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POPULAR ARTICLE

Male sterility in crop plants: The molecular key to affordable hybrid seeds

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Intricacies of the subject

Hybrid varieties, which combine two carefully chosen parents to capture the yield boost known as heterosis (hybrid vigor), are among the biggest success stories of modern agriculture. But producing hybrid seed is not easy. In crops such as rice, cotton, pigeonpea and castor, the female parent must be stopped from pollinating itself, otherwise the seed harvested is not hybrid. Traditionally this meant removing the male flower parts by hand - emasculation - a slow, skilled and expensive job that pushes up seed prices. Male sterility, the inability of a plant to produce functional pollen, solves this problem elegantly. A male-sterile plant is a ready-made female parent that simply cannot self-pollinate, so it yields pure hybrid seed when pollinated by a chosen male parent. Behind this simple idea lies a fascinating molecular machinery involving mitochondria, nuclear restorer genes and even a borrowed bacterial "poison–antidote" system. This article unpacks that machinery and explains what it means for Indian farmers and breeders.

Introduction

Every F_1 hybrid seed that reaches an Indian farmer begins with the same question: how do we stop the seed parent from fertilizing itself? The answer, deployed across millions of hectares of rice, maize, bajra, sunflower and pigeonpea, is male sterility - the precisely understood inability of a plant to produce functional pollen. What follows is a guided tour of the molecular machinery behind it and of the many ways Indian breeders put it to work.

What is male sterility?

Pollen formation in a flower follows an orderly assembly line. The stamen primordia are specified first; then the pollen mother cells form; these divide by meiosis to make haploid microspores; the microspores mature into pollen grains; and finally, the anther opens to release them. Around this assembly line stands the tapetum, a layer of nurse cells lining the anther sac that feeds the developing pollen. Male sterility results when the assembly line breaks at any step. The plant may produce no stamens at all, malformed anthers, pollen that collapses before it matures, or anthers that simply never open. In every case reported here the outcome is the same: no functional pollen, and therefore no self-fertilization.

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Male sterility is found in wild and cultivated plants of virtually all crop species, and it shares some interesting parallels with self-incompatibility, the other natural mechanism that stops a flower from fertilizing itself.

A short history

Farmers and botanists have been noticing sterile plants for centuries. The first clear scientific record goes back to 1763, when J. K. Koelreuter observed aborted anthers in species hybrids. By the 1930s and 1940s, workers had discovered cytoplasmic male sterility in maize and onion (Jones and Davis, 1944), and by the 1950s chemical gametocides had appeared. Male sterility has also been created deliberately by gamma rays, by the chemical mutagen EMS, and even by colchicine in sorghumand later by genetic engineering and cell fusion. Today hundreds of male-sterility genes and dozens of cytoplasmic sources are catalogued across almost every crop.

The Tapetum: The anther's lifeline

The tapetum is a thin layer of nutrient-rich cells that acts as a lifeline for developing pollen. It supplies sugars, lipids and proteins to the growing microspores and, at exactly the right moment, dies in a controlled manner - programmed cell death - to release building blocks for the pollen wall. Two things often go wrong in sterile plants. First, the young microspores are caged inside a callose wall (a sugar polymer) that must be dissolved by an enzyme called callase at a precise stage; if the wall is not dissolved, the microspores stay trapped and starve. Second, the tough outer coat of pollen (the exine) is built from sporopollenin, one of the most resistant biological polymers known; if its synthesis fails, the pollen walls are weak and the grains collapse. Studies also show that sterile anthers are typically poor in the amino acid proline and short of energy, and that the tapetum may die too early or too late. Many nuclear genes - among them MS1, AMS, TDF1 and MYB80 - work as master switches for these tapetal processes, and a fault in any one of them can switch off fertility.

The four families of male sterility

Breeders group male sterility into a few practical families, each with its own molecular origin. Genetic male sterility (GMS) is caused by a mutation in a nuclear (chromosomal) gene, usually recessive, and is hard to maintain because a sterile plant cannot set seed by itself. Cytoplasmic male sterility (CMS) is caused not by the nucleus but by the cytoplasm - specifically by abnormal genes in the mitochondria, which are inherited only through the seed parent; this is the workhorse of commercial hybrid seed production. Environment-sensitive GMS (EGMS) involves nuclear genes whose effect is switched on or off by temperature (thermo-sensitive, TGMS) or day-length (photo-period-sensitive, PGMS), so the same line is sterile in one season and fertile in another. Finally, transgenic and chemically induced sterility use engineered systems such as barnase - barstar, or chemical sprays called gametocides, to switch off pollen without changing the plant's chromosomes. In practice, CMS is deployed through a three-line system: a male-sterile A-line, a maintainer B-line that multiplies it, and a restorer R-line that switches fertility back on in the hybrid (Fig. 1).

Telling the systems apart

Breeders identify which system a sterile plant belongs to by studying its progeny. If a sterile plant crossed with normal pollen gives only sterile offspring, the sterility is cytoplasmic (CMS).If the offspring split roughly, one sterile to one fertile plant, the sterility is controlled by a recessive nuclear gene (GMS). And if some crosses stay sterile while others are fully fertile or segregate, the plant

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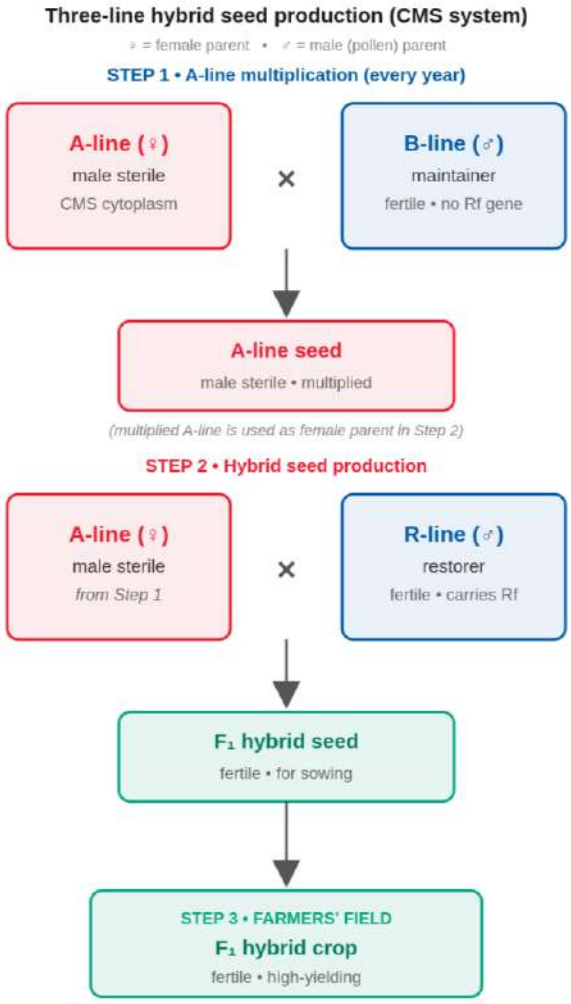
Fig. 1: Three-line hybrid seed production using cytoplasmic male sterility: the male-sterile A-line is multiplied with the maintainer B-line and then crossed with the restorer R-line to produce fertile F_1 hybrid seed for farmers.



carries cytoplasmic sterility that can be corrected by restorer genes (CGMS). This simple field test guides the breeder in choosing the right system before molecular work begins.

The mitochondrial story: How a "chimeric" gene silences pollen

Mitochondria are the power stations of the cell, and plant mitochondria have unusually large, restless genomes that frequently rearrange and recombine. Occasionally such a rearrangement stitches together pieces of existing genes into a brand-new "chimeric" open reading frame (ORF) that encodes a small, often toxic protein. Because mitochondria pass only through the seed parent, this new gene is inherited maternally. And because developing pollen and the tapetum demand enormous amounts of energy, even a small disturbance of mitochondrial function hits the anther first. The toxic protein can clog the respiratory chain, leak ions across membranes or also cause a build up of reactive and the energy-starved tapetum dies

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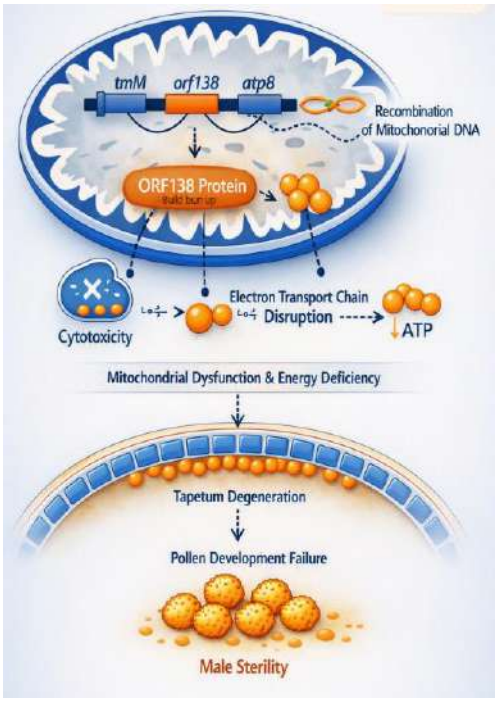
prematurely, aborting the pollen. Well-known examples include orf79 in rice (Boro-II cytoplasm), urf13 in maize (Texas cytoplasm), orf522 in sunflower and orf138 in radish (Ogura cytoplasm). These are the molecular fingerprints of CMS.

Fig. 2: Molecular basis of cytoplasmic male sterility: a chimeric mitochondrial protein (ORF138) accumulates in the tapetum, disturbs mitochondrial function and energy supply, and causes tapetum degeneration, so no functional pollen is formed



Restorer genes: Nature's fertility switch

The good news is that fertility can be switched back on by restorer-of-fertility (Rf) genes in the nucleus. Most Rf genes encode pentatricopeptide repeat (PPR) proteins, molecules built from repeated units that act as readers of mitochondrial RNA. Targeted to the mitochondrion, a restorer protein binds to the toxic CMS transcript and either cuts it, edits it or marks it for destruction, so the harmful protein is never made and normal pollen development resumes. This quiet duel between a mitochondrial "off switch" and a nuclear "on switch" is one of the clearest examples of cooperation between two genomes in a single cell. In rice, the two restorers Rf1a and Rf1b silence orf79 by different routes - cleavage versus degradation - while in radish the gene Rfo rescues the Ogura CMS, and in petunia Rf-PPR592 performs the same job. This is the molecular logic behind the three-line breeding system.

Two-line breeding: Letting the weather decide

An alternative and elegant trick uses environment-sensitive genes. In rice, TGMS lines such as Pei-Ai 64S produce no pollen above about 23 °C but become fertile in cooler weather, while PGMS lines turn sterile under long days (more than about 13 h 45 min) and fertile under short days, provided the temperature stays within 23 to 29 °C.

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Table 1: Comparison of the main male sterility systems used for hybrid seed production

Feature	Genetic Male Sterility (GMS)	Cytoplasmic / Cyto-Genetic Male Sterility (CMS / CGMS)	Environment-sensitive GMS (EGMS: TGMS / PGMS)	Transgenic Male Sterility (Barnase - Barstar)
Where the fault lies	Mutation in a nuclear gene	Chimeric gene (ORF) in mitochondrial DNA	Nuclear gene switched by temperature or day-length	Tapetum-specific transgene (barnase RNase)
Inheritance	Nuclear, usually recessive	Maternal (cytoplasmic)	Nuclear, environment-dependent	Dominant transgene
Keeping the sterile line	Difficult; fertile segregants must be rogued out	Easy - multiplied by crossing with a maintainer (B) line	Easy - same line is fertile under permissive conditions	Easy - barstar line remains fertile
Fertility restoration in the F_1	Not needed; a fertile pollinator is used	Nuclear restorer (Rf) genes in the R-line	Not needed; the environment acts as the switch	Barstarneutralisesbarnase
Hybrid seed system	Two-line (with roguing or markers)	Three-line (A, B and R lines)	Two-line	Two-line (engineered)
Indian examples	Pigeonpea ICPH 8	Bajra HB 1; rice PRH 10; sunflower BSH 1; maize DHM hybrids; sorghum CSH 1; pigeonpea ICPH 2671	Rice TGMS/PGMS lines (UPRI 95-140, UPRI 95-167)	Experimental; not yet commercial in India
Main limitation	Labour for roguing; seed-purity risk	Narrow cytoplasmic base; Rf gene needed in the pollinator	Sensitive to weather; used mainly in rice	Regulatory (GM) and public-acceptance hurdles

The same variety can therefore be multiplied as a fertile crop in one season and used as a female parent in another - no maintainer line is needed, so the system is called "two-line". Two such Indian rice lines, UPRI 95-140 and UPRI 95-167, were isolated as spontaneous mutants and registered as germplasm for this purpose.

Designer sterility: Barnase - Barstar, RNAi and CRISPR

Biotechnology lets breeders build male sterility to order. The best-known system borrows a "poison - antidote" pair from the soil bacterium Bacillus amyloliquefaciens: barnase, an enzyme that shreds RNA and kills cells, and barstar, its natural inhibitor. When barnase is wired to the TA29 promoter - a

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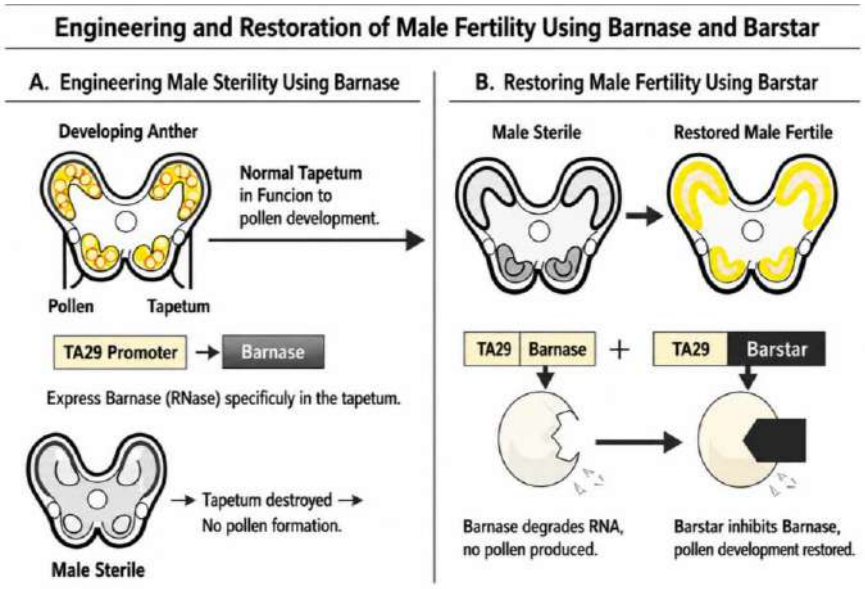
switch active only in the tapetum - the tapetum destroys itself and the plant becomes male-sterile, while the rest of the plant stays completely normal. A partner line carrying barstar remains fertile; crossing the two yields hybrid seed in which barstar neutralizesbarnase, so the hybrid crop is fully fertile. The same toolbox includes RNA interference (silencing a tapetum gene such as Bcp1) and, more recently, CRISPR–Cas editing, which can knock out pollen-development genes such as MS1, TDF1 and AMS, or even edit mitochondrial sterility genes directly. Because transgenic sterility is dominant, it is inherited simply and is easy to screen.

Fig. 3: Engineered male sterility with the barnase–barstar system: (a) tapetum-specific expression of barnase (an RNase) destroys the tapetum and prevents pollen formation; (b) introducing barstar through the pollen parent blocks barnase and restores fertility in the hybrid



Chemical hybridising agents: A non-genetic short cut

For crops where genetic systems are not yet available, breeders can spray "male gametocides" - chemicals that sterilize pollen without altering genes. The first report dates to 1950, when maleic hydrazide induced male sterility in maize. Ethephon, gibberellic acid and a few arsenate compounds have since been used in rice, wheat, cotton, onion, barley and bajra. An ideal gametocide must produce nearly complete sterility, leave the female parts unharmed, cause no mutation and leave no residue in the harvested seed. In practice, few chemicals meet all these tests, which is why chemical hybridising agents remain a niche tool used mainly as a back-up.

Applications in Indian agriculture

India was an early adopter of hybrid technology: the pearl-millet hybrid HB 1, released in 1965, was among the world's first commercially successful grain hybrids built on cytoplasmic male sterility. Since then, male sterility has quietly powered the country's seed industry. Farmers today grow CMS-based hybrids of bajra (the HB series), maize (Ganga, Deccan, DHM-107, DHM-109), sorghum (CSH1), rice (PRH 10), sunflower (BSH 1) and rapeseed-mustard (PGSH 51).

In pigeonpea (red gram), the GMS-based hybrid ICPH 8 and the CMS-based ICPH 2671 brought hybrid technology to a pulse crop for the first time; safflower hybrid DSH 129 follows a similar route, and the castor hybrid GCH 3 exploits naturally pistillate flowers. For Indian farmers the payoff is practical: cheaper and purer seed, higher and more uniform yields, and better stress tolerance - benefits that matter most to smallholders who cannot afford costly or unreliable seed. Public and private seed companies now multiply CMS-based hybrids of several vegetables and oilseeds as well, and hybrid seed production itself has become a valued source of rural employment in states such as Maharashtra, Andhra Pradesh and Karnataka. Public institutions, including State Agricultural Universities such as Mahatma Phule Krishi Vidyapeeth, Rahuri, and ICAR institutes, are actively developing new sterile, maintainer and restorer lines for regional crops, so that the benefits of hybrids reach beyond the major cereals.

Did you know?

- Male-sterile plants were first recorded more than 250 years ago - in 1763 - when J. K. Koelreuter noticed aborted anthers in species hybrids.
- The soil bacterium Bacillus amyloliquefaciens naturally makes both barnase (an RNA-shredding “poison”) and barstar (its “antidote”) - a self-defense pair that breeders borrowed to build the barnase–barstar sterility system.
- China’s hybrid-rice revolution began with a single male-sterile plant of wild rice found in 1970; its “wild-abortive” cytoplasm still underpins many modern hybrids.
- In 1970 a fungus whose toxin could punch holes through the URF13 protein devastated maize in the United States, where most hybrids then shared the same Texas (T) cytoplasm - a reminder to diversify the cytoplasmic base of hybrids.
- India’s pearl-millet hybrid HB 1 (1965) was among the world’s first commercially successful grain hybrids built on cytoplasmic male sterility.

Challenges and future prospects

Male sterility is not without weak points. CMS lines can become unstable under heat or drought stress, and if all hybrids of a crop share one cytoplasm, a single disease or toxin could threaten the entire seed chain - the 1970 Southern corn leaf blight epidemic in the United States, when a fungus exploited the uniform Texas cytoplasm of maize, remains a cautionary tale. GMS lines demand careful removal (roguing) of fertile plants, restorer genes are scarce in some crops such as pigeonpea, where only a few restorer sources are known, and transgenic sterility systems face regulatory and public-acceptance hurdles. Looking ahead, the toolkit is expanding rapidly: CRISPR-based and synthetic CMS systems, mitochondrial genome editing, genomic selection to breed better restorer lines, and artificial-intelligence-assisted pollen phenotyping all promise more robust, climate-resilient sterility systems. The goal is simple - dependable, affordable hybrid seed for every crop and every farmer.

Summary

Male sterility - the failure to produce functional pollen - is one of the quiet pillars of modern crop improvement. At its heart lies a precise molecular dialogue between the nucleus and the mitochondria: chimeric mitochondrial genes such as *orf79* and *urf13* produce toxic proteins that starve the tapetum and abort pollen, while nuclear restorer genes encoding PPR proteins silence these transcripts and switch fertility back on.

Breeders exploit this dialogue through three-line (CMS–Rf) and two-line (environment-sensitive) systems, and increasingly through engineered barnase–barstar, RNA-interference and CRISPR approaches, to mass-produce pure hybrid seed without costly hand emasculation. In India, these systems already drive hybrids of bajra, rice, maize, sunflower, pigeonpea and mustard, bringing affordable hybrid seed within reach of smallholders. With genome editing, synthetic biology and better restorer breeding on the horizon, male sterility will remain central to food security and to doubling farmers' returns.

References

1. Bohra, A., Jha, U.C., Adhimoolam, P., Bisht, D. and Singh, N.P., 2016, Cytoplasmic male sterility (CMS) in hybrid breeding in field crops. Plant Cell Rep., 35(5): 967–993.
2. Chen, L. and Liu, Y.-G., 2014, Male sterility and fertility restoration in crops. Annu. Rev. Plant Biol., 65: 579–606.
3. Kim, Y.-J. and Zhang, D., 2018, Molecular control of male fertility for crop hybrid breeding. Trends Plant Sci., 23(1): 53–65.
4. Melonek, J., Duarte, J., Martin, J., Beuf, L., Murigneux, A., Varenne, P., Comadran, J., Specel, S., Levadoux, S., Bernath-Levin, K., Torney, F., Pichon, J.-P., Perez, P., Kittiworawut, M., Whitford, R. and Small, I., 2021, The genetic basis of cytoplasmic male sterility and fertility restoration in wheat. Nat. Commun., 12: 1036.
5. Wang, Z., Zou, Y., Li, X., Zhang, Q., Chen, L., Wu, H., Su, D., Chen, Y., Guo, J., Luo, D., Long, Y., Zhong, Y. and Liu, Y.-G., 2006, Cytoplasmic male sterility of rice with Boro II cytoplasm is caused by a cytotoxic peptide and is restored by two related PPR motif genes via distinct modes of mRNA silencing. Plant Cell, 18(3): 676–687.