

THE FUNGAL SPORE: MORPHOGENETIC CONTROLS

Edited by
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and
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1981 · ACADEMIC PRESS

A Subsidiary of Harcourt Brace Jovanovich, Publishers
London · New York · Toronto · Sydney · San Francisco

ACADEMIC PRESS INC. (LONDON) LTD.
24-28 Oval Road,
London NW1

United States Edition published by
ACADEMIC PRESS INC.
111 Fifth Avenue
New York, New York 10003

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British Library Cataloguing in Publication Data
International Fungal Spore Symposium, 3rd, Gwatt,
1980

The fungal spore.

1. Fungi – Spores – Congresses

I. Turian, G II. Hohl, H R
589'.2'0446 QK601 80-49681

ISBN 0-12-703680-0

Printed in Great Britain by
Whitstable Litho Ltd., Whitstable, Kent

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PREFACE

The Second International Fungal Spore Symposium was held in Provo, Utah, USA in 1974. There, emphasis was put on questions of spore dormancy and germination. For the present Third International Fungal Spore Symposium we aimed at events accompanying spore formation without, however, neglecting recent advances in the field of spore activation and germination. Again, a major goal of the Symposium was to bring together leading authorities to assess the present state of knowledge on the ultrastructure, physiology, biochemistry and genetics of fungal spores.

It should be remembered, though, that our common denominator, the spore, represents a very diverse entity. Not only do spores differ greatly in shape and mode of formation but also functionally there is a wide gap between asexual spores and those of sexual origin which are the result of recombination mechanisms initiated by the complex interplay of mating factors. The one and all-embracing feature of spores may be recognized in their representing the end product of the transition from a vegetative, relatively undifferentiated growth condition to a reproductive, differentiated structural entity, followed by a reversal of this state during germination.

The questions raised and the problems posed by these series of transitional events are wide open and presently under study at different levels of organization. These studies cover the entire range from gene level to environmental parameters. Considered in its fullest context, spore research would encompass almost all events leading from one spore generation to another and we might have entitled the present volume 'From Spore to Spore'. For practical reasons the topics covered were restricted to those directly connected with initiation, formation and germination of spores of the major fungal groups.

Relatively simple environmental triggers such as elevated temperature (heat shock) or nutritional deficiencies (starvation) may interrupt the vegetative stage and channel the organism into developmental and reproductive pathways. Re-

search with microcycling fungi should help to answer the question of how much (or how little) vegetative growth is needed to render the organism competent for the morphogenetic switches.

Initial and basic controls of these morphogenetic processes must be based on the informational content of the organism's DNA which forms the *sine qua non* of reproducing a 'true to type' spore. Expression of gene information is conveyed by spore specific mRNAs which call into action controls at the translational and perhaps posttranslational levels to sustain synthesis of specific spore proteins, pigments and structural characteristics.

Germination, often the result of specific triggering mechanisms, represents the return to a vegetative condition, implying processes of dedifferentiation and a switch to growth which is in essence a synthesis of protoplasm and cell walls. While in some lower forms and also in early stages of spore germination in higher fungi, growth occurs in an unpolar, multidirectional fashion, in filamentous fungi the germinating spore quickly redifferentiates into an apically growing, polarized germ tube. This polarized growth pattern is maintained as long as it is enforced by the genetic potential and the environmental conditions. Eventually, morphogenetic controls will again become operative thereby imposing a return to sporogenesis. This brief outline may suffice to indicate the scope of the present volume on 'The Fungal Spore : Morphogenetic Controls'.

We would like to thank the various institutions that financially supported our meeting : Swiss National Science Foundation, Swiss Academy of Natural Sciences, Fonds Académique (Genève), Interpharma (Basel), Association Suisse des Fabricants de Cigarettes (Fribourg), University of Geneva and University of Zürich. The Symposium was sponsored by the Swiss Microbiological Society and the Swiss Botanical Society. Many thanks are due to the members of the organizing committee and the technical assistants whose untiring efforts contributed so much to the success of the meeting. They are : Erika Rüegg, Barbara Duchoud, Rosmarie Honegger, Ursula Heiniger, Marianne Hohl, Jakob Bodenmann, Mukti Ojha, Jürg Jehli, Jean Zuber, René Gees, Françoise Grange, Katja Iselin, Mehrbanou Michéa, The Can Ton-That and Bernhard Häne. We are also indebted to Academic Press for publishing the proceedings and for their cooperation and help during the editing of this volume.

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HISTORICAL INTRODUCTION

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INTRODUCTION

The Colston Research Society, a group of eminent citizens of Bristol makes an annual grant to finance a symposium on a branch of knowledge chosen by the University and held in one of its Halls of Residence. In 1966 I was asked to arrange a symposium on a mycological subject of my choice. After consultation my mycological colleagues in the Department of Botany, and I decided to adopt Dr. Madelin's suggestion that the title should be "The Fungus Spore" and that we should attempt a wide outline coverage of the subject including initiation, maturation, dispersal, dormancy, germination and the importance of fungus spores in agriculture, medicine and industry. Our guests and contributors entered into the enterprise with enthusiasm and expert knowledge. The results were published as *Colston Papers* No. 18. Later it became clear that we had initiated a continuing study. Drs. Hess and Weber arranged a second symposium in Utah U.S.A., in 1974. By then it was no longer possible to cover all aspects of the subject and the organisers wisely limited the scope of the symposium to detailed studies of the mature spore, its dormancy and germination. This second symposium was both enjoyable and stimulating. It is fitting that the present third symposium on the fungus spore should be limited to another particular aspect of the subject. Since the 1974 meeting in Utah, great advances have been made in the study of morphogenetic controls, particularly of spore initiation and development but also of activation and germination. Our present meeting is to discuss this morphogenetic control.

In a historical introduction to this fascinating and fast growing subject it is obviously not possible to cover more than a fraction of the vast literature on the development of fungi which now exists. Accordingly an attempt will be made to indicate the general principles which emerged from

earlier work on the subject and to illustrate this with selected examples to form a basis for appreciating the accounts of advanced specialist topics which are to follow.

FACTORS INFLUENCING REPRODUCTION IN FUNGI

During the first two decades of the present century little was known about factors influencing growth of fungi and still less about the events leading to the initiation of reproduction.

Apart from a few isolated papers the study of the physiology of fungi began with the pioneer work of William Brown at the Imperial College of Science in London, the results of which were published in a series of papers (Brown 1922, 1923, 1925, Brown and Horne, 1926 etc.) Brown was primarily a plant pathologist but he realised that his studies on the physiology of parasitism and the control of plant disease must be soundly based on knowledge of the factors controlling growth and reproduction of the parasite.

Brown's early work on fungal physiology was done with a species of *Fusarium* isolated from apples and then known as *F. fructigenum*, later as *F. lateritium*. This fungus grew well on most of the natural media then in general use, such as potato extract and malt extract.

Brown set out to determine the minimum nutritional requirements for growth and sporulation. From a chemical analysis of potato extract he attempted to produce a solution of defined chemicals reproducing as closely as possible the composition of the natural extract. Brown's next move was to leave out various components until he was finally left with a simple medium (containing glucose, asparagine, tri-potassium phosphate and magnesium sulphate) on which the fungus grew well. With the aid of this simple medium he studied the response of the fungus to such external factors as temperature, light, pH of the medium and aeration. It was soon evident that conditions sufficient to allow good mycelial growth were not necessarily favourable to the formation of conidia and might even inhibit spore formation. Brown and his students then attempted to grow a range of different fungi on simple synthetic media and it was soon clear that these fungi differed widely in their requirements for growth and sporulation and that fungi producing more than one type of spore needed specific conditions to produce each of these.

It was the writer's good fortune to enter Brown's laboratory in 1932 and to have the benefit of his guidance for 13 years. The starting point of the writer's researches on

reproduction in fungi was a plate of a synthetic medium (Medium A: containing 0.5% glucose, KNO_3 , KH_2PO_4 and MgSO_4) inoculated with a Pyrenomycete, *Melanospora destruens* (later shown to be a strain of *Sordaria*, *S. destruens*; Hawker, 1951). On this plate was a small contaminant colony. The *Sordaria* grew only sparsely and produced no perithecia in pure culture in medium A, but around the contaminant colony was a ring of perithecia containing viable ascospores. A number of fungi from diverse groups were then grown in mixed culture with *S. destruens* and many of them induced the latter to form perithecia. This phenomenon could have been due to one or more of a number of external factors including a mechanical barrier to growth and changes in the medium brought about by the second fungus, such as removal of nutrients, changes in pH, or the production of staling substances or of stimulating substances (growth substances). Preliminary experiments indicated that the most likely cause was the production of substances by the contaminant colony which had a stimulating effect on perithecial production by the *Sordaria* (Asthana and Hawker, 1936). Dilution of the medium was also important.

It must be remembered that in the 1930's the study of plant growth substances (auxins) was only just beginning, that the chemical nature of common vitamins was largely unknown and that pure preparations of these were not commercially available.

Nielsen (1931) had already shown that culture medium in which *Rhizopus suinus* had grown induced increased growth both of the oat coleoptile and a species of *Aspergillus*. By fractionation of the culture filtrate he showed that the factor influencing *Aspergillus* was distinct from that causing extension of the oat coleoptile (heteroauxin). Schopfer (1931, 1932) showed that growth of *Phycomyces* spp required a supply of aneurin (Vitamin B_1 , now termed thiamin). Buston and his collaborators (Buston and Pram-anik, 1931a, 1931b, Buston and Kasinathan, 1933) reported that *Nematospora gossypii* (the cotton boll rot fungus) which was unable to grow on Brown's glucose-asparagine medium, grew well with the addition of an extract of lentils to the medium. Later Kögl and Fries (1937) working with the same fungus extracted from large quantities of yeast or eggs three substances (inositol, vitamin B_1 and an unknown substance which they termed biotin). An external supply of all three was essential for growth of *N. gossypii*.

The lentil extract or its ether insoluble fraction used by Buston proved to be sufficient to permit formation of perithecia by *S. destruens*¹ when added in small quantities

to medium A. Through the kindness of K8gl and Fries the writer was provided with a small sample of biotin and was able to show that *S. destruens* did not need an external supply of inositol, showed improved growth when biotin was added to medium A and needed the further addition of vitamin B₁ for the formation of perithecia (Hawker, 1938). Later it was shown that the pyrimidine component of thiamin was as active as the whole molecule (Hawker, 1939).

Experiments with other fungi by a number of workers (listed by Lilly and Barnett, 1951, and others) soon showed that requirements varied not only between species but often also between strains of the same species. Experiments with mixed cultures showed that while all fungi required a range of growth substances for growth and sporulation they varied in their ability to synthesize these from simple chemicals. Some like *F. lateritium* could synthesise all the growth substances they needed; others like *S. destruens* were able to synthesize only small quantities of particular ones or were totally unable to synthesize one or more essential substance(s).

Parallel with these studies on the effects of growth substances were others on those of the nature and concentration of major nutrients.

It has long been recognised that a dilute medium is often more favourable to sporulation than a concentrated one. The classic experiments of Klebs (1898, 1899, 1900) with *Saprolegnia* spp and Claussen (1912) with *Pyronema confluens* showed that transfer from a medium rich in nutrients to a more dilute one induced the formation of sporangia and apothecia respectively. It is now generally accepted that such a transfer of a well fed mycelium to a medium poor in one or more essential nutrient is likely to induce sporulation.

A detailed study was made of the effects of different carbon sources at different concentrations on the production of perithecia by *S. destruens* (Hawker, 1939, 1947).

With glucose or fructose as the source of carbon, perithecia were most numerous at a sugar concentration of 0.5% and were absent at concentrations of 1.0% and higher.

The concentrations of some other carbohydrates optimal for production of perithecia were higher than that with glucose. Thus sucrose, starch and lactose were optimal at concentrations of 10.0%, 2.0% and 1.0% respectively. However, if in a liquid medium a total amount of glucose larger than 0.5% were given in small increments, fruiting increased but was still inferior to that on 10.0% sucrose.

It was concluded and supported by other experiments that fruiting was best on those more complex carbohydrates which were broken down to hexoses at a rate giving an optimal concentration of these over a relatively long period (Hawker, 1948). Since other methods of maintaining such a supply did not give such good results as sucrose, it was concluded that some intermediate stage in the inversion of sucrose stimulated the initiation of fruiting.

It had already been shown by Buston *et al.* (1953) working with *Chaetomium globosum* and by Miller *et al.* (1955) with the yeast *Saccharomyces cerevisiae* that small quantities of certain hexose phosphates favoured spore production. Perithecial formation by *S. destruens* also proved to be responsive to small quantities of glucose - 1 - phosphate or fructose - 1: 6 - diphosphate. It was concluded that the favourable effect of sucrose and some other complex carbohydrates was due to a combination of the rate of hydrolysis and the formation of particular phosphoric esters (Hawker, 1948).

The complete inhibition of formation of perithecia of *S. destruens* by high concentrations of glucose could be prevented by increasing the amount of thiamin in the medium and it was shown (Hawker, 1944) that the concentration of glucose optimal for fruiting increases with increase in the concentration of thiamin. The favourable effects of thiamin were found to be linked with an increased rate of respiration. Respiration was also greater on a sucrose rather than on a glucose medium. It was demonstrated that with *S. destruens* and some other fungi, growing on culture media, respiration reached a peak and then fell and that initiation of sporulation closely followed the fall from the peak.

The nature and concentration of nitrogen sources and the carbon/nitrogen ratio also influenced sporulation of many fungi but here the situation is complicated by the effect of toxic staling substances and changes in pH resulting from the utilization of particular nitrogen compounds.

Many trace elements also influence sporulation as has been shown particularly with *Aspergillus niger* beginning with the work of Steinberg in 1919.

Physical factors, such as light, are also important in inducing sporulation of a number of fungi. The effects were reviewed by Carlile (1965) and more recently there is a suggestion that light may act by inducing the formation by the fungus of spore-promoting substances (Leach, 1965).

Thus by the time (1966) of the first of these "Fungus Spore" symposia the general factors controlling sporulation were known. In addition, a number of specific studies in

depth on particular fungi or groups of fungi have added further information on the external and internal factors causing the change from the vegetative to the reproductive state. Such studies as those of Lilly and his co-workers (Lilly, 1966) with *Phytophthora* spp; Cantino (1956) with *Blastocladiella emersonii*; Emerson (Emerson and Fox, 1940) with *Allomyces* spp; Raper in a series of papers on *Achlya* spp (Raper, 1939, 1951) and Gooday (1973, 1974) with the biosynthesis of trisporic acid and the role of this substance in differentiation in the Mucorales, show that the study of morphogenesis in fungi is indeed a fertile field.

FACTORS INFLUENCING SPORE GERMINATION

Fungus spores vary greatly in their mode of formation; their genetic history, their ability to survive adverse conditions in a dormant state and their mode of germination. Different types of spore respond differently to particular external factors but, in general, conditions leading to germination are more exacting than those permitting vegetative growth (Brown, 1922). The physiology of spore germination was summarised by Gottlieb in 1950 and he also discussed biosynthetic processes in germinating spores at the first "Fungus Spore" symposium (Gottlieb, 1966) and at the second one (Gottlieb, 1976). Many aspects of the subject were discussed by other contributors to the Utah Symposium. The report of this symposium gives a sufficient basis for appreciation of further work to be reported later in the present meeting.

TARGETS FOR FUTURE WORK

A historical introduction must not trespass on present day studies. Hence this paper has largely ignored work in progress or done during the 70's. However, during that decade the tools available to the investigator have become increasingly sophisticated, making possible experiments which could not have been done 10 years ago and holding out the prospect of the eventual elucidation of the internal control of morphogenesis.

Two broad lines of investigation present themselves. In one, use may be made of improved micro-chemical techniques; in the other, the study of changes taking place in ultra-structure is facilitated by advances in the techniques of electron microscopy. Much has been done recently along both these lines but much more remains to be done. It is an exciting prospect.