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Microbial diversity of cellulose hydrolysis

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Enzymatic hydrolysis of cellulose by microorganisms is a key step in the global carbon cycle. Despite its abundance only a small percentage of microorganisms can degrade cellulose, probably because it is present in recalcitrant cell walls. There are at least five distinct mechanisms used by different microorganisms to degrade cellulose all of which involve cellulases. Cellulolytic organisms and cellulases are extremely diverse possibly because their natural substrates, plant cell walls, are very diverse. At this time the microbial ecology of cellulose degradation in any environment is still not clearly understood even though there is a great deal of information available about the bovine rumen. Two major problems that limit our understanding of this area are the vast diversity of organisms present in most cellulose degrading environments and the inability to culture most of them.

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Introduction

A key step in the global carbon cycle is the hydrolysis of the cellulose in plant cell walls, which is the most abundant source of carbon on land [1]. The half-life of cellulose at neutral pH in the absence of enzymes is estimated to be several million years so that microbial activity is responsible for most of the turnover of the carbon in cellulose although fire also plays a role [2]. Originally it was thought that only microorganisms produced cellulases but it is now clear that some insects, mollusks, nematodes, and protozoa also produce cellulases [3•]. Even when ruminants, shipworms or termites utilize cellulose as an energy source, microorganisms usually are involved in its degradation [4–6]. In the case of ruminants, all of their cellulose hydrolysis is carried out by anaerobic rumen bacteria, fungi, or protozoa, though for some termites both microbial enzymes and termite enzymes are utilized for cellulose hydrolysis.

Since cellulose is mostly present in plant cell walls, which are very difficult to degrade, only a small fraction of all microorganisms that are specialized for plant cell wall degradation can hydrolyze cellulose [7]. Since bacteria and fungi are unable to engulf particles, these organisms need to secrete their cellulases and most anaerobic bacteria that produce cellulosomes attach them to their outer surface. Because of the recalcitrance of plant cell walls some cellulolytic microorganisms secrete up to 50% of their total protein during growth on biomass or cellulose.

Cellulases

There are several different mechanisms that are used by cellulolytic microorganisms to degrade cellulose, although cellulases are used in all of them [8]. Cellulases are the most diverse enzymes that catalyze a single reaction, which is hydrolysis of the β-1,4 linkage joining two glucose molecules in a cellulose molecule. There are at least eleven cellulase families based on the similarities of their amino acid sequence and structural studies of the different families show that cellulases have eight different protein folds [9•]. The diversity of cellulases may result from the extreme diversity of their natural substrates, plant cell walls. Individual cellulases have very low activity on crystalline cellulose but they have a very high catalytic enhancement due to the very long half-life of crystalline cellulose. Cellulases are very different from most enzymes, as they degrade an insoluble substrate. This requires that the enzyme diffuses to the substrate and then it has to move a segment of a cellulose molecule from the insoluble particle into its active site, whereas soluble substrates diffuse to the enzyme and bind into the active site by themselves.

Almost all enzymes that degrade insoluble substrates contain a substrate binding domain, which is usually joined to the catalytic domain (cd) by a flexible linker peptide [10•]. In the case of cellulases, where this type of domain was first discovered, the domain was originally called a cellulose binding domain and then the name was changed to carbohydrate binding module (CBM), so as to include the many other types of polysaccharide binding domains. It is clear that one role of the CBM is to bind the enzyme to the cellulose so that the cd spends less time away from the substrate and it also gives the cd time to move the chain into its active site before the enzyme diffuses away from the cellulose particle. It is still not clear whether the CBM also can modify cellulose or otherwise assist cellulose hydrolysis by the catalytic domain [11].

There are a number of forms of cellulose that are used to assay cellulases; carboxymethylcellulose (CMC) is a

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soluble form that is an excellent substrate for endocellulases and its hydrolysis does not require a CBM. Amorphous cellulose, which is produced by concentrated acid treatment of crystalline cellulose is a good substrate for most cellulases and its hydrolysis is usually not affected by the CBM. Crystalline cellulose (Avicel, bacterial cellulose or filter paper), which is the main form of cellulose in most plant cell walls, requires a CBM for effective hydrolysis [12,13].

Cellulases have nonlinear kinetics on polymeric substrates, which appear to be due to substrate heterogeneity but they show Michaelis–Menten kinetics on small soluble substrates [14]. Most cellulases are endocellullases, which have an open active site so they can bind and cleave a cellulose molecule at any accessible point along the chain [15]. Endocellulases bind randomly along a cellulose molecule, make a few cleavages and then dissociate from the chain, thus they rapidly decrease the viscosity of CMC. All exocellulases have their active site inside a tunnel and they bind only at one end of a cellulose chain. They cleave off cellobiose processively from the chain end [16]. Thus exocellulases have low activity on CMC and do not decrease its viscosity. They remain bound to a cellulose chain, processively cleaving cellobiose residues from the chain end until they dissociate. There are two types of exocellulases, one class attacks the reducing end of cellulose molecules while the other attacks the nonreducing end [17]. Finally there is a third class of cellulases, processive endoglucanases that so far are found only in bacteria. Most processive endoglucanases have a unique domain structure in which the C-terminus of a family 9 cd is rigidly attached to a family 3c CBM domain [18,19]. These enzymes carry out an initial endocellulytic attack on a cellulose chain but then they processively attack the nonreducing end of the initially cleaved chain, releasing cellotetraose. Some family 5 processive endocellulases also have been identified in *Saccharophagus degradans*.

Cellulolytic mechanisms

Many aerobic microorganism use the free cellulase mechanism in which they secrete a set of individual cellulases, most of which contain a carbohydrate binding module (CBM) joined by a flexible linker to one end of the catalytic domain. The cellulases in the mixture act synergistically to degrade crystalline cellulose [20]. Cellulase synergism can result in increases in the specific activity of appropriate mixtures that are up to fifteen fold higher than that of any individual cellulase [21].

Many anaerobic microorganisms use cellulosomes, large multienzyme complexes (multimillion molecular weight), to degrade cellulose [22•]. Only a few of the enzymes in cellulosomes contain a CBM, but the protein to which they are attached (called scaffoldin) does contain a CBM, which binds the complex to cellulose. In general the cellulases produced by aerobic and anaerobic microorganisms belong to the same families, except that only aerobic fungi produce GH-7 cellulases and cellulosomes do not appear to contain family 6 exocellulases. A few anaerobic cellulolytic thermophillic bacteria such as *Caldicellulosiruptor* species secrete multidomain cellulases that contain CBMs. These organisms have a very effective plant cell wall degradation system that can hydrolyze unpretreated plant biomass unlike most other cellulolytic microorganisms [23].

Some aerobic fungi that degrade cellulose but not lignin, such as *Trichoderma reesei*, the source of most commercial cellulase, use the free enzyme mechanism while true brown rot fungi secrete both cellulases and peroxidases [24]. The peroxide and OH– radicals produced by the peroxidases and iron partially oxidize the cellulose, making it much easier for the cellulases to degrade it. Therefore brown rot fungi are able to use a set of cellulases that lack both CBMs and processive cellulases, which are needed to degrade unmodified crystalline cellulose. Both CBMs and processive cellulases are produced by aerobic microorganisms that use the free cellulase mechanism and also by anaerobic micoorganisms that produce cellulosomes. In fact, the brown rot fungus *Postia placenta* only secretes a single endoglucanase whereas free cellulolytic organisms secrete six or more cellulases and cellulosomes contain even more cellulases [25•,26,27].

There are two cellulolytic bacteria, *Fibrobacter succinogenes* an anaerobe, that is a major cellulolytic rumen bacterium and *Cytophaga hutchinsonii*, an aerobic soil bacterium, whose genome sequences contain a number of cellulase genes most of which lack CBMs and all of which are endocellulases [28,8]. Furthermore, none of these cellulases have much activity on crystalline cellulose. Both of these organisms are tightly bound to cellulose during growth and neither one secretes free cellulases or produces cellulosomes. Thus these organisms appear to use a novel mechanism for cellulose hydrolysis, which has not been determined despite extensive studies of *F. succinogenes* [29]. This mechanism is very effective, as *F. succinogenes* grows faster on cellulose than most other studied microorganisms [30]. Relatives of *F. succinogenes* are widely distributed in nature and are the major cellulolytic bacteria found in termite metagenomic sequences [31•]. As more bacterial genomes are sequenced more variations are found in the cellulase genes that they contain. *S. degradans* which has a very unusual set of cellulases, as most of them are from family 5 with a few from family 9 and both of these families contain only endocellulases. There is one family 6 cellulase but it also is an endocellulase [32]. Three of the family 5 cellulases appear to be a new type of processive endoglucanase in which processivity does not require an auxiliary domain but exactly how this organism degrades cellulose so well is not clear [33].

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Recently several new proteins have been identified that function in cellulose hydrolysis. Most cellulolytic fungi contain multiple family GH-61 genes and a few of them encode proteins having weak cellulolytic activity [34•]. A family GH-61 protein was shown to stimulate cellulose hydrolysis of pretreated biomass by crude *T. reesei* cellulase when magnesium ions were present but it did not stimulate hydrolysis of pure cellulose [34•]. *Thermobifida fusca* produces and secretes large amounts of two family 33 CBM proteins when it is grown on cellulose. One contains only a family 33 domain while the other is a family 33 CBM joined to a family 2 CBM. Both of these proteins have been shown to bind to cellulose and chitin and they give a small stimulation of cellulose hydrolysis by *T. fusca* cellulases [35]. Another *T. reesei* protein that resembles expansin called swollenen has been identified and shown to loosen crystalline cellulose [36]. A *Bacillus subtilis* homolog was cloned and shown to significantly stimulate *T. reesei* cellulase activity [37].

The diversity of cellulolytic organisms in natural habitats and their degradation functions

The best studied cellulolytic environment is the rumen which is essentially a plant cell wall degrading chemostat where the animal pretreats biomass by grinding it into small particles which then are digested by a very dense and complex mixture of anaerobic microorganisms. There are about 10^{10} bacteria per ml in the rumen but only about 10% of them are cellulolytic [38•] even though cellulose is the major carbon source available to rumen microorganisms. There are also some cellulolytic rumen fungi and protozoa but it is thought that bacteria are the major cellulose degraders. The microorganisms in the rumen that are bound to feed particles are quite different from those that are not attached and most cellulolytic microorganisms are attached to the particles [39]. However many attached microorganisms do not degrade cellulose. It is interesting that a metagenomic sequence of a leaf cutter ant colony garden contained many bacteria whose genes coding for carbohydrate degrading enzymes were most similar to those in the bovine rumen although there were clear differences between the two sets of enzymes [40].

Another cellulose degrading environment, which has been well studied is compost. The initial phase of composting occurs at moderate temperatures and it is carried out by both bacteria and fungi, then heating occurs and thermophillic bacteria dominate the community [41–43]. Cellulose degradation mainly occurs in the thermophillic phase. The community of microorganisms in compost is extremely diverse and very variable although mature compost tends to have simpler communities that are enriched in cellulolytic bacteria [43].

A serious problem in studying microbial ecology is that only a few percent of the microorganisms in most environments can be cultured and the populations are very heterogeneous. It is interesting that the bacteria in anaerobic cellulolytic environments appear to be even more diverse than the bacteria in aerobic environments. It is assumed that plant cell wall degradation is dependent on many organisms that act synergistically but this has not been not clearly shown. It is likely that some of the different polymers that are present in plant cell walls are degraded by different organisms. There are some surprising specificities seen in polymer utilization. *F. succinogenes* can hydrolyze many polysaccharides but only grow well on cellulose [44]. *Clostridium thermocellum* does not grow on xylose even though it degrades xylan well [45]. *T. fusca* cannot grow on xyloglucan even though it produces a very active xyloglucanase that completely hydrolyzes xyloglucan to soluble products [46]. This enzyme is induced by growth on cellulose and it contains a cellulose binding CBM so that it probably functions to remove xyloglucan that coats cellulose fibrils in primary plant cell walls. In fact it was shown that when bacterial cellulose was synthesized in the presence of xyloglucan, it was not hydrolyzed by a mixture of pure cellulases, unless the xyloglucanase was present [46]. In addition, although *T. fusca* can grow on either xylan or cellulose, it mainly hydrolyzes cellulose, when it is grown on biomass that contains both polymers. This is probably because the synthesis of the xylan degrading xylanases is inhibited by cellobiose, which is the inducer of all the cellulose degrading enzymes, which include a xylanase and a mannanase that each contain a cellulose binding CBM [47].

Another problem in understanding plant cell wall degradation is that we do not know the exact substrate for most organisms, as there may be several organisms that sequentially attack a given type of plant cell wall. One example of a stable mixed culture that degrades cellulose contains four organisms but only one can hydrolyze cellulose and the roles of the others are not directly linked to cellulose hydrolysis [48]. In addition to ruminants, hindgut fermenting animals like horses and humans contain cellulolytic microbes in their large intestines and even though these organisms are not as effective in cellulose degradation as those in ruminants, they do hydrolyze enough of the plant cell wall to provide some extra energy to their hosts [49•].

Conclusion

Despite the exciting new findings from the application of genomic and metagenomic techniques to the study of cellulose degrading organisms. There is still much we do not understand about the mechanism of cellulose degradation and the microbial communities that carry it out. Because of the potential of biomass as a source of renewable fuels and chemicals, there has been a rapid increase in the amount of research in this area, so that it seems likely that our knowledge about these topics should continue to increase.

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