose degradation process. Lignin constitutes a barrier preventing cellulose degradation due to its close association with cellulose in cell wall [82]. The effect of lignin on the bioavailability of other cell wall components is thought to be essentially a physical restriction, with lignin molecules reducing the surface area available to enzymatic penetration and activity [83,84]. Different factors such as seasonality, management practices, plant physiology, etc., directly or indirectly affect microbial diversity of cellulase and β-glucosidase encoding genes in soil [85,86]. These genes are responsible for producing the enzymes involved in the cellulose degradation; hence, directly or indirectly, changes in their composition or diversity influence or limit the cellulose degradation process in the soil. Although many biotic and abiotic factors significantly limit or regulate cellulose degradation in the soil, little attention has been given to how different factors directly affect or limit cellulose degradation in the soil. So our review studies strongly suggest that new studies should be carried out on factors that limit the cellulose degradation process in the soil.

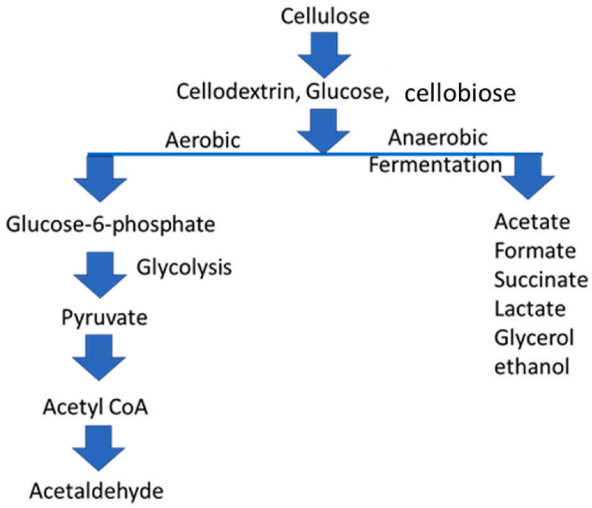


**Fig. 7.** Cellulose degradation pathway.

### *7.2. Cellulose degradation in polluted soils*

Excess amounts of toxic elements or chemicals such as pesticides, herbicides, metals, ammonia, mercury, naphthalene, and many more can cause soil pollution. Over the last decades, there is a high increase in soil pollution that further poses a risk to human and ecological health [87]. The majority of soil contamination is caused by anthropogenic activities, while some contamination occurs naturally in the soil. Soil contaminants are mainly divided into two main groups, organic pollutants (OPs) and inorganic pollutants (IPs). One of the best examples of the latter is the potentially toxic elements (PTEs) [88]. There is a long list of soil contaminants. Still, among them, heavy metals are one of the major soil pollutants because of their non-biodegradable characteristic. Once integrated into the soil, they can persist up to thousands of years [89–91].

Many studies have been done on how different intensity and types of heavy metals affect the soil microbial community and their functions such as mineralization, organic matter decomposition, respiration, etc. [85,92–94]. Rajapaksha (2004) reported that heavy metal toxicity affects the bacterial and fungal community to a different extent, increasing relative fungal/bacterial ratio with increased metal concentration [92]. Wang et al. (2007) studied the effect of heavy metals on the soil biochemical and microbial properties near a copper smelter in China [95]. Studies showed that microbial biomass and enzyme activities, especially phosphatases, were negatively affected by heavy metal stress. Moreover, heavy metal pollution had a significant impact on the bacterial and actinomycetes community. Li et al. (2017) evaluated the response of bacterial and archaea in long-term contaminated soil [96]. They reported that community composition was significantly affected by metal contamination rather than diversity. Further, bacteria showed various changes, while archaea were more tolerant to heavy metals.

Suillus luteusare is a well-known metal-tolerant ecotype of the ectomycorrhizal fungus, frequently found in pioneer pine forests in the Campine region in Belgium metal-polluted soils [94]. Beeck et al. (2015) reported that zinc and cadmium contamination is positively correlated with fungal community composition, while diversity was not affected by pollutants [94]. Additionally, *Suillus luteusare* was dominated fungal in contaminated soil. Although, otherfungal species, such asSistotremasp., Wilcoxina mikolae, and-Cadophora finlandica were also dominated. Extracellular enzymes such as ligninolytic, cellulolytic, and hemicellulolytic enzymes are significantly affected by heavy metal toxicity [85] that lead to changes in the rate of organic matter decomposition and cellulose degradation as well.

Recently, Haddad et al. (2019) reported that heavy metals are one of the most dangerous pollutants to the cellulose decomposing soil microbes [97]. The authors further demonstrated that cadmium and cobalt significantly reduce the growth of cellulose decomposing bacteria and fungi in the soil among different metals. Cadmium was the most potent inhibitor of cellulases and β-glucosidases activities. Moreover, results showed that soil texture and organic matter content are key factors influencing heavy metal stress. The highest stress or effect was observed in the clay soil compared to the sandy soil.

## 8. Cellulase enzyme system

Cellulose degradation is done by aerobic, anaerobic, and facultative anaerobic microorganisms (Fig. 7) [98,99]. The enzyme systems for cellulose degradation by microorganisms are non-complexed or complex [100–102].

### *8.1. Non-complex systems*

In the Non-complex cellulase system, an enzyme secreted by microorganisms is free and able to penetrate the cellulosic substrate. In

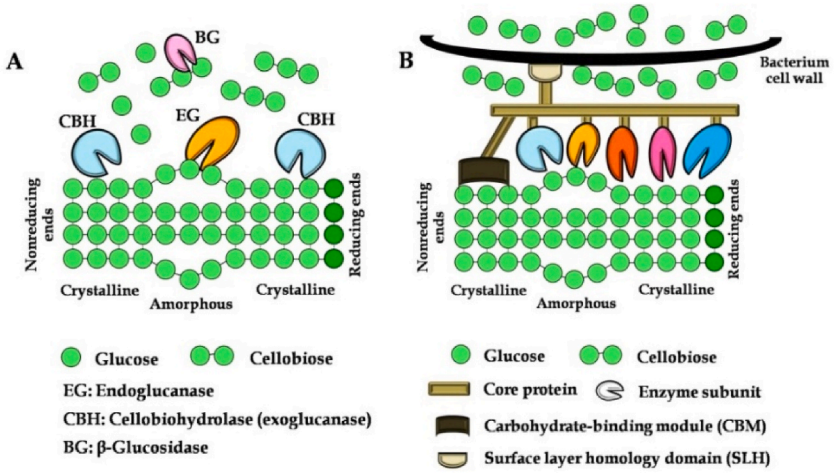


**Fig. 8.** A) Noncomplex system B) complex system [1,103]. Creative commons Attribution license (http://creativecommons.org/licenses/by/3.0).

**Table 4**
List of Anaerobic bacteria producing Cellulosome.

| Bacteria producing cellulosome | |
|---|---|
| *A. cellulolyticus* | *Clostridium saccharoperbutylacetonicum* |
| *Clostridium acetobutylicum* | *Clostridium straminisolvens* |
| *Clostridium alkalicellulosi* | *Clostridium termitidis* |
| *Clostridium bornimense* | *Clostridium thermocellum* |
| *Clostridium cellobioparum* | *Pseudobacteroides cellulosolvens* |
| *C. cellulolyticum* | *Ruminococcus bromii* |
| *Clostridium cellulovorans* | *Ruminococcus champanellensis* |
| *Clostridium josui* | *R. flavefaciens* |

this system, enzymes are easily recovered from the culture medium. The enzyme in this system is not organized on any high molecular weight adsorbing surface hence called a non-complex system. These are generally found in aerobic microorganisms, i.e., both fungi and bacteria. Cellulase from aerobic fungi, e.g.,*T. reesei, T. viride* are most studied [1]. Most aerobic bacteria are found in the soil; hence, the non-complex cellulase system is more common in soil than the complex system (Fig. 8a).

### *8.2. Complex system*

A complex system of cellulose degradation is followed by several anaerobic cellulolytic microorganisms. In this system, the cellulolytic enzyme is tightly bound to a protein structure scaffolding, which is a part of more complex macromolecular complexes termed cellulosomes [104,105]. Other than cellulases, this macromolecule can also accommodate other enzymes, hemicellulases, and pectinases [106,107]. These complexes are very stable, so they completely disassociate into an individual component. The complete dissociation of all known bacterial cellulosomes into individual components requires hard treatments, such as elevated temperatures and the presence of chaotropic agents, thus reflecting the strength of the cohesin-dockerin interaction (Fig. 8b).

## 9. Cellulosome

In the early 1980s, Bayer and Lamed first discover cellulosome in a thermophilic cellulolytic anaerobic bacterium *Clostridium thermocellum* [108,109]. Further cellulosomes have been described subsequently for a variety of anaerobic bacteria [110–112]. Anaerobic bacteria producing cellulosome listed in Table 4. Much of our knowledge about cellulosome, like its architecture, and mechanism of action, has been derived from *Clostridium thermocellum*. Cellulosome is a multienzyme complex structure usually produced by cellulolytic microorganisms, especially anaerobic bacteria. They are designed for efficient degradation of lignocellulosic biomass, notable cellulose [38,39,110,113].

Structure of *C.thermocellum* CipA scaffoldin CohI9–X-DocII trimodular fragment in complex with the SdbA CohII module [Adam et al., 2010].

Cellulosome comprises two major subunits: long flexible scaffoldin, which forms the center part containing specific binding sites cohesions, and the enzymes containing a dockerin module that binds to cohesion. Two different types of cellulosome systems are present in bacteria [114,115]. A simple system with a single cellulosome unit and a complex system combining more than one cellulosome unit with multiple types of interacting scaffoldins. Self-assembly of cellulosome complex is possible because of a high degree

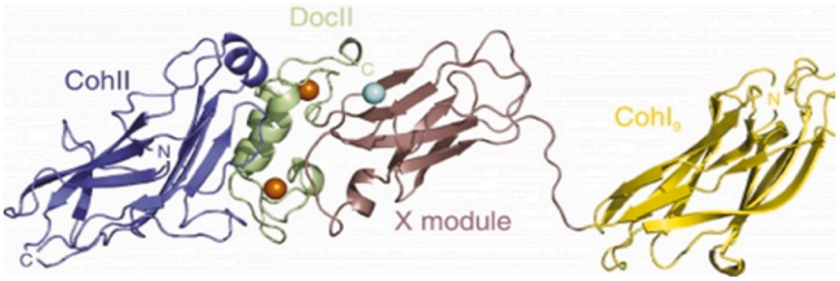


**Fig. 9.** shows below the 3D structure of Cellulosome (C. *thermocellu*m).

**Table 5**
Components of the cellulosome of *Clostridium thermocellum.*

| Cellulosome components | Description | Cellulosome components | Description |
|---|---|---|---|
| CipA (c) | Scaffoldin | XynA, XynU | Xylanase |
| CelJ | Cellulase | CelD | Endoglucanase |
| CbhA | Cellobiohydrolase | XynC | Xylanase |
| XynY | Xylanase | XynD | Xylanase |
| CelH | Endoglucanase | ManA | Mannanase |
| CelK | Cellobiohydrolase | CelT | Endoglucanase |
| XynZ | Xylanase | CelB | Endoglucanase |
| CelE | Endoglucanase | CelG | Endoglucanase |
| CelS (c) | Exoglucanase | CseP | Unknown |
| CelF | Endoglucanase | ChiA | Chitinase |
| CelN | Endoglucanase | CelA | Endoglucanase |
| CelQ | Endoglucanase | XynB, XynV | Xylanase |
| CelO | Cellobiohydrolase | LicB | Lichenase |

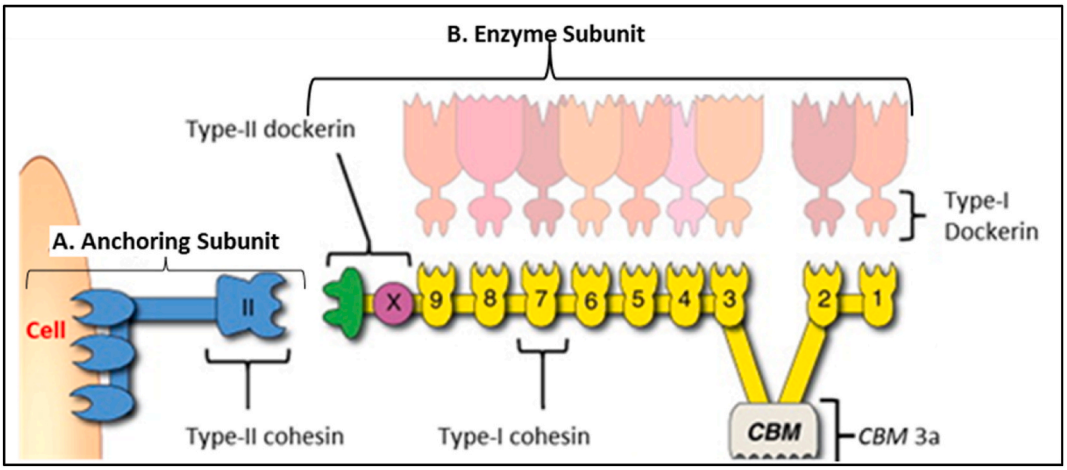


**Fig. 10.** Mechanism of Cellulosome. Organization of *Clostridium thermocellum* cellulases in cellulosomes. **Panel A (Anchoring Subunit):** The anchoring subunit on one side adhere to the cell surface peptidoglycans through their S-layer homology (SLH) domains. On other side of anchoring subunit, The type-II cohesin module (labeled II in blue colour) forms a non-covalent bond with type-II dockerin modules (Green Colour), securing the scaffoldin and its enzyme complement to the bacterial cell surface. **Panel B (Enzyme Subunit):** A central scaffold subunit comprises nine type-I cohesins, a family 3 cellulose-specific carbohydrate-binding module (CBM), an X module (pink), and a C-terminal type-II dockerin module (green) [121]. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

of affinity and recognition among specific cohesion and enzyme-borne dockerin modules [33,116]. Series of the enzyme on cellulosome provide synergistic action on crystalline substrate difficult to degrade and make it easy to degrade compared to free form. In this way, the anchoring of various cellulolytic enzymes, i.e., endoglucanases, cellobiohydrolases, xylanases, to a scaffoldin makes it a complex structure in which different enzymes work synergistically to attack heterogeneous, insoluble cellulose substrates [117,118]. Likewise, different cellulosomes are attached to common scaffoldins to form a more complex structure. The assembly of enzyme components into the cellulosome complex is governed by the cohesin-dockerin interaction (Fig. 9).

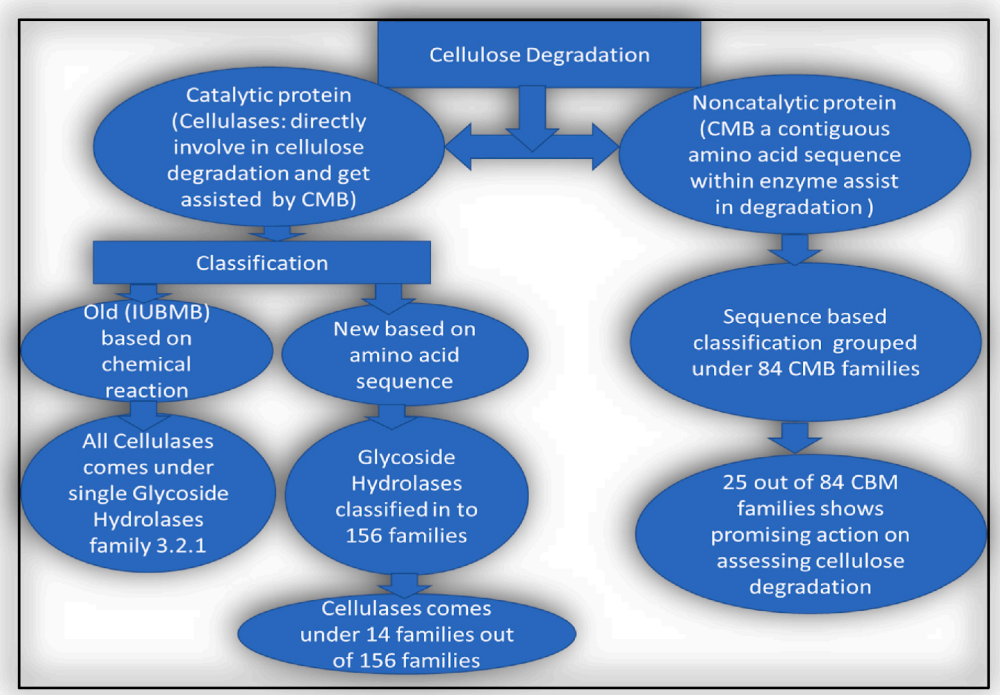


**Fig. 11.** Overview of cellulase classification.

### 9.1. *Cellulosome assembly*

Cellulosome is a multi-cellulolytic enzyme complex where different cellulytic enzymes are attached to a common scaffold in subunit through dockerin cohesion interaction, like a lock and key. Mechanism of construction of cellulosome is of great biological interest to biotechnologist, Nano biologist, with this knowledge can play a significant role in the construction of industrially significant nanomachines. Most of the studies on the mechanism of cellulosome assembly have been done on clostridia, primarily C. *thermocellum* (Table 4.). However, structural information on the components that mediate the assembly of non-clostridial cellulosomes is rapidly emerging (Table 5).

### 9.2. *Dock*

#### 9.2.1. *Dockerin*

Dockerin is an amino acid sequence that anchors the catalytic enzymes to the scaffoldin. One end of dockerin is attached to the enzyme, and another end is attached to scaffoldin. Sometimes carbohydrate-binding module (CBM) is also present between dockerin and scaffoldin. An adequate amount of Calcium ions is necessary for the structure and function of dockerin [119]. The sensitivity of dockerin to interact cohesions decreases to zero in the absence of calcium ions [120]. The dockerin can also be found in the C- terminus of scaffoldins (Fig. 10).

#### 9.2.2. *Scaffoldin subunit*

Scaffoldin is the center part of the cellulosome where different cellulolytic enzymes and carbohydrate-binding modules (CBM) are attached to it through dockerin. Scaffoldin is non-enzymatic, and it serves as a backbone of the cellulosome. Doctrine cohesion to scaffoldin is specific. Various cellulolytic enzymes are arranged similarly as their respective portions are added on the scaffoldion to interact with dockrin attached to the enzyme (Fig. 10).

#### 9.2.3. *Cohesin modules*

A repeating unit of cohesion is present on the scaffolding. Usually, more than four cohesion modules are present on scaffoldin, but its number may go up to eleven. Each cohesin binds a single dockerin domain located on the enzymes (Fig. 10).

#### 9.2.4. *Catalytic subunits*

It contains dockerin modules that serve to incorporate catalytic modules into the cellulosome complex. These catalytic modules

include polysaccharide lyases, glycoside hydrolases, and carboxylesterases (5, 6, 7) (Fig. 10).

## 10. CAZy conversion of novel sequence-based classification of cellulases

According to the Old International Union Of Biochemistry And Molecular Biology (IUBMB) system of nomenclature, Glycoside hydrolases (3.2.1) are a larger group of enzymes that hydrolyze glycosidic bonds between two carbohydrate molecules or carbohydrate and non-carbohydrate moiety [122,123] (Fig. 11). Cellulase enzyme comes under the family of glycoside hydrolases. IUBMB system of enzyme nomenclature is based on substrate specificity and occasionally on their molecular mechanism. While the new sequence-based classification is based on the structural features of enzyme and amino acid sequencing. CAZy database is dedicated to carbohydrate-active enzymes database, which describes the families of structurally related catalytic and carbohydrate-binding modules (or functional domains) of enzymes that degrade, modify, or create glycosidic bonds [124].Based on the available literature, functional and 3D structural information is added and curated regularly in the CAZy database [124].

In combination with catalytic activity estimation by sequence comparison, genome sequencing led to a revolution in cellulose degradation and gave birth to novel sequence-based enzyme classification. In a new conversion of classification, glycoside hydrolases EC 3.2.1 group is widespread into 156 families. Among 156 families, a limited number of families contain cellulolytic enzymes; these families are GH5, GH6, Gh7, GH8, GH9, GH10, GH12, GH26, GH44, GH45, GH48, GH51, GH61, GH74, GH124. Cellulases often harbor a carbohydrate-binding module (CBM), whereas cellulases with oxidoreductive catalytic modules are classified as the auxiliary activity (AA) family of proteins [86]. Even if the proteins within each family share structural properties, they have different evolutionary history and do not always share substrate specificities [66].

Family GH5 and GH9 appear to have the largest number of biochemically characterized cellulases [125]. GH5 is one of the largest CAZy-GH families and was previously known as cellulose family A [126,127]. Genes coding GH5 family enzymes are extensively distributed in Archaea, bacteria, and eukaryotes, notably fungi and plants. Zhao et al. (2013) carried out a comparative analysis of 103 representative fungi of different fungal phylum such as Ascomycota, Basidiomycota, Chytridiomycota, and Zygomycota and showed that the genome of all fungi contain GH5 genes, whereas genes of GH6, 7, 9, 12, 45 and AA9 are only present in a certain type of fungi [128]. This suggests the importance and uniqueness of the GH5 family enzyme in plant–cell- wall deconstruction and cellulose degradation [129]. GH 9 is one of the first GH family classified by hydrophobic cluster analysis and was once known as cellulose family E [126]. Encoding genes from the GH9 family are widespread among cellulolytic microorganisms (except aerobic fungi) and plants but are particularly abundant in anaerobic bacteria producing cellulosomes [130]. The GH61 family has been reclassified by CAZy into a new Auxiliary Activity Family 9 (AA9 class). The AA9 group is copper-dependent oxidative enzyme acting on crystalline cellulose. The activity of this group largely depends on the presence of a divalent copper ion in the core of the enzyme. To date, the AA9 class comprises approximately 448 members.

### *10.1. Carbohydrate-binding module (CMB)*

CBM is a specific sequence of amino acids present within the enzyme (GH). They are polysaccharide-recognizing modules of glycoside hydrolases enzyme. Initially, CMB was believed to bind to the cellulose molecule and were originally classified as CBDs (cellulose-binding domains), based on the initial discovery of several modules that bound cellulose [131]. Later CBM was discovered in a wide variety of GH enzymes other than cellulase; therefore, the group was reclassified with a more inclusive term Carbohydrate-Binding module (CMB). CAZy further classifies CBM into 84 families based on the amino acid sequence. From the name, it is apparent that not all the CMB shows cellulose-binding properties. Within CAZy only limited number of CBM families have member that can bind to cellulose; these families include CBM1, CBM2, CBM3, CBM4, CBM5, CBM6, CBM8, CBM10, CBM11, CBM17, CBM28, CBM30, CBM32, CBM35, CBM44, CBM46, CBM49, CBM63, CBM64, CBM65, CBM72, CBM76, CBM78, CBM80, and CBM81. The main role of CBM is to attach and bind the enzyme to the substrate, increase enzyme concentrations on the surface of cellulose, and quick disruption of polysaccharides [132,133].

Among all CBM families, CBM family 3 is most distinctive, diverse, and robust. CBM3s are various components of cellulases and cellulosomes that can bind firmly to crystalline cellulose. Thus CBM3s have high substrate binding capacity and play an important role in cellulose degradation [134]. Moreover, all CBM3 subfamilies consist of the shallow grove, irrespective of loss or alteration of cellulose-binding function. The role of these highly conserved shallow groves is currently unknown [134]. While CBM has been considered an essential part of cellulases, a few genomic studies of cellulose-degrading organisms showed that many of them encoded with cellulases lacking CBMs in their sequences [135]. Some present studies showed that CBMs are not necessary for cellulases' action and solely increase the concentration of enzymes on the substrate surfaces [134]. Várnai et al. (2013) reported that water content might play an important role in the evolution of various substrate-binding structures [134]. Moreover, omitting the addition of CBMs could potentially aid in solving the bottlenecks of enzymatic hydrolysis of lignocelluloses and speed up the commercialization of second-generation bioethanol [134].

## 11. Lytic polysaccharide monooxygenases (LPMOs): recent advances in cellulose degradation

In the past, cellulose degradation by the action of different cellulolytic enzymes was believed to be dependent on the synergistic activity of hydrolytic and oxidative enzymes. These classical enzymes cause slow degradation of cellulose due to the physiochemically recalcitrant and insoluble nature of cellulose. Recent work has proven that lytic polysaccharide monooxygenases (LPMOs) boost other hydrolytic and oxidative cellulolytic enzymes. Hence, it plays a vital role in cellulose degradation [136–139]. The LPMO itself is a

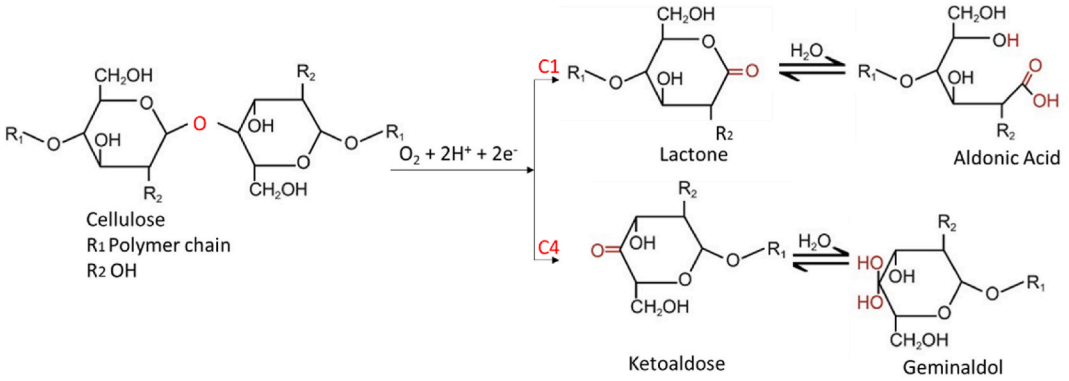


**Fig. 12.** LPMO mediated C1 and C4 oxidation of cellulose.

non-hydrolytic protein; they first notch the cellulose fiber to accelerate the action of endoglucanase. LPMO assisted cellulose hydrolysis by cellulolytic enzyme overcomes the drawbacks like slow rate of degradation and low yields.

LPMO was originally discovered for its activity on chitin [138,140].Lytic polysaccharide monooxygenase (LPMO) is a mononuclear type II copper-dependent enzyme, showed by Quinlan in 2011 [138,139,141,142]. The position of Cu molecule within LPMOs has recently been discussed by Vu et al., in 2018 [143]. LPMO catalytic activity was first proposed by Vaaje-Kolstad et al. (2010) [138] for an AA10 protein (CBP21) acting on chitin. Active sites are present near the center of lytic polysaccharide monooxygenase enzymes molecule. Catalytic metal is exposed outward and has a flat protein face. LPMO assisted cellulose degradation is a unique process that initiates with C–H activation followed by $O_2$-dependent chain cleavage [140,144–146]. Different types of LMPO may act differently by oxidation of C1 or C4 of Glycosidic bond present in cellobiose moiety (Fig. 12).

LMPO works as a redox enzyme, and it has been shown that a single oxygen atom introduced at C1 originates from molecular $O_2$. The process is assisted by LPMOs, as suggested by Vaaje et al. (2010) [138]. It is important to note that the influence of redox chemistry in the degradation of lignocellulose biomass has been identified 40 years before when Vaaje first proposed LPMO catalytic activity. Recent studies prove that LPMOs can also use hydrogen peroxide as a source of oxygen despite molecular oxygen [147].

New discoveries motivated CAZy to reclassify LPMOs into new Auxiliary Activity Family (AAs) along with other lignocellulose-acting redox enzymes [148]. GH61 was renamed AA9, CBM33 was renamed AA10, and families AA11, AA13, AA14, and AA15. Sequence base classification further subclassify AA9 into type 1 (C1-oxidizing), type 2 (C4-oxidizing). To date, the AA9 class comprises approximately 448 members.

## 12. Conclusion

In conclusion, cellulose degradation research has seen significant developments in the past decade, with a focus on eco-friendly and efficient processes. The discovery of CBM and Cellulosome has been a milestone in the cellulose degradation process. Fungal solid-state fermentation has emerged as a viable alternative to submerged fermentation. The soil microbial community plays a crucial role in cellulose degradation, and it is sensitive to various biotic and abiotic factors. Future work should focus on linking soil microbial community and their functions under different conditions, particularly in cellulose degradation. With new advanced technology, research in this area can lead to significant advancements in the development of sustainable and eco-friendly cellulose degradation processes.

## CRediT authorship contribution statement

**Rahul Datta:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing - original draft, Writing - review & editing.

## Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Rahul Datta reports financial support was provided by Mendel University in Brno. Rahul Datta reports a relationship with Mendel University in Brno that includes: employment. Rahul Datta has patent pending to n/a. no other relationship to declare.

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