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REVIEW ARTICLE

Fertility Restoration and its Inheritance Studies

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In plants, male sterility can be caused either by mitochondrial genes with coupled nuclear genes or by nuclear genes alone; the resulting conditions are known as cytoplasmic male sterility (CMS) and genic male sterility (GMS), respectively. CMS and GMS facilitate hybrid seed production for many crops and thus allow breeders to harness yield gains associated with hybrid vigor (heterosis). In CMS, layers of interaction between mitochondrial and nuclear genes control its male specificity, occurrence, and restoration of fertility. Environment-sensitive GMS (EGMS) mutants may involve epigenetic control by noncoding RNAs and can revert to fertility under different growth conditions, making them useful breeding materials in the hybrid seed industry.

Male-sterility mutants can cause abnormal development of either the sporophytic or gametophytic anther tissues. Most sporophytic male-sterility mutants affect primarily tapeta and meiocytes (cells undergoing meiosis), leading to pollen abortion or pollen less sterility. By contrast, gametophytic male-sterility mutants affect mainly the development of microspores or pollen grains.

Male-sterility plants provide crucial breeding tools to harness hybrid vigor, or heterosis, in hybrid crops and also provide important materials to study stamen and pollen development and cytoplasmic-nuclear genomic interactions. Therefore, scientists have long been interested in the genetic and molecular mechanisms of male sterility and fertility restoration.

Producing hybrid seeds of self-pollinating plants requires emasculation—the removal of functional pollen grains—to prevent self-pollination. Before the mid-twentieth century, emasculation in hybrid seed production involved manual labor, machines, or chemical treatments and thus was costly, inefficient, and even damaging to the environment. CMS and EGMS lines do not require emasculation and therefore are ideal female lines for hybrid seed production. In the 1950s, the maize CMS-T (Texas) system was first used for hybrid corn, greatly increasing the efficiency of hybrid seed production and improving maize yields. Later, CMS-based hybrid technology was developed in many other crops, including rice. Commercial hybrid rice, which increases the grain yield by over 20%, was first released in 1976 in China, and it has accounted for approximately 55% of the total rice planting area in China since the late 1980s.

CMS-based hybrid seed technology uses a three-line system, which requires three different breeding lines: the CMS line, the maintainer line, and the restorer line. The CMS line has male-sterile cytoplasm with a CMS-causing gene (hereafter termed a CMS gene) and lacks a functional nuclear *restorer of fertility* (*Rf*, or restorer) gene or genes (122), and is used as the female parent. The maintainer line has normal fertile cytoplasm but contains the same nuclear genome as the CMS line, and thus serves as the male parent in crosses for the propagation of the CMS line. The restorer line possesses a functional *Rf* gene or genes, and thus serves as the male parent to cross with the CMS line to produce F1 hybrid seeds.

Verifying CMS gene candidates requires testing their effect on male sterility. One of the main technical barriers for functionally testing CMS genes is the lack of a successful method to transform plant mitochondrial genomes. As an alternative strategy, a recombinant construct of the CMS candidate gene *orf239* in common bean fused with a 5 mitochondrial targeting signal sequence, and transferring this construct into the nuclei of tobacco plants caused male sterility, thus verifying the CMS function of *orf239*. This strategy has succeeded in functional analysis of other CMS genes, such as *orf79*, *orfH79*, and *WA352* in rice; *orf129* in sugar beet; *orf288* in rapeseed; *orf220* in mustard; and *orf456* in pepper. The use of the

mitochondrial targeting signal is critical for this method; in our experience, the mitochondrial targeting signal-encoding sequence (+1 ~ +105 base pairs) from the restorer *Rf1b* (136) works in CMS-transgenic rice and *Arabidopsis*.

Nine *Rf* genes have been isolated in seven plant species: *Rf2* (maize) (18, 86), *Rf-PPR592* (*Petunia*), *Rfo* (*Rfk1*) (radish, *Brassica*) (10, 22, 71), *Rf1a* (*Rf5*) (rice), *Rf1b* (rice), *Rf2* (rice), *Rf17* (rice), *Rf1* (sorghum), and *Rf1* (*bvORF20*) (sugar beet). *Rf-PPR592*, *Rfo*, *Rf1a*, *Rf1b*, and sorghum *Rf1* encode PPR proteins. PPRs are a group of RNA binding proteins, and most act in organellar post transcriptional mRNA processing, such as editing, splicing, cleavage, degradation, and translation.

Diversification of male sterility is necessary to avoid disease epidemics like in maize. For new CMS lines new restorers also to be identified by making suitable test crosses. The newly identified restorers can be used as male parent in hybrid development or restorer genes can be transferred to new desirable genetic background by using back cross breeding programme. The inheritance of fertility restoration varies because of presence of one or more major restorer genes and including many minor genes. Stability of restoration across different environments is because of accumulation of number of minor genes in nuclear back ground and the interaction of cytoplasmic factors with the nuclear genes.

The inheritance pattern can be clearly understood by developing the F2 or B.C or other segregating generations. Multiple generation data can give valid results in finding number of major genes responsible for fertility restoration.

Molecular markers can help in selecting individuals with major restorer gene at the seedling stage itself without the necessity of test crosses.

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