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Review

From dikaryon to diploid

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ABSTRACT

The dikaryon is the persistent vegetative phase of most basidiomycetes and arises by cell fusion of two haploids carrying different mating type alleles. The diplophase is restricted to a single cell (the basidium) where meiosis takes place. Cell fusion and karyogamy are thus temporally and spatially separated. The dikaryon is characterized by the presence in each cell of two genetically distinct nuclei in a 1:1 ratio and by clamp connections, structures involved in partitioning of the nuclei during their synchronous division. In *Coprinopsis cinerea* and *Schizophyllum commune*, with two mating type loci (A and B), heterokaryons with identical A alleles exhibit nuclear migration but no clamps, and those with identical B alleles have unfused clamps (pseudoclamps) and no nuclear migration. *Armillaria* species are exceptional among basidiomycetes because of their persistent vegetative diploid phase with no clamp connections. Cell fusion is followed immediately by karyogamy. Haploidization of the diploid nucleus may occur in the fruiting body, resulting in a new dikaryophase–diplophase. Diploids in *Ustilago maydis* were the first to be synthesized in any basidiomycete. They played a critical role in pioneering studies on DNA recombination and repair. Subsequently diploids were generated in *C. cinerea*, *S. commune*, *Microbotryum violaceum*, and *Cryptococcus neoformans*. Dikaryons (or heterokaryons) and diploids of the same genotype exhibit phenotypic differences. The reason is not known but evidence indicates that gene expression differs when the same genetic information resides in two nuclei versus one nucleus in the same cell. Diploids in basidiomycete fungi are very stable by themselves but become unstable in $2N + N$ or $2N + 2N$ dikaryons. Instability results in haploidization (gradual loss of chromosomes) of the diploid nucleus. The mechanism that triggers this instability is not known.

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1. Introduction

Most fungi in the Basidiomycota are characterized by a long-lived vegetative dikaryophase, where two genetically distinct nuclei coexist in each cell of the hypha. The dikaryon arises

after cell fusion of two haploid homokaryons carrying different mating type alleles. Under appropriate conditions, the dikaryon undergoes a complex developmental program that gives rise to a fruiting body (Kües and Navarro-González, 2015). Differentiation within the fruiting body

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leads to formation of specialized cells, basidia, where karyogamy and meiosis occur, resulting in production of four basidiospores. Meiosis can be followed by mitosis. The basidiospores can be uninucleate or binucleate. In the latter case, the nuclei may have the same or different genotype at the mating type loci (Hibbett *et al.*, 1994; Raper, 1966). Cell fusion and karyogamy are temporally and spatially separated in the life cycle of the majority of basidiomycete fungi, exemplified by *Coprinopsis cinerea* and *Schizophyllum commune*, which have long been used as model organisms for studies, among others, on mating type determination, fruiting body development, and somatic recombination (Casselton and Olesnicky, 1998; Kües, 2000; Papazian, 1954; Parag, 1962; Raper, 1966; Raudaskoski and Kothe, 2010; Stankis and Specht, 2007).

In dimorphic basidiomycete fungi, the dikaryon arises after cell fusion of two haploid yeast-like cells having different mating type alleles. Karyogamy and meiosis occur in specialized cells without fruiting body differentiation. Cell fusion and karyogamy are also temporally and spatially separated, as exemplified in *Ustilago maydis*, *Cryptococcus neoformans*, and *Microbotryum violaceum*, which have been used extensively as model organisms (among others) for the study of the mating type loci, their role in pathogenicity, ecology of plant disease, and sex chromosome dimorphism (Banuett, 1995, 2002; Feretzaki and Heitman, 2013; Giraud *et al.*, 2008; Hood, 2002; Hood *et al.*, 2013; Hull *et al.*, 2002; Lengeler *et al.*, 2002; Vollmeister *et al.*, 2012).

Basidiomycete fungi with a prolonged and stable diploid vegetative phase are of rare occurrence. In these fungi, karyogamy follows immediately after cell fusion. Thus, there is no temporal separation between the dikaryophase and the diplophase. *Armillaria mellea* is the classical example of a basidiomycete fungus with a persistent vegetative diploid phase (Anderson and Ullrich, 1982; Guillaumin *et al.*, 1991).

The persistence of a dikaryophase likely provides basidiomycete fungi with a selective advantage (Anderson and Kohn, 2007; Raper, 1966). It has been said that the dikaryophase provides plasticity not possible with diploids. Interestingly, some studies indicate that patterns of gene expression differ when identical mating type information resides in separate nuclei versus the same nucleus in the same cell (Babu *et al.*, 2005). Aside from considerations of evolutionary selective pressures that lead to a persistent dikaryophase, it is of great interest to elucidate the genetic program that controls karyogamy in fungi with a persistent vegetative dikaryophase, and to determine how this program is modified in fungi with a persistent vegetative diplophase.

In this review, I discuss dikaryons, heterokaryons, and diploids in selected members of the Basidiomycota, in particular, in *C. cinerea*, *S. commune*, *A. mellea*, and *C. neoformans* (members of the Agaricomycotina), *M. violaceum* (a member of the Pucciniomycotina), and *U. maydis* (a member of the Ustilaginomycotina). These fungi have been extensively studied and there are tantalizing observations on the behavior of dikaryons compared with diploids of the same genotype. By no means do I intend to imply that they represent the behavior of all fungi in the diverse Basidiomycota. For observations on other basidiomycetes, I refer the reader to Raper (1966).

2. Dikaryons and other heterokaryons in *C. cinerea* and *S. commune*

Mating type (or incompatibility) loci

I provide a brief description of the mating type loci in these fungi as a framework to understand the discussion that follows (for a comprehensive discussion of mating type loci, see Heitman *et al.*, 2013; Kües *et al.*, 2011).

Both *C. cinerea* and *S. commune* are heterothallic and tetrapolar, that is dikaryon establishment and maintenance are determined by two unlinked multiallelic loci, A and B (reviewed in Kamada, 2002; Kües *et al.*, 2011). These loci are complex and consist of two components, α and β ($A\alpha A\beta$ and $B\alpha B\beta$), separable by recombination, and containing two or more genes. Thousands of mating types exist due to the many possible combinations of different mating type alleles (reviewed in Kamada, 2002; Kües *et al.*, 2011). The A locus codes for homeodomain proteins and pairs of non-allelic homeodomain polypeptides interact to form an active heterodimer, which presumably acts as a major regulatory protein to control expression of target genes (Erdmann *et al.*, 2012; Inada *et al.*, 2001; Kamada, 2002). The B locus contains genes that code for pheromone and pheromone receptors, and presumably controls a G-protein coupled receptor (GPCR)-pheromone response pathway resulting in activation of target genes (Erdmann *et al.*, 2012). Most members of the Agaricomycotina have a tetrapolar mating type system, however, examples of fungi with a bipolar multiallelic or biallelic mating type system are known (James *et al.*, 2011, 2013; Lengeler *et al.*, 2002; Li *et al.*, 2004; Raper, 1966).

In the Pucciniomycotina a single mating type locus with two alleles appears to be the rule (Bakkeren *et al.*, 2008) but deviations from the bipolar and tetrapolar pattern (designated pseudobipolar) have been documented (see, Coelho *et al.*, 2010). In the Ustilaginomycotina, a bipolar mating type system is common. *U. maydis* and *Sporisorium reilianum* appear to be the exception: both have a tetrapolar mating type system, where one locus is biallelic and the other multiallelic as in *U. maydis*, or both are multiallelic as in *S. reilianum* (Bakkeren *et al.*, 2008; Banuett, 2007; Schirawski *et al.*, 2005; Vollmeister *et al.*, 2012).

Compatible, hemicompatible, and noncompatible heterokaryons

Four types of interactions are possible among haploid homokaryons of fungi with tetrapolar systems: compatible (different A and B alleles; short notation $A \neq B \neq$), hemicompatible or common A ($A = B \neq$), hemicompatible or common B ($A \neq B =$), noncompatible or common AB ($A = B =$). In bipolar systems, whether multiallelic or biallelic, only two types of interactions are possible, $A \neq$ or $A =$ (Raper, 1966).

Compatible interactions: the dikaryon ($A \neq B \neq$)

The dikaryon is a specialized type of heterokaryon characterized by a 1:1 ratio of the parental nuclei in each cell and the presence of clamp connections between adjacent cells. Clamp connections are involved in partitioning of the two nuclei during synchronous division (see below).

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