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CELLULOLYTIC ACTIVITY IN MICROORGANISMS

Raj Singh*, Anju Rani*, Permod Kumar*, Gyanika Shukla, Amit Kumar****

Author's Affiliation: *Department of Botany, K.V. Faculty of Science, Swami Vivekanand Subharti University, Meerut, UP, India. **Department of Biotechnology, K.V. Faculty of Science, Swami Vivekanand Subharti University, Meerut, UP, India.

Corresponding Author: Raj Singh
Department of Botany, K.V. Faculty of Science, Swami Vivekanand Subharti University, Meerut, UP, India.
Email- dr.rajsingh09@gmail.com
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Abstract

Cellulose is the most abundant polysaccharide occurring in plant materials. The cellulose content of higher plant is never fixed and the concentration changes with the age and type of the plant. It is specially predominant in woody substances as well as in straw, stubble and leaves. Cellulose molecules are linear polymers (unbranched long chains) of β-D-glucopyranose residues linked by β(1, 4)-glycosidic bonds. The residues in the cellulose chain are stabilized by hydrogen bonds between hydroxyl groups of adjacent glucose residues. Cellulose is soluble in acids but insoluble in alkaline solutions. Cellulose-decomposing microorganisms are found abundantly in nature. Due to cellulolytic potential these play an important role in the carbon cycle by recycling CO_2 fixed through photosynthesis. Cellulose-decomposing microbes include a variety of aerobes and anaerobes; mesophiles as well as thermophiles. Fungi and bacteria, however, are mainly responsible for cellulose degradation in nature. The details of the mechanism involved in the breakdown of cellulose have been the subject of investigation for a long time. As per currently accepted three-enzyme group hypothesis, the complete degradation of native cellulose to glucose requires three enzymes - (a) endo-β-1, 4-glucanase (EG) or cellulase (CEL, EC 3.2.1.4); (b) Cellobiohydrolase (CBH, or exo-glucanase, EC 3.2.1.91) and (c) β-glucosidase (BG, EC 3.2.1.21). EG first hydrolyses amorphous regions of cellulose fibrils. The non-reducing ends thus generated are then attacked by CBH thereby releasing cellobiose. The action of CBH then proceeds into the crystalline region. BG hydrolyses cellobiose to glucose. These enzymes work synergistically to hydrolyse cellulose..The cellulolytic activity of microbes is greatly affected by different factor *viz*. availability of nutrients, optimum pH, temperature and moisture contents have been found to be a major controlling factor in the production of cellulolytic enzymes.

Keywords: Cellulolytic activity, cellulases, cellulose, cellobiose, glucose, Microorganisms.

INTRODUCTION

Cellulose is the most abundant natural product on Earth. It is also the most abundant polysaccharide occurring in plant materials constituting about one-third of annual plants and one-half of perennial plants (Teng and Whistler, 1973). Plants synthesis about $4x10^9$ tons of cellulose annually (Coughlan, 1990). According to Whittaker (1970), cellulose constitutes about 40% or more of the total biomass present on earth. The cellulose content of higher plant is never fixed and the concentration changes with the age and type of the plant. It is specially predominant in woody substances as well as in straw, stubble and leaves. Wheat straw has been reported to contain upto 54.89% cellulose Charaya and Singh (2005); Singh *et al.(*2015). It is localized in the cell walls of plants where it occurs in close association with other substances like hemicelluloses, lignin, pectin and other polysaccharides (Norman, 1954). It is produced, in addition to higher plants, by algae, certain bacteria, marine invertebrates, fungi, slime molds and amoeba also (Richmond, 1991). However, majority of cellulose is produced as a component of plant cell walls (Tomme *et al.,* 1995).

Chemically, cellulose molecules are linear polymers (unbranched long chains) of β-D-glucopyranose residues linked by β (1, 4)-glycosidic bonds. These chains are called elementary fibrils and have a diameter of 35A. Each glucose residue is rotated 180° relative to its neighbouring molecule. Thus, the basic repeat unit is cellobiose. The residues in the cellulose chain are stabilized by hydrogen bonds between hydroxyl groups of adjacent glucose residues. These β-1, 4-D-glucan chains do not occur singly in nature. These are aligned parallel to each other to form microfibrils through hydrogen bonds between hydroxyl groups at OH-6 and OH-3 of adjacent chains. The number of glucan chains in each microfibril varies from about 36 to 200 depending upon the plant species. Inspite of different opinions regarding the structure of microfibrils (Hess *et al*., 1954; Preston and Cronshaw, 1958; Manley, 1964), it is now established that while in some parts of microfibrils, the glucan chains are arranged in an orderly fashion so that the structure is crystalline, in other parts the arrangement is less orderly so that in these regions the crystalline structure is lost (amorphous regions). In secondary cell wall, several microfibrils are joined laterally to form a macrofibril. In the primary cell wall, the microfibrils are arranged transverse to the cell axis; but in the fully developed cell wall, most of the microfibrils are in parallel arrangement. The microfibrils are usually embedded in a matrix of hemicelluloses and lignin. Cellulose is soluble in acids but insoluble in alkaline solutions. Delmer (1987), Delmer and Amor (1995), and Brett (2000) have reviewed various aspects of biosynthesis and structure of cellulose.

Cellulose-decomposing microorganisms are found abundantly in nature. These play an important role in the carbon cycle by recycling CO_2 fixed through photosynthesis. It is possible that some cellulose genes were actually borrowed by the microbes from the plants in which these appear to play a role in morphogenesis and developmental processes (Beguin and Aubert, 1994).

CELLULOSE DECOMPOSERS

Cellulose-decomposing microbes include a variety of aerobes and anaerobes; mesophiles as well as thermophiles. Fungi and bacteria, however, are mainly responsible for cellulose degradation in nature. Hopper Seylen (1883) was probably the first person to have studied the biological degradation of cellulose. In fact, this process was considered to be the domain of bacteria till de Bary (1886) found that cellulose could be decomposed by a fungus, *Peziza libertiana*. Later on, this was found to be true for a number of other fungi by Ward (1888-89, 1898), von Iterson (1904), Appel (1906), Christensen (1910), Carbone (1910), McBeth and Scales (1913) and Scales (1915). Went (1901) and Koning (1904) believed that the fungi release `cytase' (also called cellulase)

which makes cellulose available as a food to these. Since then, numerous reports have appeared on the cellulolytic ability of a large number of fungi (Coughlan, 1985;El-said,2001;Berlin *et al*.,2005; Elango and Divakaran,(2009. Gautam *et al.,*2010;Sherief *at al*.,2010;Gautal *et at*.2010;Wilson,2011;Rahman *et al.,*2011;Singh *et al.,*2015(a);Singh *et al.*2015(b,c,d). As for distribution, cellulolytic fungi are mainly concentrated among Deuteromycotina, Ascomycotina and Basidiomycotina. Outside these groups, only a few genera belonging to Chytridiales (Whiffen, 1945; Crasemann, 1954), Saprolegniales (Bhargava, 1943; Saksena and Bose, 1944; Mullins, 1973) and the Peronosporales (Mehrotra, 1949) have been reported to have cellulolytic activity. In fact, efficient enzyme systems capable of significant hydrolysis of crystalline cellulose have been isolated mainly from the genera of filamentous fungi (Teeri *et al.,* 1992;Ezekiel *et al*.,2010;Siddiqui *et al*.,2000).

MECHANISM OF CELLULOSE DECOMPOSITION

The details of the mechanism involved in the breakdown of cellulose have been the subject of investigation for a long time. Pringsheim (1912) set forth the "classical theory" for this. He showed that cellulolytic bacteria produced two products during degradation : glucose and cellobiose. He postulated that one enzyme (cellulase) cleaved cellobiose from cellulose, while a second enzyme (cellobiase) split the cellobiose into two glucose molecules. By 1940, the enzymatic cellulose decomposition was believed to be a hydrolytic process, which required at least two enzymes. It was suspected that one of these enzymes—the classic `cellulase'—had an affinity with long chains of glucose (Grassmann *et al.,* 1933). A large number of investigations were then carried out which led to the development of concept on two lines.

One group (Whitaker, 1953; Whitaker *et al.,* 1954) were able to isolate and purify by electrophoresis a single enzyme (mol. wt. 63,000) which could hydrolyze cellulose to glucose; they concluded that although cellobiose may be formed during the process, it does not necessarily act as an intermediate. Aitken *et al.* (1956) also put forward the opinion that a single enzyme converts cellulose to cellobiose, but they considered that cellobiose is necessary for the production of glucose. There is ample evidence that some wood-rotting fungi including *Collybia velutipes* and *Polyporus annosus* require a β-glucosidase in addition to cellulase to degrade cellulose to glucose (Norkrans, 1957). Thus, the possible scheme according to them is:

$$\text{Native Cellulose} \xrightarrow{\text{Cellulase}} \text{Cellobiose} \xrightarrow{\beta\text{ - glucosidase}} \text{Glucose}$$

On the other hand, in early 1950s Reese and coworkers (Reese *et al.,* 1950; Reese and Levinson, 1952; Reese, 1956) noticed that a large number of organisms are capable of hydrolyzing the soluble cellulose derivative, carboxymethyl cellulose, but relatively few are capable of efficiently hydrolyzing native crystalline cellulose. They concluded that "cellulase" systems are made up of a complex of enzymes C_1, C_X and P-glucosidase (Reese, 1963). The Ci enzyme was postulated to act on native cellulose by destroying its crystalline structure and exposing the glucan chains and, thus, making it susceptible to hydrolytic C_X enzymes, which degrade the glucan chain to cellobiose (Reese, 1956). Conversion of cellobiose to glucose also required a cellobiase or β-glucosidase. The C_1 enzyme was a nonhydrolytic one which initiated the degradation of native cellulose by breaking the hydrogen bonds between cellulose chains.Throughout the 1950's and 1960's, investigators worked to purify and characterize the C_1 and C_X enzymes (Wood, 1960; Li *et al.,* 1965; Selby and Maitland, 1967; Eriksson and Rzedowski, 1969). All these studies supported the view of Reese *et al.* (1950) that "cellulase" enzyme complex is made up of more than one enzyme.

As per currently accepted three-enzyme group hypothesis, the complete degradation of native cellulose to glucose requires three enzymes (Huang, 2001)—(a) endo-β-1, 4-glucanase (EG) or cellulase (CEL, EC 3.2.1.4); (b) Cellobiohydrolase (CBH, or exo-glucanase, EC 3.2.1.91) and (c) β-glucosidase (BG, EC 3.2.1.21). EG first hydrolyses amorphous regions of cellulose fibrils. The non-reducing ends thus generated are then attacked by CBH thereby releasing cellobiose. The action of CBH then proceeds into the crystalline region. BG hydrolyses cellobiose to glucose. These enzymes work synergistically to hydrolyse cellulose. Three types of synergism have been identified : (a) Endo-exo synergism in which EG, by random action, generates more chain ends for CBH (Exo) to attack; (b) Exo-exo synergism which refers to the effects of two exo-acting enzymes acting in concert e.g., in *Trichoderma reesei* cellulase system where CBH I and CBH II act synergistically. CBH I attacks the reducing ends of the chain while CBH II attacks the non-reducing ends of the cellulose chain (Barr *et al.,* 1996; Medve *et al.,* 1998); (c) Intramolecular synergism which refers to the relative activities of adsorbed or non-adsorbed enzymes and the extent of adsorption of catalytic and cellulose binding domains (CBD) separately. In fact, the majority of cellulolytic enzymes are modular proteins with two distinct independent domains (Gilkes *et al.,* 1991). The first domain is responsible for the hydrolysis of cellulose chain. The second domain is cellulose-binding domain (CBD) which is responsible for increasing adsorption of cellulolytic enzymes onto insoluble cellulose as well as affecting cellulose structure by helping in the reduction of particle size and increasing specific surface area. Din *et al.* (1994) found that the catalytic domain has a lower rate of hydrolysis when seperated from the cellulose-binding domain.

Overall, CBH's are one of the most important cellulolytic enzyme groups because CBH I makes up 60% of the protein mass of the cellulolytic system in *Trichoderma reesei.* (Abuja *et al.,* 1988) and its absence adversely affects the cellulase activity on crystalline cellulose by 70% (Divine *et al.,* 1994). Van Tilbeurgh (1986) demonstrated that CBH I of *Trichoderma reesei* contains two functional domains. The C-terminal glycopeptide (10 KDA) acts as a binding domain for insoluble cellulose whereas the core protein (55 KDA) contains the hydrolytic active site. X-rays scattering studies have revealed that the CBH's and EG's are tadpole-shaped—the catalytic core froming the head and wedge shape CBD at the tip of the tail (Abuja *et al.,* 1988; Rouvinen *et al.,* 1990 and Kleywegt *et al.,* 1997). The major portion of the tail is made up of a flexible, heavily-o-glycosylated linker region about 32-44 amino acids long, rich in protein, glycine, serine and threonine (Srisodusk *et al.,* 1993).

High resolution electron density mapping of CBH I (Divine *et al.,* 1994) and CBH II (Rouvinen *et al.,* 1990) has led to the development of a hypothesis to explain the activity of these enzymes (Mosier *et al.,* 1999). In CBH I, two large anti-parallel β-sheets which stack face to face occupy about one-third of this 434-residue domain. The two highly curved 13-sheets form a 40 A long flattened cylindrical tunnel which accomodates the cellulose chain with 7 glycosyl binding sites of similar aromatic residue structure. Though the catalytic core of CBH II does not have this 13-sandwich, a similar tunnel structure is formed by several long alpha helices with four similar glycosyl binding sites (Rouvinen *et al.,* 1990). However, in both CBH I and in CBH II, two acidic residues lie near the second glycosyl bond of a bound cellulose chain-one above and one below the glycosyl bond, one residue acting as a proton donor and the other acting as a nucleophile (McCarter and Withers, 1994). As a result of the cleavage of this bond, cellobiose is freed which then leaves the end of the tunnel. Thus, the enzyme remains bound to the cellulose chain while the product is released. The enzyme then progresses along the cellulose chain-CBH I proceeds towards the non-reducing ends, and CBH II proceeds towards the reducing end of the cellulose chain (Davies and Henrisaat, 1995). This mechanism explains why only cellobiose, not glucose or cellotriose or any other oligosaccharide, is produced.

Endoglucanases also have similar structure and function (like CBH). Of course, a large variety of hydrolysis products are produced. X-ray diffraction studies by Kleywegt *et al.* (1997) have confirmed the earlier belief that endo-glucanases attack by random scission of amorphous cellulose. The overall molecular architecture of EG I is very similar to CBH, the major difference being in the catalytic domain—the tunnel-forming loops are missing in EG I, resulting in an open left active site leading to less restriction in the binding of cellulose. Thus, many different hydrolytic products are formed (like glucose, cellobiose, cellotriose etc.)

The cellulose-binding domains of cellulase are highly conserved, and have been grouped into 3 families on the basis of sequence homology. Family I CBD's are found in fungi while family II and III are bacterial. Family I CBD's consist of 35 amino acids. The amino acids most likely responsible for binding are three aromatic residues (two tyrosinses and one tryptophan), and a combination of two polar residues (proline, glutamine and asparagine). These groups are arranged on two 13-sheets so that the aromatic residues may bind to the face of the sugars and the polar residues lie above the interglycosal bonds and hydroxyl group of the cellulose chain.
The independent catalytic core is bound to the CBD by a linker region, 6 to 59 amino acid residues long and rich in proline and hydroxyl amino acids (Gilkes *et al.,* 1991). It is believed that it effectively separates the catalytic core from the CBD so that they can function independently.
There have been conflicting reports about the relationship between the production of cellulolytic enzymes and colonization by fungi of plant debris. White *et al.* (1949) found that *Memnoniella echinata*, though an active cellulose-decomposer, is not a dominant colonizer on plant debris, such as leaves, stem etc. On the other hand, species of *Trichoderma and Penicillium* which are good colonizers are not active decomposers of cellulose. According to Kendrick and Burges (1962), these species are dominant colonizers due to their high spore potential. But Garrett (1975) found that the straw penetration rate by foot-rot fungi is closely related with cellulolytic rate. Jain (1989) also found a strong positive correlation between cellulolytic activity and rate of decomposition.

FACTORS AFFECTING CELLULOLYTIC ACTIVITY

Fungi differ greatly in their ability to utilize different forms of nitrogen as nutrient and the nature of nitrogen source is known to affect the production of cellulase. Cellulolytic fungi have been reported to prefer inorganic nitrogen in the form of ammonium salts or nitrates (Gascoigne and Gascoigne, 1960; Greathouse and Ames, 1945; Hirsch, 1954; Talboys, 1958; Verma and Verma, 1962; Rangaswami and Rajasekaran, 1965; Gupta and Kohli, 1967; Umezurike, 1970).

The addition of nitrogen and single super phosphate increased the decomposition of wheat crop residue by *Trichoderma lignorum* and *Stachybotrys atra.* (Singh and Charaya, 2010; Singh *et al.*2015) respectively. Inoculation of sugarcane trash with consortium of decomposer fungi and nitrogen-fixing bacteria was found to accelerate decomposition of the residues by Beary *et al.* (2002).

Magan and Lynch (1986) found that the activity of *Trichoderma* spp., *Gliocladium* spp. and *Chaetomium globosum* also decreased with decreasing water potential. The hydrogen ion concentration is also one of the most important factors influencing the secretion of enzymes. Whitaker (1953) indicated that no cellulase was produced in a medium beyond 5.0-8.0 pH range. Reese and Gilligan (1953) showed that the production of cellulase was markedly affected by the variation of hydrogen-ion concentration in the medium. The optimum pH values for the production of cellulases by most of the fungi are largely between 4.0 and 7.0 (Thomas, 1956; Venkataram, 1956; Husain and Dimond, 1958; Seo, 1959; Sehgal and Agarwal, 1964; Deschamps *et al.,* 1985; Maheshwari *et al.,* 1990). The optimum pH value varies widely for activity of cellulases secreted by various fungi and it lies within a range of 3.0-8.0 (Thomas, 1956; Sison *et al.,* 1958; Mandels and Reese, 1963; Spalding, 1963). The optimum temperature for the maximum secretion of the enzymes is believed to vary with different fungal species, inactivation taking place at high

temperatures (Saunders et al., 1948; Thomas, 1956; Sison *et al.,* 1958; Bateman, 1968; Gupta and Kohli, 1967).

CONCLUSION

Cellulose is the most abundant natural product found on the Earth. Plants synthesis about $4x10^9$ tons of cellulose annually. If this huge amount accumulated year by year on the earth, it creates a big problem on the earth as it occupies all the space. To overcome this problem microorganism play a very significant role, as they have cellulolytic potential, convert the cellulose into simpler form- Glucose, cellobiose, nutrients and CO_2. By the cellulolytic potential of microorganism fertility of soil increased and CO_2 released, utilized by green plants by photosynthesis.

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