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Mime: A Mitosis Instead of Meiosis Strategy for Synthetic Apomixis to Preserve Hybrid Vigour in Crop Plants

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INTRODUCTION

Owing to differences in cultural values, environments and technologies obtaining the universal solution for sustainable food security is difficult. However, despite these significant obstacles, there is a lot of untapped potential for improving the productivity. Heterosis in important commercial crops is being taken advantage of by using the available potent breeding methods. Three-line or two-line method of hybrid seed production has been used for a long time. Additionally, the use of CRISPR has greatly shortened the time needed for the development of hybrid seeds. Recently, a unique male fertility-related gene in Wheat Ms1 has been discovered, and the biallelic frameshift mutation caused full male sterility wheat lines. Likewise, the knockout of ZmTMS5 and OsTMS5 produced sterility in maize and rice, respectively. But a significant issue with hybrid crops has been that, unlike other crops, their progeny segregate, making the following generation unable to maintain heterosis. Due to these restrictions on sexual reproduction, apomixis is a viable option for preserving the attributes of hybrid seeds across several generations.

Apomixis and Synthetic Apomixis

Apomixis exists naturally and produces offspring, genetically identical to the mother plant. Naturally, the phenomena of apomixis are widespread but exceptional. Both sporophytic and gametophytic apomixis routes have been identified. Apomixis has the ability to maintain hybrid vigour in plant genotypes for several generations. Uncertainty surrounds the biology and development of asexual seed production, and additional research will be needed to understand the genetic makeup of this phenomenon. To combat the genetic segregation of F1 hybrids of various crops, researchers have suggested using synthetic apomixis. In various plant species, a single chromosome segment responsible for inducing apomixes has been detected.

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Nevertheless, efforts to transfer chromosomal segments responsible for the promotion of apomixis remain elusive owing to genetic evolution load. If synthetic apomixis is introduced in any crop vital for food security, it can help fix and propagate genotypes regardless of the genetic complexity in controlling a particular phenotype, ultimately enhancing the application of heterosis fixation in agriculture. Because of these enormous prospects, ingress of apomixis in commercially important crops is considered a hotspot to be studied and explored by plant biologists and the seed industry introduced synthetic apomixis in a few fruit crops, i.e., citrus and apple; however, epigenetic modifications involve severe seed abortion, leading to the failure to transfer apomixis in major crops.

Approaches for Synthetic Apomixis

There are three most common approaches in plant breeding to convert crop plants from sexual to apomictic modes of reproduction:

1. Wide crosses with apomictic wild relatives
2. Mutation breeding
3. Genetic transformation techniques

Mitosis Instead of Meiosis (Mime): A Novel Strategy for Synthetic Apomixis

Meiosis and mitosis are distinguished based on three integral characteristics. First, DNA double standard breaks (DSBs) are induced with recombination and pairing between homologous chromosomes. Second, the first cell division leads to monopolar orientation of kinetochores of sister chromatids. Third, after genome duplication, the division of cells takes place two times. The genetic factors controlling these three developmental processes have been identified in plants. The genes SPO11-1, SPO11-2, HOMOLOGOUS PAIRING ABERRATION IN RICE MEIOSIS1 (PAIR1), PUTATIVE RECOMBINATION INITIATION DEFECT1 (PRD1), PUTATIVE RECOMBINATION INITIATION DEFECT2 (PRD2), MEIOTIC TOPOISOMERASE VIB-LIKE (MTOPVIB), DSB FORMATION (DFO), CENTRAL REGION COMPONENT 1 (CRC1), and $P31^{comet}$ are indispensable for the induction of DSBs in plants. The induced mutations in the abovementioned genes disrupt the normal pairing and recombination of homologous chromosomes. The monopolar orientation of kinetochores during the first meiotic division is mainly regulated by the meiotic cohesion complex controlled by a major component REC8. The genes OMISSION OF SECOND DIVISION (OSD1) and TARDY ASYNCHRONOUS MEIOSIS (TAM) control entry into the second division of meiosis. Mutations in any of these genes impact the second division, leading to the production of diploid gametes in both males and females. The spo11-1 and rec8 double mutant produced a mitotic-like first meiotic division. The osd1, rec8, and spo11-1 triple mutant and tam, rec8 and spo11-1 triple mutant exhibited apomeiosis phenotypes in which meiosis switched into mitosis-like division, and this genotype was called MiMe.

The MiMe strategy helped in the development of viable diploid gametes and their successful transfer into rice by combining mutations in the genes (PAIR1, REC8, and OSD1) involved in the same process, suggesting that this strategy could be widely applied in flowering plants. Clonal seeds were generated by crossing MiMe plants with the engineered genome elimination (GEM) line and ultimately opening a plethora of options for clonal reproduction through seeds with mechanisms similar to apomixis.

Crispr Helpful to Develop Mime Phenotypes

When genome editing to substitute the mitosis for meiosis (MiMe) phenotype is combined with the expression of BBM1 in the egg cell, clonal progeny can be obtained that retain genomewide parental heterozygosity. The synthetic asexual-propagation trait is heritable through multiple generations of clones. Moreover, multiplex editing of three (REC8, PAIR1 and OSD1) key meiotic genes

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in hybrid rice leads to the production of clonal diploid gametes and tetraploid seeds. Next, editing of the MTL gene involved in fertilization results in the induction of haploid seeds in hybrid rice. By simultaneous editing of these four endogenous genes in hybrid rice using the CRISPR/Cas9 system, plants able to propagate clonally through seeds were obtained. The quadruple AOP (Apomictic Offspring Producer) mutants obtained through the knockout of OsSPO11-1, OsREC8, OsOSD1 and OsMATL produced the MiMe phenotype. The mutant has the ability to produce apomictic plants. However, thus far, the number of viable clone seeds with their original hybrid genetics intact are much lower than expected and this area needs further research. The MiMe phenotypes is achieved through disruption of gene controlling meiosis II which leads towards unreduced embryo sac essential for apomeiosis.

Limitations of Synthetic Apomixis

The utilization of the CRISP/Cas system for synthetic apomixis has been successfully employed in rice; however, seed production with intact hybrid vigor was significantly reduced. However, Wang et al. (2020) reported the MiMe does not significantly reduce the seed production whereas, the mutation in MTL leads toward haploid induction at expense of seed production in rice.

CONCLUSION

Understanding the phenomenon of apomixis remains challenging for plant geneticists; however, its potential benefits remain a focus of enormous interest for plant breeders. A combined strategy that can target apomeiosis, parthenogenesis and seed formation might be of the utmost importance to exploit the full potential of apomixis to eliminate breeding barriers. In summary, the successful application of genome editing technology for targeted mutagenesis has opened further avenues of research for understanding the molecular mechanisms controlling apomixis. The efficiency of clonal propagation in crops, particularly in rice, has been limited by the frequency of parthenogenesis. However, this could be improved in the future by studying different promoters of genes or incorporating specific alleles that exhibit full or partial dominance.

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