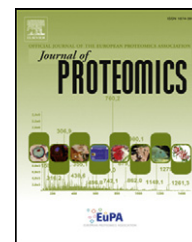


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Review

Comparative analysis of secretomes in basidiomycete fungi



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ARTICLE INFO

Article history:

Received 23 December 2013

Accepted 3 March 2014

Available online 12 March 2014

Keywords:

Secretome

Bioinformatic secretome

Basidiomycete

Lignin degradation

ABSTRACT

Lignocellulose, the major reservoir of organic carbon on Earth, is recalcitrant to turnover and resistant to microbial and enzymatic attack because of the protective action of lignin and the crystalline structure of cellulose. Basidiomycetes are the only organisms known to degrade lignocellulose using two alternative degradation strategies: white rot basidiomycetes break down the lignin moiety extensively before attacking the cellulose, whereas brown rot basidiomycetes cause limited lignin alteration while primarily degrading cellulose. These strategies depend on complex portfolios of extracellular enzymes whose production and export are environment and substrate dependent. More than 265 fungal genomes (more than 90 corresponding to basidiomycetes) have been sequenced. These sequences can be bioinformatically screened to identify presumptive secreted proteins that, however, differ from the experimental data, stressing the importance of using complementary approaches for analyzing these complex systems. The study of fungal secretomes from the scope of their different lignin degradation strategies and lifestyles would facilitate their use in the treatment of lignocellulose as carbon feedstock for biofuel production and further biorefinery processes. In this article, we carry out a comparative review of the analytical tools and strategies used for studying basidiomycetes' secretomes and compare the available results from these two points of view.

Biological significance

In this article, we review the tools and strategies used in the analysis of basidiomycetes' secretomes and we compare the secretome data available for this type of fungi with a special emphasis on the enzymes involved in lignocellulose degradation. This comparative study provides a basis for distinguishing different lifestyles (saprotrophs, symbionts and parasites) on the basis of their respective secretomes.

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1. Introduction

The fungal lifestyle depends on the absorption of environmental nutrients that are made available via the action of sets of secreted hydrolyzing enzymes. Consequently, protein secretion is crucial for fungal life and growth. This high capacity of enzyme secretion has been exploited by industry, where compounds secreted by fungi have been used for decades [1,2]. The secretome is defined as the set of proteins secreted by a cell or an organism at a given time [3]. There are two points that must be kept in mind in this context. First, in a broad sense, the secretome includes both the proteins that are released into the surrounding medium and those that remain bound to the membrane or cell wall or that are integral membrane proteins. Second, the secretome, like the transcriptome, is highly variable depending on environmental conditions, including the growth substrate, temperature and growth phase. Although the number of fungal transcriptomic studies is steadily increasing, it is not sufficiently large to draw global conclusions to explain how a secretome is modulated in response to environmental conditions in different species. Hence, in this article, we review the characteristics of the secretomes of some model organisms that are representative of different basidiomycete lifestyles, paying special attention to the enzymes involved in lignocellulose degradation.

Lignocellulose, the major reservoir of organic carbon on Earth, is recalcitrant to turnover and resistant to microbial and enzymatic attacks because of the combination of the protective action of lignin, the cementing action of hemicellulose and the crystalline structure of cellulose. From the perspective of a geological time frame, lignocellulose could have served as a major carbon sink until the appearance of saprophytic lignin-degrading fungi at the end of the Carboniferous period [4]. Filamentous fungi play an important role in carbon cycling because some of these fungi, grouped in the phylum Basidiomycota, secrete large amounts of lignocellulose-degrading enzymes. These fungi are the only organisms known to degrade lignocellulose at a global scale. Lignocellulolytic basidiomycetes use two alternative strategies for attacking lignocellulose. White rot basidiomycetes degrade the lignin moiety extensively before attacking cellulose, whereas brown rot basidiomycetes cause limited alterations of lignin while primarily degrading cellulose. These two processes are carried out by complex portfolios of secreted enzymes whose production and export are modulated in response to environmental and substrate changes.

White rot basidiomycetes attack the lignin moiety of lignocellulose using oxidative enzymes classified as manganese peroxidases (MnP, EC 1.11.1.13), versatile peroxidases (VP, EC 1.11.1.16), lignin peroxidases (LiP, EC 1.11.1.14) and

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