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Unisexual versus bisexual mating in *Cryptococcus neoformans*: Consequences and biological impacts

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ABSTRACT

Cryptococcus neoformans is an opportunistic human fungal pathogen and can undergo both bisexual and unisexual mating. Despite the fact that one mating type is dispensable for unisexual mating, the two sexual cycles share surprisingly similar features. Both mating cycles are affected by similar environmental factors and regulated by the same pheromone response pathway. Recombination takes place during unisexual reproduction in a fashion similar to bisexual reproduction and can both admix pre-existing genetic diversity and also generate diversity *de novo* just like bisexual reproduction. These common features may allow the unisexual life cycle to provide phenotypic and genotypic plasticity for the natural *Cryptococcus* population, which is predominantly α mating type, and to avoid Muller's ratchet. The morphological transition from yeast to hyphal growth during both bisexual and unisexual mating may provide increased opportunities for outcrossing and the ability to forage for nutrients at a distance. The unisexual life cycle is a key evolutionary factor for *Cryptococcus* as a highly successful global fungal pathogen.

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1. Introduction

Sex is ubiquitous throughout biology. Numerous fungal species were long considered clonal or asexual, for example, the human fungal pathogens *Candida albicans* and *Aspergillus fumigatus*. However, bioinformatic studies of whole genome sequences revealed the existence of both opposite alleles of the mating-type locus (*MAT*), and population genetics studies revealed genetic recombination within the population. These advances first suggested sexual reproduction is an integral life cycle feature for these and other fungal species that have been thought to be asexual (Butler et al., 2009; Ene and Bennett, 2014; Heitman, 2006).

Sexual identity in fungi is defined by *MAT*, which contains genes that regulate cell identity and sexual reproduction (Ni et al., 2011). Mating can be either heterothallic, involving mating between partners harboring different mating type alleles with high DNA sequence dissimilarity, or homothallic, which involves sexual reproduction of solo cultured individual isolates. Homothallism can also involve selfing, or same-sex mating/unisexual reproduction. Heterothallism and homothallism in fungi have been reviewed in detail (Lee et al., 2010; Ni et al., 2011). Table 1 lists some classic

examples for different types of heterothallic and homothallic mating in fungi.

Heterothallic mating occurs either in a bipolar or a tetrapolar system. The bipolar mating system contains a single bi-allelic *MAT* locus that controls mating between partners of opposite mating types, such as the genetic model *Neurospora crassa*, the prominent human fungal pathogenic basidiomycetes *Cryptococcus gattii* and *Cryptococcus neoformans*, and the ascomycetes *C. albicans* and *A. fumigatus* (Galagan et al., 2005; Hsueh et al., 2011b; Hull and Johnson, 1999; Metzenberg and Glass, 1990). Many basidiomycetes, such as *Coprinopsis cinerea*, *Cryptococcus heveanensis*, and *Ustilago maydis* exhibit tetrapolar mating systems which contain two unlinked, multiallelic *MAT* loci that control mating between partners of different mating types that differ at both *MAT* loci (Cassleton and Kues, 2007; Metin et al., 2010; Spellig et al., 1994). Tetrapolar mating systems restrict inbreeding more than bipolar mating systems because they reduce the chances of mating between the progeny to 25% versus 50% in a bipolar mating system (Fig. 1) (Ene and Bennett, 2014). Homothallism involves sexual reproduction of solo isolates without a partner and there are at least five different types of homothallism in different fungal species, including pseudohomothallism, mating type switching, two fused or linked *MAT* loci, two unlinked *MAT* loci, and one *MAT* locus (Ni et al., 2011). Pseudohomothallism occurs in *Neurospora tetrasperma* and *Podospora anserina*, and refers to selfing of spores that contain two nuclei of different mating types (Merino

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Table 1
Examples of fungal mating strategies.

	Phylum	Species	Reference
<i>Heterothallism</i>			
Bipolar	Ascomycota	<i>Aspergillus fumigatus</i> <i>Candida albicans</i> <i>Neurospora crassa</i>	Galagan et al. (2005) Hull and Johnson (1999) Metzenberg and Glass (1990)
	Basidiomycota	<i>Cryptococcus neoformans</i> <i>Ustilago hordei</i>	Hsueh et al. (2011b) Lee et al. (1999)
Tetrapolar	Basidiomycota	<i>Coprinopsis cinerea</i> <i>Cryptococcus heveanensis</i> <i>Ustilago maydis</i>	Casselton and Kues (2007) Metin et al. (2010) Spellig et al. (1994)
<i>Homothallism</i>			
Pseudohomothallism	Ascomycota	<i>Neurospora tetrasperma</i> <i>Podospora anserina</i>	Merino et al. (1996) Picard et al. (1991)
Mating type switching	Ascomycota	<i>Kluyveromyces lactis</i> <i>Saccharomyces cerevisiae</i> <i>Schizosaccharomyces pombe</i>	Butler et al. (2004) Herskowitz et al. (1992) Nielsen and Egel (2007)
Two fused or linked opposite MAT loci	Basidiomycota	<i>Agrocybe aegerita</i>	Labarere and Noel (1992)
	Ascomycota	<i>Cochliobolus</i> spp. <i>Didymella zae-maydis</i> <i>Neurospora</i> spp. (<i>N. pannonica</i> ; <i>N. terricola</i>) <i>Stemphylium</i> spp. <i>Sordaria macrospora</i>	Yun et al. (1999) Yun et al. (2013) Poggeler (1999) Inderbitzin et al. (2005) Poggeler (1999)
Two unlinked opposite MAT loci	Ascomycota	<i>Aspergillus nidulans</i> <i>Neosartorya fischeri</i>	Galagan et al. (2005) Rydholm et al. (2007)
One MAT locus	Ascomycota	<i>Candida albicans</i> <i>Neurospora</i> spp. (<i>N. africana</i> ; <i>N. dodgei</i> ; <i>N. galapagonensis</i> ; <i>N. lineolata</i>) <i>Stemphylium</i> spp.	Alby et al. (2009) Poggeler (1999) Inderbitzin et al. (2005)
	Basidiomycota	<i>Cryptococcus neoformans</i>	Lin et al. (2005)

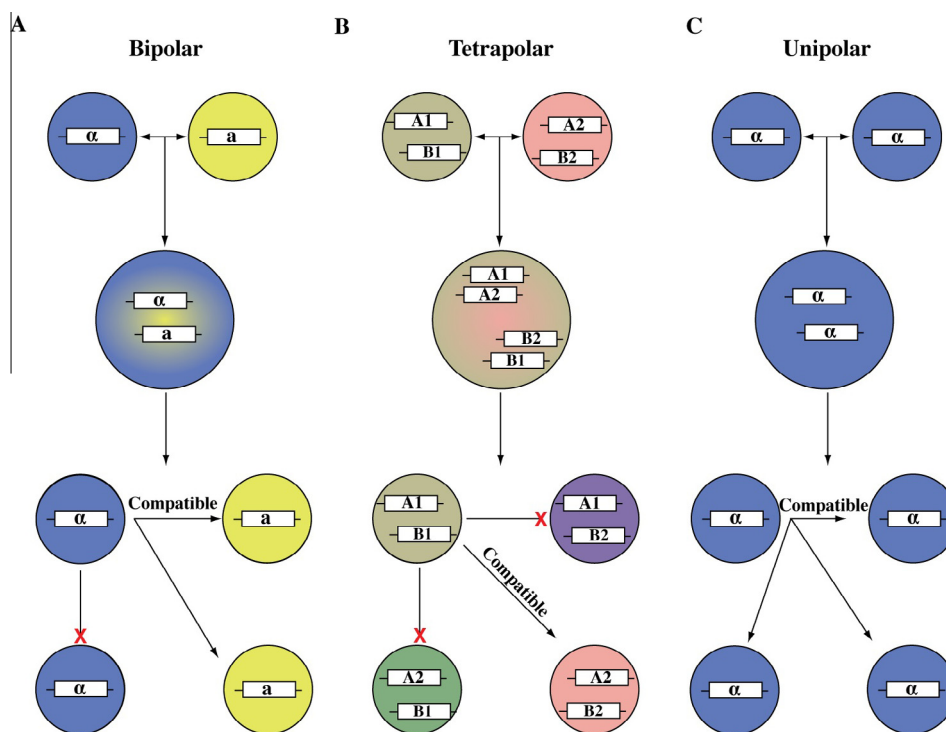


Fig. 1. (A) Bipolar mating type systems encode mating type determinants at one locus. Alleles for the MAT locus must be different for heterothallic mating to occur and diploids to be formed. The resulting spores are able to mate with 50% of their siblings in a tetrad. (B) Mating type determinants are encoded at two unlinked loci in tetrapolar mating systems. Cells must carry different alleles at both MAT loci for mating to occur and spores can only mate with 25% of their sibling meiotic products. (C) *C. neoformans* has a unisexual cycle, in addition, to the standard bipolar heterothallic mating cycle. α cells are able to mate with other α cells to produce diploids that are homozygous at the MAT loci. These diploids are able to sporulate and produce inter-fertile spores.

et al., 1996; Picard et al., 1991). Mating type switching refers to a daughter cell mating with the mother cell that has converted its mating type through endonuclease facilitated recombination in response to DNA double-strand breaks, and it occurs in *Kluyveromyces lactis*, *Saccharomyces cerevisiae*, and *Schizosaccharomyces pombe* (Butler et al., 2004; Herskowitz et al., 1992; Nielsen and

Egel, 2007). Even though pseudohomothallism and mating type switching facilitate mating within the same cell, or among cells from an asexually derived colony, mating still occurs between two nuclei of the opposite mating types. In certain fungal species, both alleles of the MAT locus are present in one nucleus enabling the fungus to be self-fertile. The MAT loci can be fused or linked

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