

## Advancements in understanding the role of mating type genes in fungal sexual reproduction

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### Abstract

Fungi perform various reproductive strategies, including sexual and asexual reproduction, with the latter being essential for genetic recombination and evolutionary processes. Sexual reproduction encompasses heterothallism, homothallism, and pseudohomothallism, all governed by genes located at the mating type locus. These genes perform a pivotal function in sexual reproduction, encode transcription factors that regulate various aspects of fungal growth and reproduction. This review provides insights into the structure, molecular function, and regulatory mechanisms of mating genes in fungal sexual reproduction.

**Keywords:** Fungi, Genes, Molecular function, Mating, Sexual reproduction.

### Introduction

There are many types of fungi in nature, with up to  $1.6 \times 10^6$  species, belonging to Chytridiomycota, Zygomycota, Glomeromycota, Ascomycota, Basidiomycota, and the newly established phylum Cryptomycota (Jones *et al.*, 2011; Mora *et al.*, 2011). Fungal species correspond to various reproduction methods. These methods are diverse, encompassing both asexual and sexual categories. While nearly all fungi can reproduce sexually, asexual reproduction is more commonly observed. Sexual reproduction, on the other hand, is a diverse phenomenon in nature, characterized by varying modes and frequencies of occurrence (Beukeboom and Perrin, 2014; Nieuwenhuis and James, 2016; Ali *et al.*, 2022). In fungi, asexual reproduction occurs without the need for karyogamy and meiosis. Instead, somatic cells produce asexual spores through processes such as fragmentation, fission, or budding. Sexual reproduction involves the development of specialized sex cells called gametes, which give rise to varied progeny through processes such as karyogamy and meiosis. These reproductive cells exhibit exceptional durability, even under extreme circumstances. Moreover, sexual reproduction enhances genetic diversity by eradicating harmful mutations and facilitating the dissemination of advantageous genes. Furthermore, genotypic diversity arises from the recombination of

genetic material during hybridization of the species. This diversity is beneficial for fungal species, as it improves their environmental adaptation and selection. Hormonal mechanisms that regulate both male and female gametes, as well as cells with sex, are monitored by mating-type genes, which are the primary regulators of sexual reproduction in fungi. These genes play an important role in sexual differentiation, development, and the production of the ascus shell. As a result, extensive research on these genes is critical for gaining a better understanding of fungal sexual behaviors, which is critical for illuminating these organisms' reproductive strategies and determining the origins of biological reproduction (Nieuwenhuis and James, 2016).

### Sexual reproduction

In fungi, the mating type (MAT) locus controls sexual characteristics. Both MAT $\alpha$  and MAT $\alpha$  connect to the mating types of *Neurospora crassa*. Similarly, complementary mating types designated MAT $\alpha$  and MAT $\alpha$  have been observed in *Saccharomyces cerevisiae* and *Cryptococcus neoformans*, respectively. This indicates that MAT1-1 and MAT1-2 are frequently expressed in different kinds of fungal mating (Ni *et al.*, 2011; Whittle *et al.*, 2011; Ene and Bennett, 2014). The distribution of haploid cells in fungi and the categorization of

their sexual traits are significantly influenced by mating-type genes. Reproduction methods are divided into three types: pseudohomothalium, homoclan mating (homothalium), and heterothallic mating (heterothalium) (Szewczyk and Krappmann, 2010; Ali *et al.*, 2023). Bipolar heterothallic and tetrapolar heterothallic coordination are the two types of offspring that are classified by allotropic mating, which is controlled by mating-type incompatibility factors. Only two mating types are present in bipolar heterothallic fungi, which typically can be determined by a single pair of loci (Kück and Pöggeler, 2009). Four mating types, identified by two sets of mating type loci ( $A\alpha/A\beta$  and  $B\alpha/B\beta$ ), are the characteristics of tetrapolar heterothallic fungi. Bipolar traits are present in most *heterothallic Ascomycota* fungi that have been found previously (Kück and Pöggeler, 2009; Gross *et al.*, 2012). Sexual reproduction in *heterothallic* fungi occurs when strains with opposing mating types with one another. The fundamental mechanism of sexual reproduction in these fungi is this mutual mating process. However, among *homothallic* fungi, there are compatible species in which the genes for mating type coexist in the same cell nucleus, suggesting that self-fertilization is possible. Secondary homothalium is the term for this self-fertility phenomenon, in which a single sexual reproductive cell simultaneously harbors the haploid nuclei of two complimentary mating types. These fungi can reproduce sexually spontaneously due to their special genetic coordination. Studies have also shown that under environmental and genetic conditions, cooperation is promoted within a specific group. Even within the same species, it's not unusual for various groups to work together interchangeably. Furthermore, two different coordinating strategies might operate side by side (Lin and Heitman, 2007; O'Gorman *et al.*, 2009). In fungi, sexual reproduction consists of multiple stages: selecting suitable partners, fusing cells to form a fertilized egg, rearranging chromosomes during meiosis, and generating new haploid organisms. Recombination has two main functions: it first speeds up adaptation by allowing advantageous alleles that are not found in the same genome to come together; it additionally facilitates the combination of destroying mutations that are associated with beneficial mutations (Wallen and Perlin, 2018). Experimental findings indicate that sexually reproducing groups exhibit quicker adaptability in individuals compared to asexual groups. Recent evolutionary experiments tracking new mutations in baker's yeast have provided evidence for this. Indeed, the integration of advantageous mutations and the elimination of harmful ones from the genetic makeup can enhance the rate at which fungi adapt to novel environments (McDonald *et al.*, 2016). Despite the fundamental pattern of sexual reproduction being consistent, significant variations exist among different fungal

groups in nature, particularly during various stages of the reproductive process. Fungi can switch from asexual to sexual reproduction under specific environmental conditions. This mode of reproduction, which involves the formation of sexual structures and spores, performs a pivotal function in the onset of various plant diseases, as it often serves as the primary source of initial infection. An example of this is the ascomycete fungus *Villosiclava virens*, which after infecting rice, propagates vegetatively to produce rice false smut balls. Efficient fusion between strains of different mating types occurs when the ambient temperature is favorable. This leads to the formation of sclerotia, most of which can sprout into fruiting bodies. Upon maturation of the fruiting body, an ascus sac is developed, containing several asci. Each mature ascus houses eight linearly arranged ascospores (Yong *et al.*, 2018). Based on their morphology, the fruiting bodies of fungi can be categorized into several types: ascothecia (belonging to the class Sclerotinia), ascomata (found in the class Discomycetes), cleistothecia (associated with the class Anthecothecia), and pseudothecia (part of the Coelomycetes). Despite the variations in morphology and size among these ascomycete fungi, the developmental processes within their fruiting bodies are remarkably similar (Kues and Navarro-González 2015; Ali *et al.*, 2024).

#### MAT locus and structure

In the sexual reproduction of fungi, genes known as mating types, the mating type genes significantly impact gender control and genetic evolution. The mating type region encompasses the mating type gene along with adjacent sequences. This is because the gene homology at the MAT locus is notably low, and the genes are not uniformly positioned across different organisms. Consequently, this unique genetic arrangement is referred to as an idiomorph, rather than an isomorph, due to its distinct structure (Lu *et al.*, 2010). In heterothallic *ascomycetes*, strains typically possess one pair of highly heterologous mating type loci if they are of opposite mating types. Conversely, *homothallic strains* contain both alleles within this pair. These alleles are commonly discussed as MAT1-1 and MAT1-2. In nature, the occurrence ratio of these two forms is generally 1:1. In synthallic *Ascomycetes*, MAT1-1 and MAT1-2 loci are situated connected on the same chromosome. However, in most cases, these two MAT loci are found on separate chromosomes and segregate independently during sexual reproduction. The first mating type gene in *Saccharomyces cerevisiae* was cloned from the fermented species. In *Saccharomyces cerevisiae*, there are two mating types, represented by the loci MAT $\alpha$  and MATa. The MAT $\alpha$  locus encodes two proteins, MAT $\alpha$ 1p and MAT $\alpha$ 2p. MAT $\alpha$ 1p has a role that extends beyond controlling the mating type;

it also regulates the expression of cell-type specialized genes. Together with the Mcm1 protein and the STE12 protein, MAT $\alpha$ 1p forms a protein complex that activates the transcription of  $\alpha$ 1 domain-specific genes. In various fungal species such as *Magnaporthe grisea*, *Ophiostoma quercus*, *Cochliobolus heterostrophus*, *Cryphonectria parasitica*, and *Villosiclava virens*, the heterologous mating-type loci are known as MAT1-1 and MAT1-2. These loci collaborate differently within each species. In the *Pleurosporium* group, there are three types of mating type loci configurations: either only MAT1-1, only MAT1-2, or both MAT1-1 and MAT1-2%. Additionally, in this group, MAT1-1 is inverted and fused with MAT1-2 (Inderbitzin *et al.*, 2005; Ahmed *et al.*, 2018).

Two mating type loci are present in *Mycomyces*: The P/R locus encodes genes related to pheromone and pheromone receptors, while the other locus encodes HD transcription factors that regulate sexual development (David-Palma *et al.*, 2016; Sun *et al.*, 2017). The homologous genes in *Curvularia crescentus* are CIMAT1-1-1 and CIMAT1-2-1, respectively, encoding proteins with the  $\alpha$ -box and HMG-box domains (Wilken *et al.*, 2017; Haseeb *et al.*, 2019a). In fungi, algae, and certain protozoa, mating-type genes are essential genetic elements that establish the compatibility of mating between individuals from the same species. The proteins that control sexual differentiation and reproductive functions are encoded by these genes. With a primary focus on model organisms like *Saccharomyces cerevisiae* (baker's yeast), *Schizosaccharomyces pombe* (fission yeast), and other fungal species, this article explores the locus and structure of mating type genes. The evolutionary flexibility of sexual reproduction mechanisms is demonstrated by the variation in the composition and arrangement of mating type loci across species. Different mating types have probably evolved to increase genetic diversity and adaptation, which are essential for species survival in some environments. The locus and structure of the mating type genes vary greatly amongst organisms, which is indicative of their complex functions in controlling sexual reproduction and maintaining genetic variety. Research on these genes provides light on the molecular processes that underlie eukaryotic sexual differentiation and reproduction. Three proteins are encoded by the *Saccharomyces cerevisiae* MAT1-1 gene. The first, encoded by the MAT $\alpha$  mating type gene, is an  $\alpha$ -domain protein called MAT1-1-1. This protein is homologous to the second protein (MAT $\alpha$ 1p), which also has an acidic  $\alpha$ -helix. According to Shiu and Glass (2000), the third protein, MAT1-1-3, is a highly mobile HMG-1 protein that attaches to chromatin and is essential for the organization and control of gene expression. Studies show that most Ascomycetes under study have a generally conserved MAT1-1 locus, that

usually codes for an  $\alpha$ -domain protein. However, the  $\alpha$ -domain protein is exclusively encoded by a subset of Ascomycota MAT1-1 loci. The MAT1-2 locus encodes HMG-2, a highly mobile protein, in addition to the acidic  $\alpha$ -helical protein and HMG-1 protein encoded by the MAT1-1 locus (Kanamori *et al.*, 2007; Haseeb *et al.*, 2019b; Sun *et al.*, 2024b,d). The findings of the research show that different fungi have different mating type locus MAT1-1 ways of action. Most of the functions of the proteins expressed by the MAT locus are upstream regulatory factors in regulatory pathways. They are involved in the subsequent process of meiosis as well as the recognition and control of cell fusion, or mating, between cells of various mating types. HMG-1 and the  $\alpha$ -helical protein may be involved in sexual development (Haseeb *et al.*, 2019c; Sun *et al.*, 2024 a,c).

It has been possible to successfully clone several mating-type genes in fungi. The conserved MAT1-2 region of *Cochliobolus heterostrophus* has an HMG-box domain, a highly mobile DNA-binding regulatory protein, while the conserved MAT1-1 region contains an  $\alpha$ -box domain protein. A single mating-type gene, either MAT1-1-1 or MAT1-2-1, is present in each region that wraps around its corresponding site. These genes are essential for identifying type 2 nuclei (Lu *et al.*, 2011). The mating-type genes MAT1-1 and MAT1-2 of *Xanthomonas zeae* have been cloned; they encode the  $\alpha$ -box and HMG-box DNA-binding domains, respectively, and contain the same flanking sequences for both segments. The research revealed that the translation product of *Xanthomonas zeae*, MAT1-1, exhibits increased homology with the proteins produced by MATA and the MAT $\alpha$ 1 gene in *Saccharomyces cerevisiae*, aligning with MAT1-1 of *Podospora* and *Neurospora crassa*. There are A and a mating type strains of the heterothallic fungus *Pseudomonas cornis* as well as Aa hermaphrodite mating type strains. This fungus is found in nature. The  $\alpha$ 1 transcription factor and high mobility protein are encoded by the mating type genes StMAT1-1 and StMAT1-2, respectively (Mathias *et al.*, 2004; Haber, 2012).

Mating type (MAT) genes encode transcription factors with highly conserved DNA-binding sequences and are essential for reproduction in various kinds of fungi. The MAT1-1-1 gene encodes  $\alpha$ 1 transcription factors in Faecalimycete fungi, including *Podospora anserina*, *Sordariomycetidae*, and *Neurospora crassa*. Meanwhile, the MAT1-1-3 and MAT1-2-1 genes encode proteins that have HMG-box domains. One of the proteins produced by the MAT1-1-2 gene has a PPF structure. A single gene, such as MAT1-2-1 in *Gibberella*, FPR1 in *Podospora*, or mata-1 in *Neurospora*, is typically present in the MAT1-2 locus of *Discomycetes* and *Sclerotinia*. In contrast, the MAT1-1 locus contains three genes: FMR1,

SMR2, and SMR1 in *Podospora*; *matA-1*, *matA-2*, and *matA-3* in *Neurospora*; and MAT1-1-1, MAT1-1-2, and MAT1-1-3 in *Gibberella* (Debuchy *et al.*, 2010; Wilson *et al.*, 2019).

Two closely related MAT loci are present in *Fusarium graminearum*: MAT1-2, which contains MAT1-2-1 and MAT1-2-3, and MAT1-1, which contains MAT1-1-1, MAT1-1-2, and MAT1-1-3. While *Podospora*'s SmtA-3 protein lacks an HMG domain, its MAT1-1-3/SmtA-3 gene sequence of *Macrospora*. The four MAT genes found in *Chaetomium globosum* include MAT1-1-2, which codes for a PPF-structured protein. MAT1-1-1 and MAT1-2-1 are the genes found in *Huntia omanensis*; MAT1-1 has the MAT1-1-1 and MAT1-1-2 genes, while MAT1-2 contains the MAT1-2-1 and MAT1-2-7 genes. In contrast, the MAT1-2 locus of *Huntia moniliformis* has just two genes (Wilson *et al.*, 2022).

In *Phytophthora citrus*, MAT1-1-1 and MAT1-1-4 make up the MAT1-1 locus, whereas MAT1-2-1 and MAT1-2-5 make up the MAT1-2 locus. Most species in the *Clavicepsaceae* family have the MAT1-1 and MAT1-2 loci, however, certain species, like *Verticillium fungicola* and *Cordyceps militaris* do not have the MAT1-1-3 gene (Yokoyama *et al.*, 2006; Zhang *et al.*, 2011). The mating-type locus in binding *Mucor* features a single high-mobility group (HMG)-domain transcription factor gene, either *sexM* or *sexP*, flanked by RNA helicase and triose phosphate transporter genes. The conserved domains in the *SexM* and *SexP* proteins are highly similar, with *SexM* also containing a nuclear localization sequence. *Aspergillus oryzae*, a heterothallic fungus, has two loci: MAT1-1, which includes partial sequences of MAT1-1-1, MAT1-1-2, MAT1-1-3, and MAT1-2-1; and MAT1-2, which contains MAT1-2-1 and a novel gene, MAT1-2-8. *Magnaporthe oryzae* has the same genes in MAT1-1, with MAT1-2 also containing MAT1-2-2. In *Thielaviopsis* species, MAT1-1 includes MAT1-1-1, while MAT1-2 contains MAT1-2-1, MAT1-2-7, and MAT1-1-2 (Wilson *et al.*, 2021).

### Molecular functions of mating type genes

Research indicates that the proteins encoded by the MAT locus function as transcription factors. These fungal mating-type genes are not limited to regulating the mating process; they also influence the growth of parental strains of contradictory mating types, the sexual reproduction process, and the formation of ascospore heterokaryons. Even in the absence of sexual reproduction, these genes hold significant importance in fungi. Bohm discovered that in *Penicillium*, the MAT gene is crucial for hyphal morphology, conidial morphology, seed formation, and penicillin production. It also plays a role in controlling mechanisms related to sexual reproduction (Table 1). In the absence of the mating type phase, when the MAT1-1-1 gene is deactivated,

the *S. sclerotiorum* mutant fails to produce sclerotia. Tingting noted that the expression level of the *S. sclerotiorum* MAT-2 gene is lowest in hyphae, but significantly higher in sclerotia stages 5 and 6 compared to other stages. After the MAT-2 gene is knocked out, the mutant exhibits denser hyphae, altered sclerotia numbers, and changes in the branch angle and number of hyphae. Consequently, its pathogenicity is notably reduced. (Doughan and Rollins, 2016) The study revealed that knocking out the genes MAT1-1-1, MAT1-1-5, and MAT1-2-1 in *S. sclerotiorum* results in complete sterility of the organism. Mutants with the MAT1-2-4 gene knocked out exhibit delayed germination of the fruiting body, along with changes in stroma and ascospore formation. Additionally, these mutants produce a reduced number of male gamete subunits. Changes in the expression of the *Ppg-1*, *PreA*, and *PreB* genes among these four gene mutants suggest that the MAT genes are involved in sexual reproduction, gene regulation, meiosis, and morphogenesis (Doughan, 2013; Doughan and Rollins, 2016).

In *Neurospora crassa*, the expression of *matA-3* (MAT1-1-3) is very low when the ascus is formed. Mutants of *matA-1* and *matA-1* are sexually sterile, whereas *matA-2* and *matA-3* mutants show only a slight decrease in fertility. Double knockout mutants of *matA-2* and *matA-3* remain fertile, but there is a significant reduction in the number of ascothecia, and the state of the ascospores changes. This indicates that the functions of these genes during the sexual development stage partially overlap (Zheng *et al.*, 2013; Tarique *et al.*, 2020). Wang *et al.* (2014) research demonstrated that mating-type genes are communicated throughout the asexual reproductive development stages of *Neurospora crassa*. It was also found that the *matA* phenotype is associated with a higher expression of certain genes.

In *Faecalibacterium macrospora*, knocking out the  $\alpha$ -domain or the small open reading frame gene does not disturb the nutritional development and reproductive growth of the bacteria. However, mutants of *SmtA-2* (MAT1-1-2) are unable to produce mature ascothecia, indicating that the deletion of the *SmtA-2* gene blocks the formation of ascocysts during the early stages of sexual reproduction (Klix *et al.*, 2010; Huang YuFei *et al.*, 2018). In *Podospora anserina*, mutants of opposing mating types lacking the  $\alpha$  or HMG domain genes are incapable of fertilizing after mating. They are nevertheless capable of producing asci by parthenogenesis. According to this, growth following fertilization does not require the HMG and  $\alpha$  domain genes, but sexual reproduction requires. It has been demonstrated that drastically altering the expression of MAT1-1-1 and MAT1-1-2 genes, either alone or concurrently, has an impact on colony expansion in *Ulocladium botrytis*. Important for the fungi

reproductive process, these genes affect the size and number of conidia (Liu *et al.*, 2022).

Mating type flipping is a mechanism by which cells can change their mating type in species such as *S. cerevisiae* and *S. pombe*, thereby increasing variation in genetics. The silent HML $\alpha$  or HMRA loci act as templates to replace the MAT sequence in *S. cerevisiae* because of a double-strand break caused by the HO endonuclease at the MAT locus. Like this, recombination moves genetic material from the silent mat2-P and mat3-M loci to the active mat1 locus in *S. pombe*. Mating-type genes in yeasts, such as *S. cerevisiae*, control the development of mating projections, or shmoos, which aid in cell fusion during mating. Mating-type genes in filamentous fungi control the growth of specialized structures like conjugation tubes, which permit the fusing of hyphae from different types of mating (Klix *et al.*, 2010). In fungi, sexual reproduction is a complicated process controlled by multiple genes. For example, the deletion of MAT1 and MAT2 genes in *Aspergillus nidulans* indicates their critical function in sexual reproduction. Comparably, in *Curvularia crescentus*, the genes MAT1-1-1 and MAT1-1-2 are essential for sexual reproduction; moreover, MAT1-1-2 controls the germination of conidia. Following induction, the expression of the MAT1-1-1 and MAT1-1-2 genes in *Fusarium graminearum* increases quickly, peaking on day 4, suggesting a shared bidirectional promoter (Wilson *et al.*, 2019; Ramsak and Kuck, 2022). The regulatory role of the SMR2 and FPR1 genes is identified in the nucleus of *Podospora anserina*. In both the cytoplasm and nucleus of *Schizosaccharomyces pombe* and *Saccharomyces cerevisiae*, the fusion process involves the Mat1-Pc and Mat-Mc genes as well as the MAT $\alpha$ 1 gene. The  $\alpha$ 1 transcription factors MCM1 and STE12 in *S. cerevisiae* activate genes unique to  $\alpha$  and control genes involved in sexual reproduction. The proteins Mcm1 and Ste12 interact with SmtA-1, the mating type gene, in *Macrospora faecalis*. In addition to having more hyphal branching, Mcm1 knockout mutants show decreased biomass and shorter hyphal intervals. These mutants are unable to produce ascospores or fruiting bodies. On the other hand, while the loss of the Ste12 gene hinders the development of ascospores and asci, it does not affect fruiting body production or vegetative growth. This suggests that in *Macrospora faecalis*, Mcm1 and Ste12 are both necessary for sexual reproduction.

Mutants of MAT1-1-2 and MAT1-1-3 in *Fusarium* remain fertile, while MAT1-2-1 and MAT1-1-1 mutants exhibit defects in male and female fertilization, respectively. The mat1-2-1 mutant also reduces the expression of the FgSO gene and hinders hyphal fusion. All MAT locus genes interact to form a protein complex essential for sexual reproduction. MAT1-1-1 and FgMcm1 are

involved in cell recognition and sexual development. Although these mutants do not affect wheat pathogenicity, mat1-1-1 and mat1-2-1 mutants show decreased disease in corn stalks, suggesting a role in host specificity. In *Botrytis cinerea*, knocking out the MAT1-1-1, MAT1-1-5, MAT1-2-1, and MAT1-2-10 genes does not change growth rate or morphology, but MAT1-1-1 and MAT1-2-1 are necessary for initiating sexual reproduction. The mat1-1-5 and mat1-2-10 mutants cannot produce ascus discs or ascospores despite normal production. Transcriptome analysis reveals that sexual reproduction onset often involves gene clusters, with 35 upregulated and 99 downregulated (containing over 900 genes) in ascospores. These changes align with expression alterations in genes encoding chromatin organization enzymes, indicating extensive epigenetic regulation during sexual reproduction (Duan *et al.*, 2023; Ran *et al.*, 2023; Sun *et al.*, 2023). In the study of sexual reproduction in fungi, the MAT locus genes play a pivotal role. Transcriptome analysis of RNA extracted from the fruiting bodies and mycelium of *Aspergillus oryzae* revealed that the expression levels of MAT1-1-2 and MAT1-1-3 are significantly higher in the fruiting body than in the mycelium, indicating their importance in regulating sexual reproduction in the rice smut fungus. These genes not only regulate sexual reproduction but also control cell recognition, fusion (mating), and the reduction division process necessary to produce sexual spores. This process requires the appropriate signaling between environmental stimuli and strains, involving multiple functional molecules.

Proteins such as HMG-1 and HMG-2, after being expressed, undergo further modifications like acetylation, phosphorylation, methylation, and glycosylation to become functional. Cell mating type recognition, fusion, and the transmission of mating-related pheromone signals are often mediated by pheromone receptors. Currently, seven pheromone receptors and more than twenty related pheromones have been identified. In the bipolar heterothallic coordination system, the expression of pheromones and pheromone receptor genes is regulated by mating gene-encoded transcription factors. When fungi are stimulated by related factors, pheromone receptors activate the highly conserved MAPK pathway, inducing a response from mating gene-encoded transcription factors. In *Cryptococcus neoformans*, the pheromone receptor gene Cpr2 can activate the G-protein signal to regulate mating, while the receptor genes STE2 and STE3 are crucial for sexual identification. In *Candida tropicalis*, the Wor1 transcription factor controls morphological transformation and filament formation. Pheromones secreted by strains of opposite mating types allow cells of the same mating type to mate and form tetraploid offspring, which can then mate with the opposite mating type strain to produce hexaploid

offspring. This mechanism generates polyploidy and genetic diversity, aiding in adaptation to environmental changes. The information has been modified so that the discussion of the function of the MAT locus genes in *Aspergillus oryzae* appears first, then the basic methods of fungal sexual reproduction regulation, and finally, specific examples from *Candida tropicalis* and *Cryptococcus neoformans*. From the function of genes in a single species to the larger context of fungal reproduction, the paragraph now makes sense (Ojeda-Lopez *et al.*, 2018).

## Conclusion

In fungi, mating-type genes are essential regulators of the process of sexual reproduction. Mating-type genes from a variety of fungi have been successfully cloned by researchers worldwide, and their molecular roles have been thoroughly examined. These investigations have clarified how

mating-type genes affect several phases of the sexual reproduction process. Mating type genes can transition from encouraging cooperation across distinct mating types to cooperation within the same type. These genes show a high frequency of interspecific alterations and are evolving quickly. However, there remains a lack of comprehensive studies on the mechanisms of action of mating type genes and their signalling systems.

## Contribution of authors

MBA wrote and edited the manuscript, MI and ABS conceived the idea, AL and JK searched literature, MIM and WA, correction and supervision.

## Conflict of interests

The authors declare that there is no conflict of interest.

**Table 1:** Genes and their functions of mating type gene in fungal sexual reproduction.

Genes	Functions
MAT locus proteins	Act as transcription factors; regulate mating process, growth of parental strains, sexual reproduction, and ascospore formation
MAT1-1-1 ( <i>Penicillium</i> )	Crucial for hyphal and conidial morphology, seed formation, penicillin production, and sexual reproduction control
MAT2 ( <i>S. sclerotiorum</i> )	Influences hyphal density, sclerotia formation, and pathogenicity
MAT1-2-4 ( <i>S. sclerotiorum</i> )	Affects fruiting body germination, stroma, ascospore formation, and male gamete production
matA-3 ( <i>Neurospora crassa</i> )	Low expression during ascus formation; partial overlap in sexual development functions
matA-2 ( <i>Neurospora crassa</i> )	Associated with higher gene expression during asexual reproductive stages
SmtA-2 ( <i>Faecalibacterium macrospora</i> )	Essential for mature apothecia formation
HMG and $\alpha$ domain genes ( <i>Podospira anserina</i> )	Required for sexual reproduction but not post-fertilization growth
MAT1-1-1 and MAT1-1-2 ( <i>Ulocladium botrytis</i> )	Impact colony growth, conidia size, and quantity
Mating type switching ( <i>S. cerevisiae</i> , <i>S. pombe</i> )	Enhances genetic diversity

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