

Transcriptional regulation of plant cell wall degradation by filamentous fungi

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Abstract

Plant cell wall consists mainly of the large biopolymers cellulose, hemicellulose, lignin and pectin. These biopolymers are degraded by many microorganisms, in particular filamentous fungi, with the aid of extracellular enzymes. Filamentous fungi have a key role in degradation of the most abundant biopolymers found in nature, cellulose and hemicelluloses, and therefore are essential for the maintenance of the global carbon cycle. The production of plant cell wall degrading enzymes, cellulases, hemicellulases, ligninases and pectinases, is regulated mainly at the transcriptional level in filamentous fungi. The genes are induced in the presence of the polymers or molecules derived from the polymers and repressed under growth conditions where the production of these enzymes is not necessary, such as on glucose. The expression of the genes encoding the enzymes is regulated by various environmental and cellular factors, some of which are common while others are more unique to either a certain fungus or a class of enzymes. This review summarises our current knowledge on the transcriptional regulation, focusing on the recently characterized transcription factors that regulate genes coding for enzymes involved in the breakdown of plant cell wall biopolymers.

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Keywords: Cellulase; Ligninolytic enzyme; Hemicellulase; Transcriptional regulation; Cre; ACEI; ACEII; PacC; Hap complex

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1. Introduction

Plant cell wall consists mainly of polysaccharides such as cellulose, hemicelluloses and pectin, which together with proteins and lignin form a complex and rigid structure. It is estimated that approximately 4×10^9 tons of cellulose is formed annually, however, its amount on earth does not accumulate due to fungi and bacteria that efficiently degrade plant cell wall materials. These microorganisms play a key role in the recycling of carbon back into the ecosystem. Degradation of plant cell wall compounds is a complex process involving the synergistic action of a large number of extracellular enzymes. In filamentous fungi, these plant cell wall degrading enzymes, cellulases, hemicellulases, pectinases and ligninases provide the fungus with the means to obtain energy and nutrients from plant cell wall biopolymers. In addition, plant cell wall degrading enzymes are believed to contribute to the action of plant pathogenic fungi [1,2]. Carbohydrate polymer degrading enzymes may also play a role in the ability of antagonistic fungi to attack their target fungi due to hydrolysis of the host cell wall [3].

Many of the biopolymer degrading enzymes have received considerable attention because of their potential applications in food, feed, textile, and pulp and paper industries [4–8, and references therein]. Several applications, such as bleaching of pulp by xylanolytic enzymes, clarification of juices with pectinases and bio-bleaching of textiles with cellulases are currently in use. The use of fungal lignocellulose degrading enzymes for total hydrolysis of plant biomass to sugars is under intensive study. Liberated sugars could serve as raw material in the bioproduction of chemicals and fuels by microbes. For instance, bio-ethanol production by yeasts and bacteria from hexose and pentose sugars derived from agricultural waste materials could replace part of the fossil fuel use with a more sustainable alternative.

Industrial production strains of *Aspergilli* and *Trichoderma* can produce extremely high amounts of extracellular enzymes, several tens of grams per litre [9,10]. The

existence of hypersecreting strains and strong promoters, such as cellulase promoters, make filamentous fungi potential hosts for heterologous protein production as well. These fungi are easy and inexpensive to grow in large bioreactors and they possess good secretion capacity capable of carrying out similar type of protein modifications as occurs in many higher eukaryotes. As an example, calf chymosin, used in the dairy industry is produced at commercial levels in *Aspergillus niger* [11].

The importance of fungi for the global carbon cycle, the significance of extracellular enzymes in the life of these organisms and the biotechnological importance of filamentous fungi and their enzymes have promoted an interest towards understanding the regulation of expression of the extracellular enzymes and especially the characterization of the transcription factors involved. The most studied filamentous fungi in respect to biopolymer degrading enzyme production are brown-rot fungi *Trichoderma reesei* (*Hypocrea jecorina*), *A. niger* and *Penicillium* and the ligninolytic white-rot fungus *Phanerochaete*. Full genomic data is now available for *Phanerochaete chrysosporium* (<http://www.jgi.doe.gov/programs/whiterot.htm>), *Aspergillus nidulans* (<http://www-genome.wi.mit.edu/annotation/fungi/aspergillus/index.html>) and *T. reesei* (<http://shake.jgi-psf.org/trirel/trirel.home.html>).

2. Plant cell wall polysaccharides and lignin

Plant cell wall consists of cellulose, hemicelluloses and pectin and the phenolic polymer lignin. Cellulose is the most abundant polysaccharide in nature and the major constituent of plant cell wall providing its rigidity. Cellulose consists of β -1,4 linked D-glucose units that form linear polymeric chains of about 8000–12000 glucose units. In crystalline cellulose, these polymeric chains are packed together by hydrogen bonds to form highly insoluble structures. Hemicelluloses, the second most abundant polysaccharides in nature, have a heterogeneous composition of various sugar units. Hemicelluloses are usually classified according to the main

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