

Essential Fungal Genetics

Springer

New York

Berlin

Heidelberg

Barcelona

Hong Kong

London

Milan

Paris

Singapore

Tokyo

David Moore LilyAnn Novak Frazer

Essential Fungal Genetics

With 59 Illustrations



Springer

David Moore
School of Biological Sciences
The University of Manchester
Manchester M13 9PT
UK
david.moore@man.ac.uk
www.oldkingdom.org

LilyAnn Novak Frazer
Response Environmental Technologies
Limited
Abbeyfield House
Blyth Road
South Yorkshire S66 8HX
UK
Lily.Nfrazer@response-uk.com

Library of Congress Cataloging-in-Publication Data

Moore, D. (David), 1942–

Essential fungal genetics/David Moore, LilyAnn Novak Frazer.

p.;cm.

Includes bibliographical references and index.

ISBN 0-387-95367-1 (h/c: alk. paper)

1. Fungi—Genetics. I. Frazer, LilyAnn Novak, 1965– II. Title.

[DNLM: 1. Fungi—genetics. 2. Genome, Fungal. QK 602 M821e 2002]

QK602 .M66 2002

579.5'135—dc21

2001054910

Printed on acid-free paper.

© 2002 Springer-Verlag New York, Inc.

All rights reserved. This work may not be translated or copied in whole or in part without the written permission of the publisher (Springer-Verlag New York, Inc., 175 Fifth Avenue, New York, NY 10010, USA), except for brief excerpts in connection with reviews or scholarly analysis. Use in connection with any form of information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed is forbidden.

The use in this publication of trade names, trademarks, service marks, and similar terms, even if they are not identified as such, is not to be taken as an expression of opinion as to whether or not they are subject to proprietary rights.

Production coordinated by Chernow Editorial Services, Inc., and managed by Francine McNeill; manufacturing supervised by Jerome Basma.

Typeset by SNP Best-set Typesetter Ltd., Hong Kong.

Printed and bound by Maple-Vail Book Manufacturing Group, York, PA.

Printed in the United States of America.

9 8 7 6 5 4 3 2 1

ISBN 0-387-95367-1

SPIN 10853243

Springer-Verlag New York Berlin Heidelberg

A member of BertelsmannSpringer Science+Business Media GmbH

Preface

Our intention in writing this book is to provide a text that offers a succinct but comprehensive account of the genetics of Kingdom Fungi. We do not pretend that this is a monographic textbook, nor do we intend it to be a laboratory manual. Rather, we hope that it will be a user-friendly guide that can be used as a supplement to general genetics texts.

Most genetics textbooks deal adequately with plant and animal genetics. Even at an elementary level, a description of Mendel's experiments with peas is rapidly followed by the description of Morgan's experiments with the fruit fly. Thus, right from the start plant and animal work is well integrated in the learner's mind.

This treatment unfortunately leaves the student ignorant of an entire kingdom of organisms. There are three major kingdoms of eukaryotes on Earth: plants, animals, and fungi. For the most part, fungi feature regularly in only two areas of traditional genetics teaching. On the one hand, we can find the ascus segregations that contributed so much to developing an understanding of the mechanism of recombination in the 1960s. On the other hand is the contribution work on yeast (as a model eukaryote) is currently making to understanding "cell cycle control" and its genetic regulation. As a result, most introductory genetics texts will leave the reader/student with the impression that fungi are of use when peculiarities of their structure or lifestyle suit them to particular experimental approaches, but are not worth mentioning otherwise!

We cannot redress the balance totally, but we hope we have produced a book that displays the genetics of fungi in a way that will be attractive and challenging, comprehensive yet succinct. This book will provide the tools for integrating fungal genetics into current teaching by complementing the major textbooks used in courses on general genetics, general organismal biology, general microbiology, and general mycology.

Our aim is to preserve the concepts that characterize fungal genetics, revealing the mixture of facts, techniques, and experimental approaches that distinguish fungal genetics as a study in its own right. We believe we have incorporated the full range of genetic information so that all aspects

of eukaryote genetics appropriate to fungi are described here in a way that is easily understood and memorable.

Without attempting to be a laboratory manual, this book has an instructional “how to do it” tone and will therefore have a practical value for anyone who has a mind to start genetic analysis of any fungus. Instead of dwelling on technical details like laboratory recipes, this book deals with the details of the ideas and concepts underlying basic approaches to fungal genetics so that these are on record and easily accessible rather than being lost in history, or buried by the great mountains of molecular methodologies.

We have tried to maintain a readable style of presentation, and to that end, there are no reference citations in the text; however, we provide a range of reference materials at the end of each chapter, and the number of references increases in later chapters as we touch on wider topics. We have favored review articles and Websites for these reference lists, so that the interested reader can very quickly penetrate deeper into the literature. More recent publications are also emphasized, but we also recognize the value of the history of the science and give references to some historical publications. For some of us (DM included), “history” is unfortunately deemed to start in about the 1980s. Doesn’t time fly!

Another unusual aspect is that the examples we have chosen to illustrate various features tend, whenever possible, to favor basidiomycetes and the less-often referenced fungi. We have done this because it is relatively easy to find information about the main “models,” like *Neurospora* and *Aspergillus*, so we prefer to describe other species. Of course, we can’t escape “yeast,” the ultimate model eukaryote, and the first eukaryote to have its genome completely sequenced. We try to emphasize, however, that no matter how much we learn about *Saccharomyces cerevisiae*, it is not the end of the story. No matter how important it is as a “model,” this yeast is not adequately representative of filamentous fungi, nor does it represent other yeasts. When you know everything there is to know about *S. cerevisiae*, you will still be ignorant about fungal genetics. So read on, and get an impression of the full story!

David Moore
LilyAnn Novak Frazer
Manchester, United Kingdom
August 2001

Contents

Preface	v
Chapter 1 Why Study the Genomes of Fungi?	1
Revision Concepts	1
1.1 Origins	2
1.2 Diversity in the Kingdom Fungi: Chytridiomycota, Zygomycota, Ascomycota, and Basidiomycota	8
1.3 Fungi in Nature	14
1.4 Fungi in Technology	17
1.5 Fungi as Models	19
1.6 Genes to Genomics	21
Publications and Websites Worth a Visit	24
Historical Publications Worth Knowing About	25
Chapter 2 Genome Interactions	26
Revision Concepts	26
2.1 Fungal Lifestyles: Hyphal Fusions Are the Key to Advanced Hyphal Systems	28
2.2 Population Biology Aspects of Compatibility Systems	34
2.3 Compatibility and the Individualistic Mycelium	39
2.4 Nuclear Migration	44
2.5 Other Incompatibility Reactions	48
2.6 Structure and Function of Mating-Type Factors: Mating-Type Factors in <i>Saccharomyces cerevisiae</i>	51
2.7 Structure and Function of Mating-Type Factors: Mating-Type Factors of <i>Neurospora</i>	55
2.8 Structure and Function of Mating-Type Factors: Mating-Type Factors in <i>Ustilago maydis</i>	59
2.9 Structure and Function of Mating-Type Factors: Mating-Type Factors in <i>Coprinus cinereus</i> and <i>Schizophyllum commune</i>	62
2.10 Overview: Biology of Incompatibility Factors	67

	Publications and Websites Worth a Visit	69
	Historical Publications Worth Knowing About	70
Chapter 3	Wild Types and Mutants	71
	Revision Concepts	71
3.1	Phenotypes and Genotypes: Variations and Mutations	72
3.2	Molecular Nature of Mutation	74
3.3	Natural Variation and Spontaneous Mutation	76
3.4	Generating Mutants: Mutagenesis	77
3.5	Generating Mutants: Irradiation	79
3.6	Generating Mutants: Chemical Mutagens	81
3.7	Types of Functional Mutant	83
3.8	Isolating Auxotrophic Mutants	84
3.9	Resistance Mutations	89
3.10	Reverse Mutation: From Auxotroph to Prototroph	90
3.11	Molecular Variants	91
	Publications and Websites Worth a Visit	93
	Historical Publications Worth Knowing About	94
Chapter 4	Segregation Genetics: The Indirect Approach	96
	Revision Concepts	96
4.1	Complementing Mutants	97
4.2	Adenine Auxotrophs of <i>Coprinus</i>	98
4.3	Functional Allelism	104
4.4	Gene Segregation Depends on the Behavior of Chromosomes During Nuclear Division	106
4.5	Meiosis	107
4.6	Analyzing Gene Segregations from Random Spores	109
4.7	Use of χ^2 Tables	111
4.8	Testing for Homogeneity	113
4.9	Detecting Linkage	118
	Publications and Websites Worth a Visit	120
	Historical Publications Worth Knowing About	121
Chapter 5	Recombination Analysis	122
	Revision Concepts	122
5.1	Linkage Studies Make Maps	124
5.2	Multipoint Crosses	126
5.3	Rules of the Three-Point Crosses Game	129
5.4	A Three-Point Cross in <i>Coprinus</i>	130
5.5	Mapping Centromeres Using Gene Segregations in Tetrads and Eight-Spored Asci (Octads): Single Gene Segregations	132
5.6	Mapping Using Multiple Gene Segregations in Tetrads and Octads	135

5.7	Unordered Tetrads	140
5.8	Linkage Analysis to Linkage Map	145
5.9	Tetrad Segregations Leading to Secondary Homothallism	146
5.10	Gene Segregation During the Mitotic Division Cycle	147
5.11	Cytoplasmic Segregations: Mitochondria, Plasmids, Viruses, and Prions	154
	Publications and Websites Worth a Visit	159
	Historical Publications Worth Knowing About	160
Chapter 6	Mechanisms of Recombination	161
	Revision Concepts	161
6.1	Gene Conversion	162
6.2	Hybrid- or Heteroduplex-DNA	164
6.3	A Basic Mechanism for Recombination	166
6.4	Correction of Base Mismatches in Heteroduplex-DNA Generates Aberrant Segregation Ratios	170
6.5	Modifying the Basic Recombination Model	172
6.6	Models and the Real World	177
	Publications and Websites Worth a Visit	182
	Historical Publications Worth Knowing About	183
Chapter 7	The Physical Genotype	184
	Revision Concepts	184
7.1	Molecular Markers	186
7.2	DNA Polymorphisms	187
7.3	Restriction Fragment Length Polymorphisms	188
7.4	Polymerase Chain Reaction	192
7.5	PCR Primers: AP-PCR and RAPD	193
7.6	Single-Strand Conformation Polymorphisms	195
7.7	DNA Fingerprinting	196
7.8	Microsatellites	199
7.9	Minisatellites	200
7.10	Transposable Elements	201
7.11	Genes and Spacers	204
7.12	Electrophoretic Karyotypes	205
	Publications and Websites Worth a Visit	207
	Historical Publications Worth Knowing About	209
Chapter 8	Genes to Genomics: Mapping the Fungal Genome	211
	Revision Concepts	211
8.1	Genes and Maps: The Story So Far	212
8.2	Physical Maps	215
8.3	Restriction Mapping: A Real-Life Example	216
8.4	Optical Mapping	223

8.5	DNA Cloning: Plasmids, Cosmids, BACs, and YACs	225
8.6	Chain Termination Sequencing	227
8.7	The First Complete Eukaryotic Genome Sequence: <i>Saccharomyces cerevisiae</i>	233
8.8	Comparisons Between Genomes	236
	Publications and Websites Worth a Visit	240
	Historical Publications Worth Knowing About	243
Chapter 9	Systematics, Phylogeny, and Evolution	245
	Revision Concepts	245
9.1	Phylogenetics: Inferring Evolutionary Development	246
9.2	The Molecule Is the Message	248
9.3	Inferring Relationships	251
9.4	Making Trees Make Sense	256
9.5	Horizontal Transfer of Genetic Information	261
9.6	Genes in Populations	262
9.7	Genes in Fungal Populations	266
9.8	Genetic Variation in Hosts and Pathogens	270
9.9	Evolution in Captivity: Natural and Artificial Selection	273
9.10	Mycotechnology	275
	Publications and Websites Worth a Visit	279
	Historical Publications Worth Knowing About	281
Chapter 10	The Genetics of Fungal Differentiation and Morphogenesis	282
	Revision Concepts	282
10.1	Differentiation and Morphogenesis	284
10.2	Genetic Approaches for Analyzing Gene Regulation	286
10.3	Regulating Gene Expression: DNA-Binding Proteins	288
10.4	Regulating Gene Expression: Chromatin Remodeling	290
10.5	Regulating Gene Expression: Transcription	292
10.6	Galactose Utilization in Yeast: The Epitome of Eukaryote Regulation	295
10.7	Regulating Gene Expression: Repression and Silencing	298
10.8	Regulating Gene Expression: High-Level Control Mechanisms, DNA Modification, and Epigenetics	300
10.9	Posttranscriptional Regulation: Spliceosomes, Proteasomes, and Protein Networks	305
10.10	Shape, Form, and Differential Gene Expression	310
10.11	Yeast–Mycelial Dimorphism	311
10.12	Conidiation: Translational Triggering and Feedback Fixation	315

10.13	Sexual Reproductive Structures in Ascomycetes and Basidiomycetes	321
10.14	Genetic Control of Morphogenesis of Fungal Fruit Bodies	332
	Publications and Websites Worth a Visit	339
	Historical Publications Worth Knowing About	341
	Index	343