Extracellular Enzymes of *Penicillium*

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1. INTRODUCTION

The wide range of extracellular enzymes produced by species of *Penicillium* play an important role in the microbiological breakdown of organic materials. Notable examples of hydrolases of *Penicillium* include various cellulolytic enzymes and other polysaccharases, such as α- and β-glucanases, hemicellulases, and pectic enzymes, together with a variety of lipases and proteolytic enzymes that are recognized as being responsible for the development of the characteristic flavors in ripened cheeses. Despite this plethora of extracellular enzymes, surprisingly few species of *Penicillium* have so far been adopted for industrial enzyme production. Indeed, Godfrey and Reichelt (1983) point out that most industrial microbial enzymes are produced from no more than 11 fungi, 8 bacteria, and 4 yeasts. This restriction is largely explained by the fact that only a few microorganisms are approved for use in the food industry, and enzyme manufacturers are usually keen to include food processing as a potential market for their products. Nevertheless, the use of microbial enzymes in industrial processes has expanded considerably in recent years, and the *Penicillia* would seem to be particularly well placed to have an increasing part to play in the future manufacture of these enzymes.

2. CELLULOSE-DEGRADING ENZYMES

Many microorganisms produce extracellular enzymes that catalyze the hydrolysis of water-soluble cellulose derivatives, such as carboxymethyl- or hydroxyethylcellulose of relatively low degrees of substitution, and of highly...
swollen forms of cellulose, e.g., phosphoric-acid-swollen cellulose, but relatively few have the ability to hydrolyze highly ordered crystalline cellulose, as typified by cotton (Wood et al., 1980). Included among the cellulolytic microfungi that are able to hydrolyze highly ordered cellulose are members of the genus *Penicillium* (Selby, 1968; Wood and McCrae, 1977; Somani and Wangikar, 1979).

### 2.1. The Cellulase Complex

As long ago as 1950, Reese et al. (1950) proposed that the cellulase complex contains three major enzyme components. The first of these components, which is produced only by organisms that are able to degrade crystalline cellulose, was termed $C_1$, so named because it was believed to act first on the highly ordered arrays of cellulose molecules in the elementary fibrils by deaggregating the cellulose chains, making them available for subsequent hydrolysis by the $\beta$-1,4-glucanases. This latter group of hydrolytic enzymes forms the second major component of the cellulase complex, generally referred to as $C_x$, the $x$ reflecting the fact that normally there are several of these enzymes present in culture filtrates of cellulolytic microorganisms. The $C_x$ component contains both endo- and exo-$\beta$-1,4-glucanases that are responsible for hydrolysis of soluble derivatives of cellulose or swollen and partially degraded cellulose, but are without effect on crystalline cellulose in the absence of the $C_1$ component. The products of the action of the $C_x$ enzymes are short-chain cellobiooligosaccharides, cellobiose, and glucose. The third component of the cellulase complex, the $\beta$-glucosidases ($\beta$-d-glucoside glucohydrolases), convert the cellobiooligosaccharides and cellobiose to glucose. The proposed actions of the various components are summarized in Fig. 1.

The cellulase complex of *P. funiculosum* was shown by Selby (1968) to conform to Reese’s concept. Selby also demonstrated cross-synergism between the $C_1$ and $C_x$ components of *P. funiculosum* and *Trichoderma viride*; the $C_1$ of *P. funiculosum*, when recombined with the $C_x$ of *T. viride*, was almost as effective at solubilizing crystalline cellulose as the recombined $C_1$ and $C_x$ from *P. funiculosum* only.

While the $C_x$ components from *P. funiculosum* exhibit the classic exo- and endo-$\beta$-1,4-glucanase activities (Wood and McCrae, 1977), the action of the $C_1$ component remains unclear. Following the development of improved fractionation methods and the discovery that the $C_1$ fraction appears to possess cellobiohydrolase activity, several groups of workers reversed the original concept of Reese et al. (1950) by suggesting that it is the endo-$\beta$-1,4-glucanase that attacks first, in a random manner, to produce chain ends for subsequent attack by the exoenzyme, $\beta$-1,4-glucan cellobiohydrolase. However, Reese (1976) critically questioned the implication that $C_1$ and this