# The Filamentous Fungi

## Volume 3 Developmental Mycology

Edited by:
JOHN E. SMITH, D.Sc., F.I. Biol. F.R.S.E.
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# Preface

The unique morphology of the filamentous fungi inevitably requires that their development involves unique solutions to the problems of growth and differentiation. In this volume we have aimed at bringing together concepts and evidence from the variety of disciplines, *viz.* biochemistry, physiology, genetics and cytology which can contribute to our understanding of fungal development. Furthermore, we have aimed to avoid lengthy and detailed descriptions of morphogenetic events in the fungi which can so easily cloud rather than clarify the principles involved.

We believe that it is self evident that a good understanding of fungal development is essential to a complete appreciation of the behaviour of fungi in an industrial or academic situation. This volume is an attempt to provide research workers in each of these fields with an integrated perspective of the subject of fungal development. As with the previous two volumes in this series we have aimed to make each chapter an entity in itself rather than a survey of recent advances.

*1977*

J. E. S.
D. R. B.

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# Contents

CHAPTER 1

# Concepts of Differentiation

**BARBARA E. WRIGHT**



## 1.1 Introduction

The purpose of this introductory chapter is to arrive at a useful definition of 'biochemical differentiation'. The approach will be to examine various types of differentiation in order to see what they have in common, so that we may distil or select those characteristics applicable in most cases. When the word 'differentiation' is in quotation marks, it refers to the word or symbol; when not in quotation marks, it refers to the phenomenon being described. In the latter case, I should be pointing to the phenomenon, rather than speaking or writing the word—to avoid the semantic sin of identifying a symbol with the object it represents. A symbol or definition must of necessity be an abstraction or selection of only a few of the countless characteristics (some unknowable) which together constitute the phenomenon. A symbol *is not* identical with the object. Those who argue about the 'nature' or 'cause' of (') biochemical differentiation (') should realize that such arguments usually stem from a lack of awareness that different definitions are being used, or from a confusion between, and/or identification of, symbol and phenomenon.

Neither phenomena nor definitions can be right or wrong. Phenomena can only be described, and a definition is arbitrarily made, based on criteria such as conventionality, clarity and usefulness. For excellent discussions regarding the nature of definitions see Lotka (1956) and Korzybski (1958). There are different kinds of definition; the one we seek is called a connotative definition, which describes selected characteristics common to similar phenomena.

Phenomena referred to as examples of 'differentiation' can cover a very broad range. Indeed, even enzyme induction in bacteria has been included. For our purposes, however, more complex systems will be used because they are more representative of what most investigators in our field would consider to be cases of 'biochemical differentiation'. As we are interested not in mere correlations, but in biochemical mechanisms underlying

'differentiation', examples have been chosen which offer at least some indication as to the rate-limiting steps (*i.e.*, critical variables) controlling the specific transformation in question. For the purpose of the points to be made, I have taken the liberty of making certain assumptions and simplifications regarding the systems to be described.

## 1.2 The Accumulation of Fibroin in *Bombyx mori*

The first and in certain respects simplest example is the accumulation of the silk protein, fibroin, in the silk worm *Bombyx mori* (Suzuki, Gage & Brown, 1972; Suzuki & Brown, 1972; Lizardi & Brown, 1975). When the silk gland cells cease cell division, an enormous increase in the amount of DNA occurs; when DNA synthesis stops, only fibroin (300 $\mu$g/cell) is made. Elegant analyses have shown that the fibroin gene is not amplified in the silk gland, but is present as a constant fraction of the haploid genome, and represents 0.0022% of the DNA from all parts of the silk worm. The messenger RNA (mRNA) for the fibroin protein has been isolated (80%–90% pure) and analyzed by partial sequence analysis. The sequence found could actually be predicted, because the protein has a simple primary structure. This mRNA comprises about 1% of the total RNA in the silk gland at the end of the larval life of the animal, when fibroin is the predominant protein synthesized in this tissue. A simplified picture of the sequence of events which culminates in the accumulation of fibroin protein are summarized in Fig. 1.1.

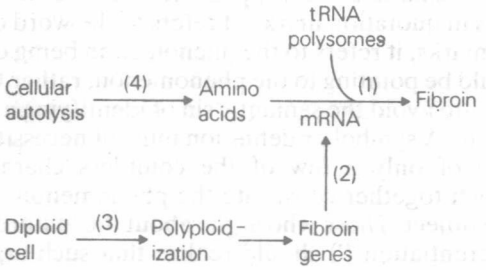


**Fig. 1.1** Sequential events essential to the accumulation of silk protein (fibroin) in *Bombyx mori*.

Cellular autolysis, which supplies amino acid precursors for fibroin synthesis (4 in Fig. 1.1) and polyploidization in the silk gland cells, which results in ten times more DNA and hence fibroin gene per cell (3 of Fig. 1.1), occur many days prior to fibroin accumulation (1 of Fig. 1.1). Thus, we shall assume that these events are not rate-limiting when fibroin accumulates, and that the content and activities of cellular tRNA and polysomes are also optimal for the protein synthesis which will occur. Presumably, the critical event occurring during the 3–4 days prior to fibroin accumulation is the production of $10^4$ molecules of mRNA by each gene (2 of Fig. 1.1). Each mRNA molecule is then translated into $10^5$ silk protein molecules during the last 4 days of larval life (1 of Fig. 1.1). Thus, the critical variable controlling the synthesis and accumulation of this structural protein is gene activation.

## 1.3 Chitin Synthesis in *Saccharomyces cerevisiae* and *Mucor rouxii*

The next example to be considered is chitin synthesis during septum formation in the budding yeast, *Saccharomyces cerevisiae* (Cabib & Farkas, 1971; Cabib & Ulane, 1973) and during hyphal or cell wall growth in the mould *Mucor rouxii* (Bartnicki-Garcia & Lippmann, 1972; Bartnicki-Garcia, 1973; Ruiz-Herrera & Bartnicki-Garcia, 1974). In both systems, the enzyme is present largely in an inactive state and can be activated by an activating factor (AF) or proteolytic enzyme (2 of Fig. 1.2). The protease, AF, is liberated from vesicles at the site of septum formation and the inactive enzyme or zymogen is then transformed to active chitin synthase.

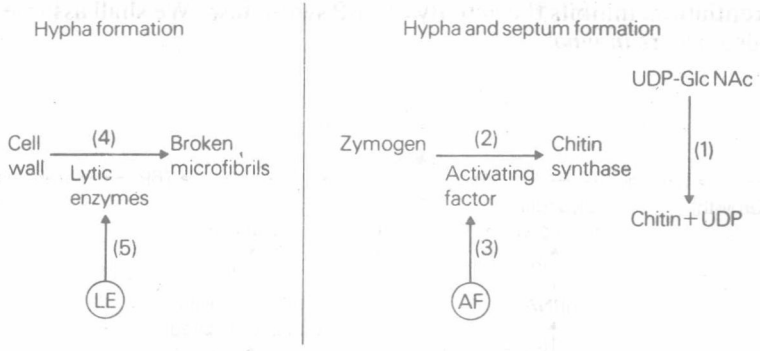


**Fig. 1.2** Prior events necessary to the accumulation of chitin in *Mucor rouxii* and *Saccharomyces cerevisiae*.

In the case of hyphal growth, presumptive evidence has been obtained for the critical role of wall lysis coupled with synthesis. Lytic enzymes attack the microfibrillar skeleton by splitting either inter- or intramolecular bonds, thus facilitating the extension of old chains or the production of new ones (4 of Fig. 1.2).

In the case of septum formation, the total amount of chitin synthase, as measured after proteolytic activation, is constant, regardless of growth medium, growth phase or stage of the cell cycle. Therefore, the critical variables for chitin synthesis with respect to this enzyme do not involve gene activation, mRNA synthesis or stabilization. (Zymogen and/or active enzyme may well be turning over, but that would be irrelevant in our present context, as inactive and active enzyme concentration is a constant before and during septum formation). The AF-carrying vesicle fuses with the plasma membrane at the site of septum formation, resulting in the transformation of zymogen to active enzyme. Thus, the production of broken microfibrils (4 of Fig. 1.2) as 'primers' for new synthesis and the liberation of an activating factor (3 of Fig. 1.2) are the critical variables controlling structural polysaccharide formation during differentiation in these two systems.

## 1.4 Glycogen phosphorylase and trehalose in *Dictyostelium discoideum*

The last two examples are taken from the cellular slime mould, *Dictyostelium discoideum*, and were chosen because they involve two other kinds of products of 'differentiation': an enzyme (glycogen phosphorylase) and a