Fungal Physiology

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Preface

The field of fungal physiology, like other fields of science, has exploded in the past twenty years. This explosion has occasioned an increasing number and frequency of symposium volumes, advanced treatises, and review articles summarizing many important aspects of this field. Also, several introductory mycology texts now include significant coverage of fungal physiology. This book is intended to fill the gap between these two levels of presentation in order to provide the teacher and student of fungal physiology with a book suitable for a semester course.

The book is aimed at the senior-graduate student level and assumes a working familiarity with general and organic chemistry, physics, and calculus. A course in general or cellular physiology would also be useful, as would some familiarity with fungal structure, reproduction, and classification. However, the first chapter is a general introduction to the fungi; this explains the mycological terminology to students without a detailed knowledge of the fungi, and provides a common basis of understanding of fungal reproduction and of the classification I have used.

In writing this book I have deliberately spent little space on those aspects of physiology and biochemistry that are common to most of biology, assuming that these will be studied in greater detail in other courses. They are presented here only in sufficient detail that a student need not have course backgrounds in biochemistry and cytology to use this text. I have tried to concentrate on those aspects of physiology where fungi are significantly different from, and often unique among, other organisms.

While it is important for students to know the current status of concepts of physiology, it is more important to understand how these concepts were derived, and thus how they may be changed in the future. There are two approaches to this kind of understanding, the historical and the experimental. I have not attempted to produce a historical account of the field of fungal physiology, but I have tried to discuss the subject from the experimental point of view. Showing reasoning behind the experimental approaches that can be taken to solve the problems of fungal physiology is an important part of this book, as is the illustration of these experiments by original data. This approach allows students to see and interpret for themselves the results of this process. I also recommend that students read and discuss original research papers to extend this experience beyond that permitted by the confines of this book.

Review articles are referred to wherever possible, for economy of space, to limit the extent of reference citations interrupting the reader's thought, and to provide a guide to the larger body of literature. This means that the student will have to seek out this secondary literature in order to find the original works. The primary literature is cited where specific data is used and where clarity requires it. Also, I have not attempted, necessarily, to cite the most recent papers on a topic (although I have tried to be as current as possible), but rather I have chosen references as examples of the kinds of work being done and for their originality and interest.

I would like to thank my colleagues, especially Drs. Robert Zabel and Daniel Walton, for their encouragement, discussions, and reviews of portions of the manuscript. These have been a tremendous aid in producing this work. I would also like to thank Penny and Regina for their diligent work in typing, retyping, and typing again this text as it evolved to its end. I am sure that they are as happy as I to have it finished.

DAVID H. GRIFFIN

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CHAPTER 1

Introduction to the Fungi

The fungi are an important group of organisms whose significance to humanity has been recognized for only a little more than a century, although some have been successfully domesticated for thousands of years without the realization of their existence. Being microorganisms, they do their work both for and against the interests of humanity in hiding, and become readily apparent only during their reproductive phases.

The fungi are important as primary agents of decay in the cycling of carbon, nitrogen, and other nutrients in the biosphere and in the deterioration of useful materials and products. They cause serious diseases in plants and animals, including people, not only by their direct attack and invasion, but also indirectly through the secretion of toxins. Their abilities to synthesize many strange and wonderful compounds significant to us is not limited to deleterious activities, but includes the production of many materials important to the food, drug, and chemical industries.

Although the control of the diverse activities of fungi in preventing their deleterious activities and promoting their useful ones has been managed to some extent empirically, greater success can be expected from an informed basis of understanding their physiology and life cycles. Because the physiological properties of the fungi are often intertwined with their life histories, and because it is hoped that this book will be useful and interesting not only to students of mycology but also to students without a detailed background in the fungi, the general properties and reproduction of fungi is described here to provide a common background and reference for the succeeding chapters.

ORGANIZATION OF THE THALLUS

The fungal kingdom is a diverse assemblage of organisms with a great variety of structural types. All organisms that we recognize as fungi have the basic characteristics of eucaryotic cells, the cytochemical details of which are dealt with in Chapter 3. The cellular basis of thallus organization ranges from unicellular forms without cell walls to multicellular structures with a considerable degree of differentiation.

Hyphae

The vast majority of fungi are composed of hyphae—unique, threadlike, tubular structures, bounded by walls, and forming extensive, branched, anastomosing systems called mycelia. The hyphae of most fungi are segmented by septa that divide the mycelium into units similar to cells, but the presence of pores through the septa allows the mass movement of cytoplasm and organelles and the migration of nuclei through the mycelium to distant parts. This communication has important consequences for the physiology of the fungus. Of the variety of septal pore structures found among the fungi, two are very common (Fig. 1), the simple pore typical of the mycelial Ascomycetes and Deuteromycetes, and the more complex dolipore septum typical of many Basidiomycetes. Although there is cytoplasmic continuity through these pores, the parenthesome and septal swelling at the pore of the dolipore septum and Woronin granules or other inclusions in simply septate fungi may act to occlude the pores, preventing the free movement of materials between segments.

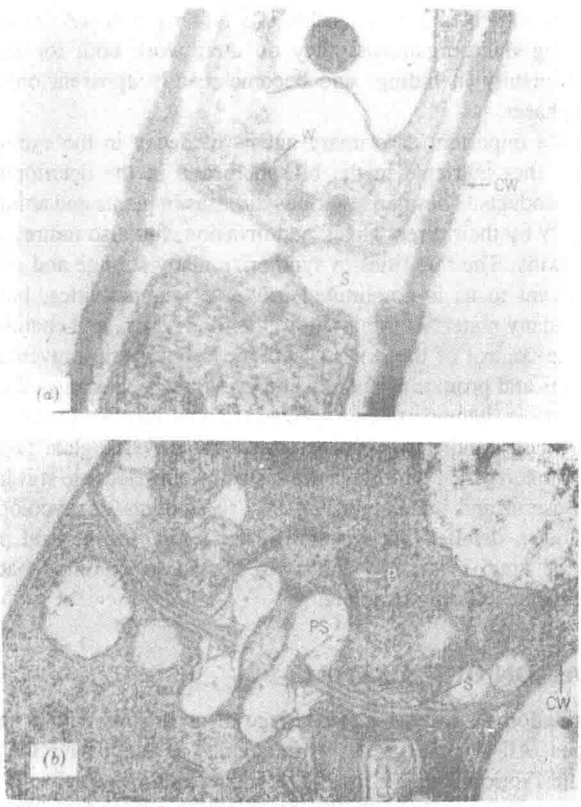

Figure 1 Septal pore structures of fungi. *(a)* Simple pore of *Oidiodendron griseum* (Deuteromycetes), magnification 36,000 × (courtesy of F. Terracina). *(b)* Dolipore of *Poria latimarginata* (Basidiomycetes), magnification 35,750 × (courtesy of H. Hoch and E. Setliff). Symbols: CW, cell wall; S, septum; W, Woronin granule; PS, septal pore swelling; P, parenthesome.

However, it is clear from observations with the light and electron microscopes, and from studies of nuclear migration with genetically marked nuclei, that considerable freedom of movement of nuclei and other hyphal constituents does occur under the appropriate circumstances.

The numbers of nuclei per segment are also variable (Kühner, 1977; Trinci, 1978). In some fungi the nuclei are strictly regulated to one per segment, but in many the numbers are variable. Often there is a large number, 100 or more, in the apical segment and progressively fewer nuclei in subapical segments so that only a few segments from the tip there is one nucleus per segment. The dicaryotic mycelium of the Basidiomycetes typically has two nuclei per segment that divide coordinately in a carefully regulated fashion. The very particular behavior of these nuclei is often, but not always, accompanied by the formation of specialized branches, the clamp connections, formed in association with the septa of these hyphae (Fig. 2).

The ready occurrence of anastomosis between hyphae and the subsequent nuclear migration between the fused mycelia creates heterocaryons, mycelia with two or more genetically different types of nuclei, adding to the genetic capabilities of the organism and permitting the asexual recombination of genetic material between nuclei in the hyphae. This phenomenon, known as parasexuality, occurs in place of or in addition to the normal sexual cycle of the fungus. It is genetic recombination without meiosis, thus the term, parasexuality. Mycelial fungi are able to maintain genetic variability within a single thallus with an extraordinary degree of flexibility, which is not found anywhere else among living things.

Hyphae forming the somatic body of the fungus are normally undifferentiated and unorganized. Differentiation normally occurs during reproduction, especially in the fleshy fruited fungi of the Ascomycetes and Basidiomycetes. However, some fungi produce differentiated somatic structures as well. There are two basic types (Fig. 3)—the rootlike mycelial strands and rhizomorphs, and the more compact hyphal masses, sclerotia.

The degree of differentiation of hyphae within these structures is quite varied,

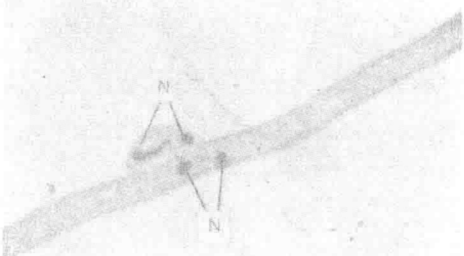

Figure 2 Clamp connection of *Coriolus versicolor* (Basidiomycetes), showing four nuclei (N) just after coordinate division, magnification 1700 × (courtesy of A. Robinson).

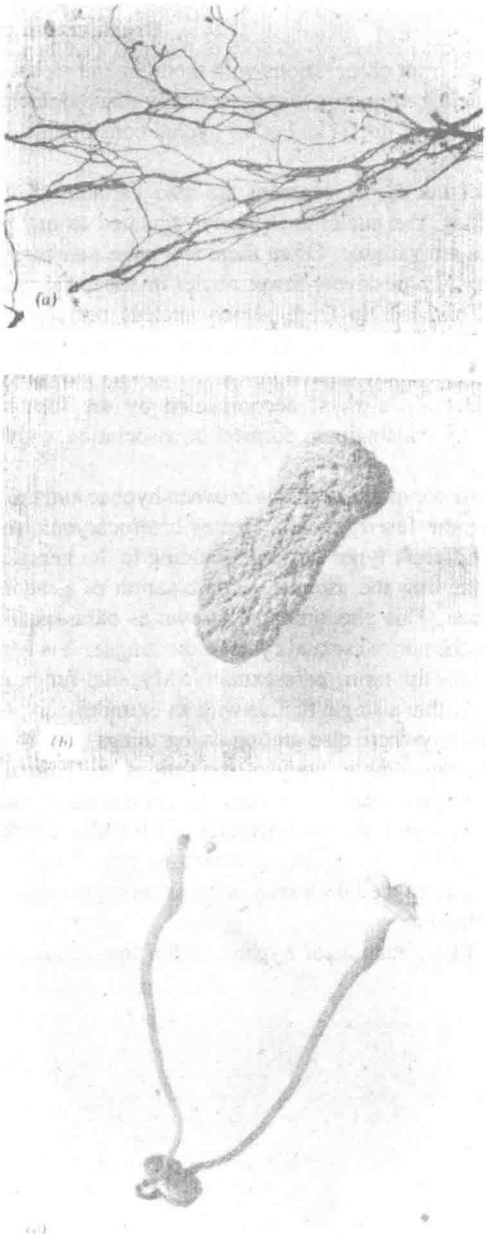

Figure 3 *(a)* Rhizomorphs of *Armillaria mellea* (Basidiomycetes), magnification 0.5 ×. *(b)* Sclerotium of *Sclerotinia sclerotiorum*, magnification 3.0 ×. *(c)* Sclerotium with apothecium of *S. sclerotiorum*, magnification 2.0 × (*b* and *c* courtesy of J. van Etten).

depending on the fungus. Hyphae may be easily recognizable in the structure of relatively undifferentiated strands and sclerotia, being only loosely aggregated. In more highly differentiated forms of these structures, the branching and septation of the hyphae becomes so intense that the filamentous character of the mycelium is no longer recognizable, and distinctly different tissue zones may also be formed. Sclerotia may be strictly vegetative structures, or they may be sites of sporulation in some Deuteromycetes, Ascomycetes, and Basidiomycetes.

Yeast

Yeast is a unicellular fungal form that has a cell wall and a single nucleus per cell. Yeast forms are widespread through many different fungal groups, although the term is often used as a common name for the yeastlike Ascomycetes. Many mycelial fungi are dimorphic. They have yeast stages in their life histories, and have the ability to grow either as yeast or as mycelium, depending on environmental conditions, giving another functional dimension to these organisms.

Although there is considerable variation in the form of yeast cells, there are two basic types, depending on the mode of cell division. The most prevalent type is the budding yeasts, in which cell reproduction occurs by the blowing out of a small portion of the cell wall and the subsequent growth of this bud into a full sized cell (Fig. 4-a). Septum formation at the isthmus separates the mother cell from the bud. The fission yeasts, the other form, do not bud, but elongate. Septum formation near the middle of the cell then divides the yeast into two daughter cells (Fig. 4-b).

Chytrid Thalli

Among the Mastigomycota there is a variety of nonmycelial thallus forms that are generally coenocytic in nature. The simplest, the holocarpic chytrid, is a single, saclike, multinucleate cell with no appendages or branches. Eucarpic chytrids have rhizoidal branches attached to the expanded portion of the thallus, which may itself be simple or branched (Fig. 5). Most chytrids have a determinant, limited growth habit, but others form a mycelium-like thallus, a rhizomycelium, of unlimited extent, consisting of a series of multinucleate centers connected by rhizoids. Many Mastigomycota form true mycelia; these generally lack septa.

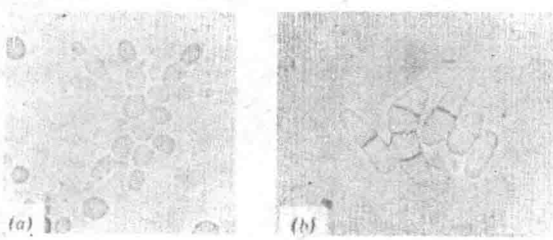

Figure 4 *(a)* Budding yeast cells of *Saccharomyces cerevisiae*, magnification 500 ×. *(b)* Fission yeast cells of *Schizosaccharomyces octosporus*, magnification 500 × (courtesy of C. J. K. Wang).

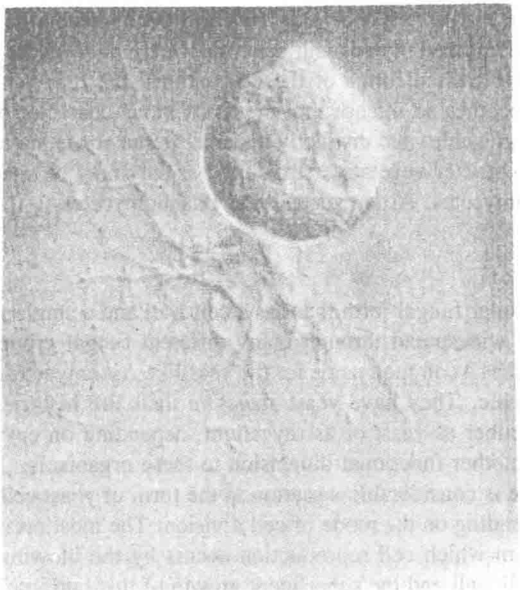

Figure 5 Eucarpic thallus of ***Rhizophydium sphaerotheca***, magnification 130 × (Gauriloff, 1978).

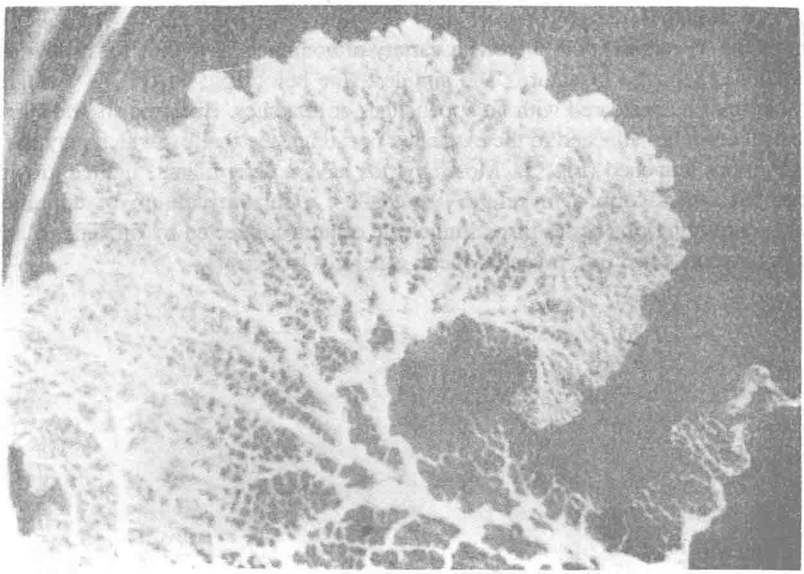

Figure 6 Plasmodium of ***Physarum gyrosum***, magnification 3 × (courtesy of C. J. Alexopoulos).

Plasmodia

Plasmodia are naked amoeboidal thalli, lacking cell walls. True plasmodia of the Myxomycetes may become very large, like mycelia (Fig. 6). They are diploid, multinucleate, and the nuclei divide synchronously. Plasmodia are much like mycelia in that they can fuse together, potentially forming heterokaryons and sharing genetic information within the same thallus through the anastomosing network of protoplasmic strands comprising them.

Another naked thallus type is the pseudoplasmodium of the Acrasiomycetes (Fig. 7). In this form the amoebae are the basic unit of structure; they are separate at first but then aggregate into multicellular masses that show differentiation and specialization of cells like a multicellular organism.

REPRODUCTION

The sexual reproduction of fungi is the primary basis for classification with asexual reproduction and, to a lesser extent, somatic structures used as secondary characters. The sexual reproduction of the fungi frequently, but not always, requires two genetically different individuals to achieve sexual combination. Such fungi are said to be heterothallic. When a single genetic strain of the fungus is capable of completing the sexual cycle by itself, it is said to be homothallic. In this section I briefly review the reproductive biology of the fungi in relation to their classification with representative life cycles for those fungi whose physiology has been studied extensively.

Gymnomycota

These are amoeboid organisms lacking cell walls in their somatic stages, and feeding by engulfment. They are more animal-like than fungal, but have traditionally been studied by mycologists. All form cell walls about their spores and supporting structures during sporulation. The division Gymnomycota is divided into three classes, Acrasiomycetes, Myxomycetes, and Protosteliomycetes. Only the Acrasiomycetes and Myxomycetes have been studied by physiologists.

The Acrasiomycetes, typified by *Dictyostelium* (Fig. 7), produce uninucleate amoebae upon spore germination; these amoebae feed and divide, increasing their numbers. They may form a multicellular mass called a pseudoplasmodium, or grex, by the aggregation of a population of amoebae to a central location. The grex is a truly multicellular organism which moves, responds to stimuli, and ultimately forms spores on a structure called a sorocarp.

The Myxomycetes, represented by *Physarum*, form myxamoebae or swarm cells on germination of their spores. Myxamoebae and swarm cells are interconvertible amoeboid forms; the swarm cells are flagellate and the myxamoebae are nonflagellate forms. These cells may feed and divide, or they may fuse in pairs forming diploid cells that no longer divide after nuclear division, but instead grow into multinucleate giant amoeboid thalli called plasmodia (Fig. 6). Plasmodia may fuse with others, or they may break up into smaller plasmodia. Plasmodia sporulate by forming spores within a sporangiumlike structure with an outer wall and a noncellular stalk.

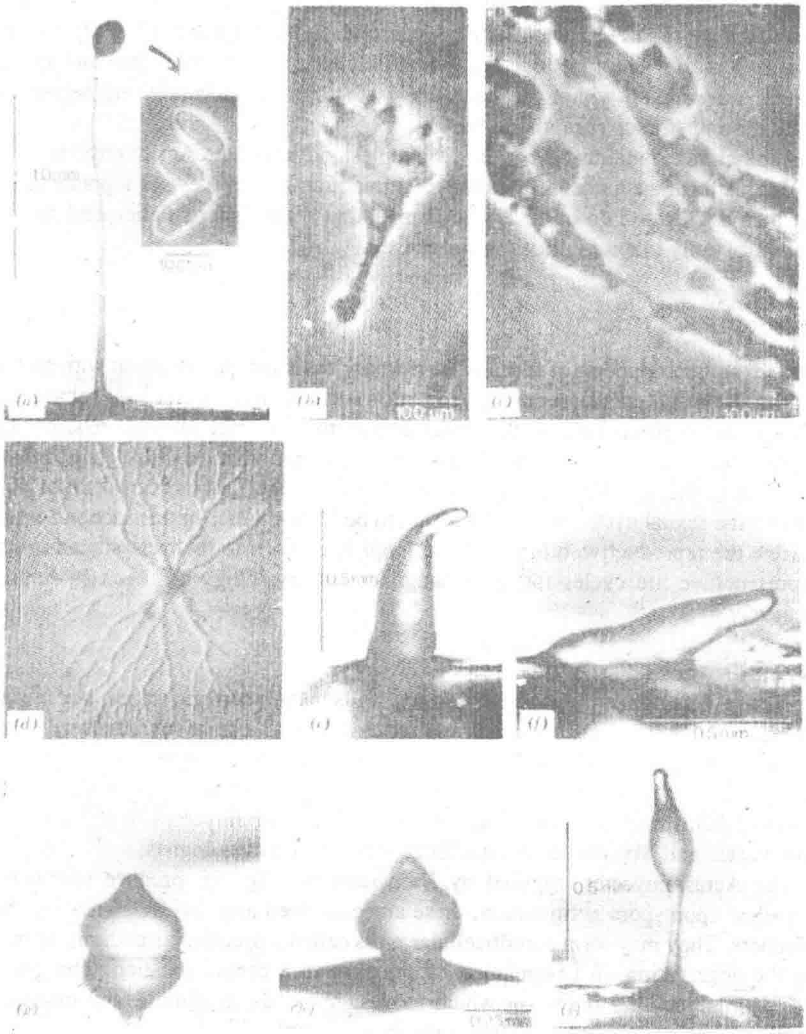

Figure 7 *Dictyostelium discoideum* (Gregg, 1966). *(a)* Mature sorocarp and spores. *(b)* Vegetative amoeba. *(c)* Amoebae in aggregation streams. *(d)* Pattern of aggregation. *(e)* Late aggregation. *(f)* Grex. *(g)* Preculmination. *(h* and *i)* Culmination.