The Sordaria cell cycle affords several advantages for the study of meiosis

Sordaria macrospora is a morphologically complex multicellular organism with several cell types that differ in morphology, physiology and developmental origin especially during the sexual cycle (Fig. 1). Its life cycle is completed in seven days, by the end of which ripe ascospores are formed. Vegetative growth consists of multinucleate tip-growing syncytial filaments (hyphae) separated by perforated septa that allow the passage of the haploid nuclei, mitochondria and other organelles.

S. macrospora produces spores only through a sexual cycle involving classical meiosis. It does not produce mitotically derived asexual spores/conidia. The sexual cycle of *S. macrospora* is initiated by the formation of ascogonial coils, which develop into protoperithecia when surrounded by enveloping vegetative hyphae. Protoperithecia further develop into a flask-shaped perithecium also called fruiting body [1]. Within perithecia, multi-nucleate ascogonial cells give rise to dikaryotic ascogenous hyphae, whose two nuclei divide synchronously several times before finally forming, on their tip a hook-shaped cell, called a crozier (Fig. 1). The two haploid nuclei of the crozier undergo a simultaneous mitosis, with spindles positioned such that one daughter nucleus from each pair is present in the crook portion of the crozier. Septa form on each side of the crook, resulting in a basal and a lateral cell flanking the binucleate ascus-mother cell. Karyogamy takes place as the ascus mother cell begins to elongate. This unique diploid phase in the life cycle is followed immediately by the long prophase of the first meiotic division. DNA replication occurs by the time of nuclear fusion.

In contrast to *N. crassa*, which is heterothallic (haploid cultures from single spores are unable to enter the sexual cycle), *S. macrospora* is homothallic and thus able to enter the sexual cycle from a single ascospore. In fact all strains of our laboratory are issued from a single ascospore from a strain originally selected for its longevity and high fertility. *Sordaria* homothallism is due to the fact that its mating type (*Mat*) locus contains both *Mat* idiomorphs [2]. Self-fertility is interesting for at least three purposes. (i) It allows the direct recovery of recessive and dominant mutants after mutagenesis as well as to

directly obtain haploid (and then homozygous diploid) versions molecularly transformed strains. (ii) Homothallism guarantees that the two genomes in a diploid are isogenic. However, because of self-fertility, crosses produce both parental and hybrid fruiting bodies, a handicap for recombination tests, which can, however, be easily prevented by the use of non-allelic self-sterile but cross-fertile mutants [3,4]. (iii) Although *N. crassa* has a long history of genetic analysis, *S. macrospora* is better suited for studying meiosis, because all perithecia contain 100% of 8-spored aci and 100% viable ascospores while sporulation in *N. crassa* is more variable with ascospore death often found in routine laboratory crosses [5].

Finally, although there is no indication of a direct link with homothallism, in contrast to heterothallic *N. crassa, S. macrospora* did not develop "checking and cleaning mechanisms" during its sexual cycle, allowing therefore easier recovery and screening of integrated foreign DNA or tagged genes. Thus: First, there is no premeiotic mechanism like RIP (irreversible repeat-induced-point mutation) that scans the haploid genome for DNA sequences present in more than a single copy and converts C/G base pairs to A/T pairs in the duplicated sequences during karyogamy (review in [6]). Second, although containing clear orthologs of the genes involved in the mechanism, *S. macrospora* has also not developed a process called MSDU (meiotic silencing by unpaired DNA), which, during *N. crassa* meiotic prophase, detects and inactivates all asymmetrical situations, such as a deletion or an insertion in one of the homologous chromosomes. MSUD acts on all paired and unpaired copies of the sequence/gene in the genome and holds also for even number of copies, even when inserted at different positions along the chromosomes [7]. The mechanism appears to be post-transcriptional, i.e. involving an RNA intermediate [7,8].

References

- [1] Lord KM and Read ND. Perithecium morphogenesis in *Sordaria macrospora*. Fungal Genet Biol 2011;48:388-399.
- [2] Kück U, Pöggeler S, Nowrousian M, Nolting N, Engh I. Sordaria macrospora, a model system for fungal development. In T. Anke & D Weber (Eds) The Mycota XV, Physiology and Genetics Berlin, Heidelberg: Springer, 2009, pp 17-39.

- [3] Leblon G, Zickler D, Le Bilcot S. Most U.V. induced reciprocal translocations in Sordaria macrospora occur in or near the centromere regions. Genetics 1986;112:183-204.
- [4] Zickler D, Moreau PJ, Huynh AD, Slezec AM. Correlation between pairing initiation sites, recombination nodules and meiotic recombination in *Sordaria macrospora*. Genetics 1992;132:135-148.
- [5] Perkins DD, Barry EG. The cytogenetics of *Neurospora.* Adv. Genet. 1977;19:133-285.
- [6] Selker EU. Repeat-induced gene silencing in fungi. Adv. Genet. 2002;46:439-450.
- [7] Shiu PK, Raju NB, Zickler D, Metzenberg RL. Meiotic silencing by unpaired DNA. Cell 2001;107:905-916.
- [8] Decker LM, Boone EC, Xiao H, Shanker BS, Boone SF, Kingston SL et al. Complex formation of RNA silencing proteins in the perinuclear region of *Neurospora crass* Genetics 2015;199:1017-1021.