

Soil Biology 36

Benjamin A. Horwitz
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Christian P. Kubicek *Editors*

Genomics of Soil- and Plant- Associated Fungi

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Editors

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Foreword

Fungi, the “fifth kingdom” of living beings, comprise a wide variety of eukaryotic heterotrophs including mushrooms, rusts, truffles, morels, molds, yeasts, and many more families, genera, and taxa that are less well known. Their total number has been estimated to be in the range of 1.5 million species. Fungi have traditionally been considered to be microorganisms, because of the tiny hyphal filaments that are formed in laboratory cultivations. However, these hyphae can form extensive networks in their natural habitats, whose biomass is not smaller than that of large animals or plants.

Fungi have also developed numerous lifestyles: saprotrophs break down dead organic material and thus importantly contribute to nutrient cycling within the ecosystem. Yet many other fungi are biotrophs and form symbiotic associations with plants (mycorrhizae), algae (lichens), arthropods, and even prokaryotes. In fact, more than 80 % of the vascular land plants are obligatorily dependent on mycorrhizal symbioses with fungi. More recently, facultative and obligate endophytes of various plant tissues have also been discovered, and there is evidence that they can protect the plants against biotic and abiotic stress.

In order to be successful in their habitats, fungi have developed various successful strategies such as the ability to export hydrolytic enzymes to break down biopolymers or to produce chemicals that can antagonize competing organisms. Some of these properties have been exploited by humans for the production of goods for a long time: production of ethanol by the yeast *Saccharomyces cerevisiae* is the oldest example of the use of fungi for mankind and is experiencing a revival in this decade because of the interest in production of biofuels from renewable resources. Other 60-and-more-year-old examples are penicillin production by *Penicillium chrysogenum* and citric acid production by *Aspergillus niger*. These processes led to a more systematic exploitation of fungi and consequently the development of a number of biotechnological processes for the production of enzymes (such as cellulases, amylases, lipases, and glucose oxidase); platform

chemicals such as citric acid, itaconic acid, and gluconic acid; and numerous secondary metabolites that proved successful in medicine (e.g., penicillin, cephalosporin, cyclosporine, lovastatin). Due to the high secretory capacity that was detected in the enzyme producers, fungi have also been used as workhorses for the production of mammalian and plant proteins, which are only of limited availability from their native producer (e.g., chymosin). Finally, because fungi share a significant part of their gene repertoire with higher organisms, but can easily be studied and manipulated in the lab, some of them (e.g., *S. cerevisiae*, *Schizosaccharomyces pombe*, *Aspergillus nidulans*, *Neurospora crassa*) have extensively been used as model systems for basic biological processes such as the cell cycle, reproduction, or the circadian rhythm.

On the other side, many fungi also have negative impacts on mankind: the majority of contemporary plant diseases are caused by fungi and can achieve epidemic dimensions like the Dutch elm disease caused by *Ophiostoma ulmi* or chestnut blight by *Cryphonectria parasitica*. They also lead to large losses of nutritionally required crop plants by either affecting plant biomass formation (like the rice pathogen *Magnaporthe grisea*) or simply due to the secretion of mycotoxins (such as aflatoxin formation by *Aspergillus flavus*) and thus spoiling the harvest. Many other fungi can act as parasites of animals including humans, such as *Cryptococcus neoformans* that causes fungal meningitis. More recently, several fungi have proven to be opportunistic facultative pathogens, which do not target animals or humans regularly but can establish themselves in the body of immunocompromised individuals. In addition, many fungi have developed mechanisms to settle in the most extreme habitats and can occupy, e.g., building walls, thereby giving rise to “indoor contamination,” or simply cause biodeterioration of materials, particularly manufactured wood.

In view of all these diverse activities, it is not surprising that fungi have also been intensively investigated towards detecting the mechanisms that form the basis of the various positive or negative effects. The final aim is to find tools that can be used either to increase their beneficial action or to combat their negative impact. This was, however, significantly impeded in those fungi where appropriate genetic systems to map mutations and cross mutants were unavailable. Today, the development of techniques to sequence, assemble, and annotate whole genomes and to functionally analyze their contents by systems biological approaches (transcriptomics, proteomics, metabolomics, and other “omic” technologies) has eliminated this bottleneck. The first major fungal genomics milestone was the publication of the whole genome sequence of the yeast *S. cerevisiae* 17 years ago. Today, more than 100 fungi had their genomes sequenced, and although this number is dominated by fungi of medical importance, genomic insights are already available for many other fungi. Today, we have arrived in several cases at first systematic insights into how fungi use their genetic repertoire for their specific behavior.

This book reviews the current state in our genomic understanding of those fungi which are primarily soil inhabitants and also those which interact with plants, whereby both positive and negative interactions will be covered. The comparison of their genomes reveals the various strategies, by which fungi use a basically similar repertoire of genes for differing purposes, and offers fascinating possibilities for future research.

Vienna, Austria

Christian P. Kubicek

Preface

Fungi have a major role in natural ecosystems and in agriculture. This is particularly relevant for fungal species whose main niche is either soil, rhizosphere, plant roots, or above-ground plant tissues. The sequences of fungal genomes provide a new window to observe and understand how fungi recycle organic material in the soil, engage in positive and negative interactions with plant roots, and attack plants as pathogens. An unprecedented amount of sequence information has accumulated over the past decade, and researchers are now looking for ways to extract biological information. We assembled this volume in the hope that comparison across species will help bring focus to what is similar or different in the genomes of soil saprophytes, symbionts, and plant pathogens. There are now so many sequences that any attempt to catalog what is known for all fungi would require not one but tens of volumes and would quickly become out of date. Rather, we chose examples of species where particular principles can be illustrated. The reasons are diverse: from importance in ecology, agriculture, or medicine to model species that may have been convenient for applying a certain technique. If the approaches from one species eventually lead to fruitful work in another, we will be able to look back on a successful contribution to the science of fungi in its new genomic framework.

We are grateful to the authors of the chapters of this volume for all their thoughts and efforts. In particular, each chapter develops a unique approach that often reflects not only the fungal species studied but also the viewpoint, research priorities, and expertise of the research community studying each species. The fungal genome sequencing projects are the source of this book, which two decades ago would have been difficult to even imagine. Many of the contributors have been central participants in the genome projects or guiding future ones, and we hope to share the satisfaction of seeing a growing contribution of the genomics of soil, rhizosphere, and plant-interacting fungi to ecology, biotechnology, and sustainable agriculture. We would like to express our sincere thanks to the series editor Prof. Dr. Ajit Varma for supporting this project from the start and for his help in

bringing this volume to completion. It has been a pleasure to edit the volume, primarily due to the stimulating cooperation of the contributors. We wish to thank Hanna Hensler-Fritton and Jutta Lindenborn, Springer Heidelberg, for their generous assistance and patience in finalizing the book.

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Chapter 1

Genomic Contributions to the Study of Soil and Plant-Interacting Fungi

Benjamin A. Horwitz, Prasun K. Mukherjee, Mala Mukherjee,
and Christian P. Kubicek

1.1 Introductory Remarks

The first filamentous fungal genome published was of *Neurospora crassa* (Galagan et al. 2003), one of the classical genetic model systems (Davis and Perkins 2002; Perkins 1992). It is obvious, though, that not everything can be learned from the genome of a single species. Fungi are very versatile and degrade almost any substrate. The niche occupied by a given fungal species can be anywhere from very wide to very narrow. It was logical, therefore, to ask whether the genomes of plant pathogens would differ from saprophytes, and how. The sequence of rice blast as “the” model plant pathogen (Dean et al. 2005) indeed began to provide insight into what makes a pathogen different, with expanded families encoding signal transduction machinery, secondary metabolism, and possible virulence-related proteins. Later, though, the choice of species to sequence followed a more complicated path, guided by medical or agricultural importance, or by the activity of the research groups working on a particular group of fungi. Although different questions have been pursued in different species, there are unifying themes. Some of these themes are set by basic biology, for example, protein kinase genes related to the cell cycle, or the fundamental structure of the fungal cell wall. Others are related to interaction with other organisms: small secreted proteins that act as

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