FUNGAL PATHOLOGY

Fungal Pathology

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SPRINGER-SCIENCE+BUSINESS MEDIA, B.V.

Library of Congress Cataloging-in-Publication Data

Fungal pathology / edited by J.W. Kronstad.
p. cm.
ISBN 978-90-481-5483-8 ISBN 978-94-015-9546-9 (eBook)
DOI 10.1007/978-94-015-9546-9
1. Mycoses. 2. Medical mycology. I. Kronstad, James Warren.

QR245 .F8535 2000
579.5'165--dc21

00-033061

ISBN 978-90-481-5483-8

Printed on acid-free paper

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PREFACE

This book brings together twelve chapters on fungal pathogens with the goal of presenting an overview of the current areas of activity and the common themes that pervade research on these important organisms. The timing of the book is appropriate because we have gained sufficient insight from molecular genetic analyses to begin to make some comparisons between different fungal pathogens and to discuss the key advances that have been made. The chapters provide a broad survey of the important topics in fungal pathogenesis including morphogenesis, virulence, avirulence, and signaling. The reader also will find clear discussions of parasitism, mutualism, symbiosis, evolution, phylogeny and ecology for those fungi where these issues are especially important. Finally, many of the chapters in this book illustrate the fact that we are on the verge of a revolution in our understanding of fungal pathogens because of the application of genomics to these organisms and their hosts.

The fungi included in this book represent many of the most intensively investigated fungal pathogens of plants; in this regard, a chapter is also included for pathogens in the *Phytophthora* group, even though these organisms are no longer classified as fungi. It is appropriate to include *Phytophthora* for historical reasons and, in addition, the insights in terms of pathogenesis and host-specific interactions are important to keep in mind when considering fungal pathogens. Chapters are also included on pathogens of insects and humans, as well as endophytic fungi. The endophytic fungi provide fascinating examples of the impact of fungi on human activities and food production including the influence on livestock. The chapters on the pathogens of insects and humans (*Aspergillus fumigatus*) are useful to provide comparisons with plant pathogens. It is clear that fungal pathogens share common suspected virulence properties (e.g., degradative enzymes) whether they attack plants or animals. These chapters also provide a perspective on how similar experimental questions and problems face investigators working on any fungal pathogen, no matter what the host. Although not included in this book, other fungal pathogens of animals have emerged as important models for understanding virulence. For example, information on *Candida albicans* and *Cryptococcus neoformans* is valuable for scientists working on plant pathogens to consider, particularly in the areas of attachment to host tissue and signal transduction. However, in this book we have limited ourselves to fungi that primarily display a filamentous growth morphology.

Space limitations and other constraints prevented the inclusion of chapters for other prominent plant pathogens such as the powdery and downy mildews, *Fusarium*, *Ophiostoma*, *Rhyncosporium*, and *Rhizoctonia*. These fungi will undoubtedly soon be included in other books on this subject. Fungicide resistance is also largely untouched in these chapters although some information on drug resistance is included for *A. fumigatus*. The reader is referred to an excellent web site for information on other plant

pathogens and links to mycology resources to investigate these fungi (http:www.ifgb.uni-hannover.de/extern/ppigb/ppigb.htm)

Taken together, the chapters in this book present an excellent survey of the areas of investigation at the forefront of fungal pathogenesis. As the reader will note, many but not all of these chapters begin with a description of the interaction of the fungus with the host during the initiation of infection. Typically this involves the attachment or adhesion of a spore followed by germination, formation of infection structures or an infectious cell type and penetration of the host. The formation of infection structures such as appressoria have received considerable experimental attention. This is particularly true for *Magnaporthe grisea*, *Colletotrichum* spp., the insect pathogens and the rust fungi. In this regard, it is interesting to note the similarities between plant and insect pathogens (e.g., Chapters 7 and 8). The best view of appressorium formation has been developed for *M. grisea* and the genomic efforts with this fungus soon will undoubtedly reveal a detailed and complete view of the process in this fungus. The similarities between many of the fungal plant pathogens (and the insect pathogens) suggest that *M. grisea* will emerge as the paradigm for this process. It will be interesting to see whether the information from *M. grisea* will be applicable to fungi such as *Botrytis cinerea* where there is still debate about whether true infection structures are formed.

There are two other areas of note in the context of fungal differentiation during infection. These are the formation of the infectious dikaryon during the entry of *Ustilago maydis* (Chapter 12) into maize tissue and the formation of haustoria by rust fungi and other biotrophs (Chapter 10). The work on *U. maydis* provides interesting insight into the specialized role of mating-type loci in the disease process and the interconnections between pathogenesis, morphogenesis and sexual development. The chapter by Hahn (Chapter 10) provides an up to date view of haustoria in the rust fungi and the considerations for a molecular description of this process. This chapter provides an excellent description of the use of molecular approaches to identify fungal genes that are induced during the interaction of the rust with the host. A picture is emerging of the molecular details of nutrient transfer during the biotrophic interaction. Good comparisons can also be made with biotrophic growth for both *U. maydis* and *Cladosporium fulvum* (Chapter 3). Along with the work on rusts, these fungi also provide good examples of the efforts to identify and characterize fungal genes whose transcription is induced during the biotrophic interaction with the host. Similar information is also provided for *Phytophthora* spp. in Chapter 9. In addition, these chapters include information on the nutritional challenges that fungi face upon entry into the host. For example, Chapter 3 describes the results of a search for genes that are induced by starvation in *C. fulvum*. Biotrophic development also is described for *Colletotrichum* spp. in Chapter 5.

The identification and evaluation of virulence factors is a common theme for many of the chapters in this book. Restriction enzyme mediated insertion (REMI) has been a powerful tool for identifying virulence genes for a number of pathogens including *A. fumigatus*, *C. heterostrophus*, *U. maydis* and *Colletotrichum*. As noted in Chapter 3, the technique has not worked to date for *Cladosporium*. The best examples of virulence factors continue to be the host specific toxins defined for

Cochliobolus species, although toxins may also be important for *Botrytis cinerea*, *A. fumigatus* and for some of the insect pathogens. Other virulence factors include cell wall degrading enzymes and proteases as well as factors to avoid the host defense response (e.g., suppressins and antioxidant enzymes). Degradative enzymes are discussed in detail in the chapters on *A. fumigatus*, *B. cinerea*, the rust fungi, and the insect pathogens. The description of hypovirulence in *Cryphonectria parasitica* (Chapter 6) provides a fascinating example of how hypoviruses can attenuate fungal virulence. The detailed investigation of hypovirulence illustrates the importance of signal transduction in the interaction of fungi with their hosts (see below). An emerging and potentially novel story for virulence concerns the work on the path-1 mutant of *Colletotrichum magna* described in chapter 5. This mutant is able to colonize host plants but fails to cause disease. Interestingly, the mutant may stimulate a defense response and provide protection from infections by other pathogens. Other factors involved in virulence include the production of phytohormones (described for *B. cinerea* and *U. maydis*), the formation of melanin as a protective agent (*A. fumigatus*) or as part of infection structure formation (*M. grisea, Colletotrichum*), and the synthesis of hydrophobins by several pathogens.

Investigators are starting to accumulate avirulence genes from fungal pathogens and we will hopefully reach a level of understanding similar to that available for bacterial plant pathogens in the near future. Of course, the best studied system continues to be the *C. fulvum* - tomato interaction in which both avirulence gene products and the corresponding R genes in tomato have been characterized. Avirulence genes from *M. grisea* have also been characterized in detail and corresponding host R genes have been identified (Chapter 8). Information is also accumulating rapidly for avirulence elicitors in *Phytophthora* (Chapter 9). The chapters on rust fungi and *B. cinerea* also include information the interaction of the pathogens with the host defense response including elicitation and evasion of the host defense response. An interesting aspect of *B. cinerea* infections is the initiation of quiescent infections in which there is a delay in the formation of discernible symptoms. Host specialization, as describe in Chapter 11, also is an interesting aspect of the interactions between clavicipitaceous symbionts and grass species.

One area that has received tremendous attention in recent years is the role of signal transduction as a key aspect of fungal pathogenesis. Much of this work focuses on signaling and morphogenesis in *C. parasitica, M. grisea, U. maydis, Colletotrichum*, and the insect pathogens. This aspect of fungal pathogenesis has also proven to be very important in animal pathogens such as *Candida albicans* and *Cryptococcus neoformans*. As mentioned above, the story of hypovirulence for *C. parasitica* has provided an excellent illustration of the importance of signaling in virulence. Much of the work to date on fungal pathogens has involved identifying components of the signaling pathways (e.g., MAPK module genes, cAMP pathway genes). It will be particularly interesting to use our understanding of the signaling pathways to identify the upstream signals that will provide insight into the key features of the host that are perceived by pathogens. Also the detailed description of the downstream targets of the signaling pathways should provide a view of the connections

between protein kinases (e.g., MAP kinases and PKA) and key factors involved in morphogenesis and virulence.

Finally, it is important to point out the common theme of genomics that pervades the chapters in this book. The chapters on *Phytophthora*, *C. heterostrophus* and *M. grisea*, in particular, include interesting information of genome structure. This is just the first glimmer of big things to come. Genomics projects are underway for many fungi and host species including most of the ones described in this book. For example, a review of the chapters will reveal discussions on genomics for *U. maydis*, *M. grisea* (and rice), *A. fumigatus*, *Phytophthora*, *Cochliobolus*, and the rust fungi. The application of genomics to fungal pathogenesis will open up a tremendous number of avenues of investigation and it is clear that we are on the verge of an amazing leap forward in our understanding of the pathogens and their interactions with hosts. In addition to the collection of EST and genomic sequence information, we will soon see microarray experiments with these fungi and their hosts.

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