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Mini review

Sordaria macrospora, a model organism to study fungal cellular development

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ABSTRACT

During the development of multicellular eukaryotes, the processes of cellular growth and organogenesis are tightly coordinated. Since the 1940s, filamentous fungi have served as genetic model organisms to decipher basic mechanisms underlying eukaryotic cell differentiation. Here, we focus on *Sordaria macrospora*, a homothallic ascomycete and important model organism for developmental biology. During its sexual life cycle, *S. macrospora* forms three-dimensional fruiting bodies, a complex process involving the formation of different cell types. *S. macrospora* can be used for genetic, biochemical and cellular experimental approaches since diverse tools, including fluorescence microscopy, a marker recycling system and gene libraries, are available. Moreover, the genome of *S. macrospora* has been sequenced and allows functional genomics analyses. Over the past years, our group has generated and analysed a number of developmental mutants which has greatly enhanced our fundamental understanding about fungal morphogenesis. In addition, our recent research activities have established a link between developmental proteins and conserved signalling cascades, ultimately leading to a regulatory network controlling differentiation processes in a eukaryotic model organism. This review summarizes the results of our recent findings, thus advancing current knowledge of the general principles and paradigms underpinning eukaryotic cell differentiation and development.

Introduction

Fungi represent a separate eukaryotic kingdom which is clearly distinct from plants and animals. Currently, about 100,000 fungal species have been described, but conservative predictions suggest that there are around 1.5 million fungal species on earth (Burton et al., 2002; Hawksworth, 2001; Stajich et al., 2009). Fungi have a high relevance for basic as well as applied science. For example, they are pathogens of humans, animals or plants, live in symbiotic relationships with plants, and are beneficial as producers of, e.g. antibiotics in the pharmaceutical or food industry. Evidence from molecular work on DNA and proteins has shown that fungi are more closely related to animals than to plants, thereby making them favourable models for human cells. Thus, fungi are attractive organisms to investigate fundamental processes of the eukaryotic cell and several eukaryotic model organisms can be found in the class of ascomycetes, a major fungal subkingdom-level taxon.

Irrespective of their taxonomy two morphological groups of fungi can be distinguished: yeasts and filamentous fungi. While yeasts are mostly unicellular fungi which show a quite simple morphological differentiation, filamentous fungi form a broad variety of cellular structures. During sexual development, for example, they form complex fruiting bodies which are characterized by specialized tissues harbouring and protecting the meiosporangia. Although fruiting body formation is a major developmental process during the sexual life cycle, only few molecular details are known about factors governing this differentiation process. Usually, two types of sexually propagating ascomycetes can be distinguished: hetero- and homothallic fungi. Heterothallic fungi are characterized by two mating types that are designated with either plus and minus or A (or alpha) and a. Mating can only occur between partners of the opposite mating type. In contrast, no different mating type strains are known from homothallic fungi; every strain is able to complete the sexual life cycle simply by a selfing process. At the genomic level, these phenotypic differences are represented by mating type loci. In heterothallic fungi, strains of different mating type carry different mating-type loci usually encoding transcription factors with conserved DNA-binding motifs such as HMG boxes or alpha domains. Although the mating-type loci are present at homologous sites on the chromosome, they show no sequence similarity and therefore are called "idiomorphs" (Metzenberg and Glass, 1990; Pöggeler, 2001). In contrast, strains of homothallic fungi are not distinguishable by their mating-type loci. Some carry both, MAT-1 and MAT-2 specific genes, but most have a single mating-type locus representing a hybrid locus that encodes mating-type genes with similarity to both

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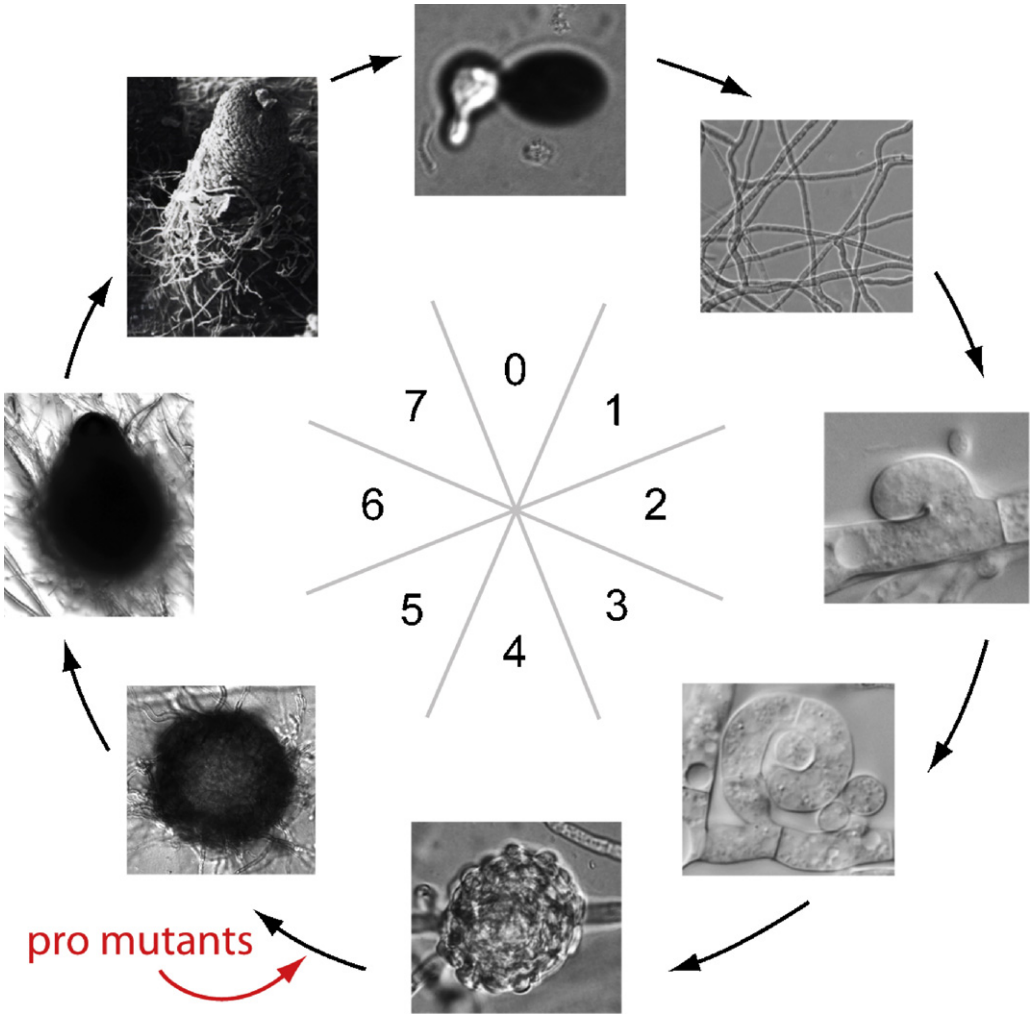

Fig. 1. Life cycle of *Sordaria macrospora*, which can be completed in the laboratory within 7 days. Figures represent different stages that can be observed at individual days. Note that figures are not shown to scale. The final stage, the perithecium, is shown as a scanning electron micrograph.

idiomorphs of heterothallic species (Debuchy and Turgeon, 2006; Pöggeler et al., 1997b). A well-studied example is the chimeric mating-type locus of the homothallic fungus *Sordaria macrospora*. Recently, functional analysis of this fungus has shown that the mating-type genes are involved in the regulation of cellular development (Klix et al., 2010; Pöggeler et al., 2006). Moreover, it is known that the conditions that initiate the sexual cycle are species specific. For example, a light/dark cycle, a nutritional deficit or addition of fatty acids may be able to trigger the formation of sexual organs in e.g. *Pyronema confluens*, *Pyronema domesticum* and *Neurospora crassa*, respectively (Moore-Landecker, 1979; Nowrousian and Kück, 2006; Nukina et al., 1981). Homothallic fungi usually generate female reproductive structures called ascogonia. These develop further into spherical protoperithecia which protect ascogenous hyphae emerging from the ascogonium. In the tip of ascogenous hyphae, two nuclei pair up to form the dikaryotic state. This dikaryotic mycelial phase is followed by karyogamy of two haploid nuclei, resulting in a diploid nucleus. The formation of a diploid nucleus is a prerequisite in enabling meiotic division to take place. After meiosis, the four haploid nuclei undergo a post-meiotic mitosis. As a result, every ascus contains eight nuclei, each of which will be the starting point for ascospore formation.

The homothallic life cycle harbours several experimental advantages for studying fruiting body development, since all stages of this complex developmental process can be investigated in a single individual strain. No mating of two partners carrying opposite mating types is necessary to complete the life cycle. Likewise, developmental mutants with defined developmental blocks can be easily recognized. To decipher factors that specifically control fruiting body formation, we have recently started a programme to identify the molecular determinants regulating complex cellular differentiation processes during sexual development. As a model, we chose the ascomycete *S. macrospora* that has been used since the 1950s for conventional genetic studies (Esser and Kuenen, 1967).

Sordaria macrospora as an experimental system

Sordaria macrospora is a coprophilic homothallic ascomycete that is closely related to two other model organisms, *Neurospora crassa* and *Podospora anserina*. In contrast to these two species, *S. macrospora* does not form any asexual spores and, as outlined above, does not require a mating partner with an opposite mating-type locus for completion of the sexual life cycle. The life cycle starts by germination of a meiospore, the product of meiosis. Germinating ascospores, as shown in Fig. 1, generate a haploid mycelium which after 2–3 days forms ascogonia, the female gametangia. These cells are enveloped by sterile hyphae to form fruiting body precursors, the protoperithecia. The round-shaped young fruiting bodies with a size of about 20–55 μm subsequently differentiate after 4–5 days into mature fruiting bodies with an outer pigmented peridial tissue and, following karyogamy, inner ascus initials. These will mature to about 50–300 eight-spored asci. Fruiting bodies contain several