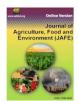


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Review Article



Maternal inheritance: A new pathway for the industrialization of plant breeding

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ABSTRACT

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An imagine character named CMS found in different plant species and has been utilized in hybrid cultivars development. CMS is linked to incorporation of specific fertility restoring genes, which are donated by the restorer line. In recent years, efforts to understand the factors inducing sterility and the associated fertility determinants (*Rf*) in plants. The creation of hybrids utilizing a CMS line has been successfully adopted across various plants. In addition, CMS can be engineered by currently developed *CRISPR-Cas* gene editing, which allows for the knockout of specific genes responsible for male gamete development. An environment-insensitive genic male system known as 3rd-generation hybrid rice technology (TGHRT) is effectively addressing the inherent challenges of two-line as well as three-line systems. Hence, the inception of TGHRT, a multitude of discoveries and innovations have emerged. This review tries to provide insights into the mechanisms underlying the development of CMS, along with their potential and future prospects in the industrialization of plant breeding.



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INTRODUCTION

Genetic inheritance serves as the foundation of plant breeding. In genetics, inheritance is generally interpreted through Mendelian laws, which dictate the transfer of nuclear genes. The inheritance of traits in plant genetics has been conventionally understood via Mendelian principles, where genes located on nuclear chromosomes, the offspring are received genetic composition from both parents equally, predictable outcomes across Nevertheless, there exists an additional non-Mendelian form of inheritance, referred to as cytoplasmic or extranuclear inheritance, which is significant in the transmission of certain traits (Laurentin Táriba 2023). In the majority of eukaryotes, cytoplasmic DNA is predominantly transmitted through the maternal line, meaning it is inherited from the mother to the offspring, unlike nuclear DNA, which adheres to Mendelian inheritance patterns (Birky and William 2001). The maternal nature of cytoplasmic inheritance arises from the fact that, in most plants, the egg cell provides the bulk of the cytoplasm to the zygote. This inheritance type is regulated by genes found in mitochondria and chloroplasts, which are maternally inherited in most angiosperms and exist as independent, circular, self-replicating DNA molecules (Kuroiwa 2010). These genes influence character like sterility; this unique form of inheritance carries significant genetic and breeding implications (Hanson and Bentolila 2004). Cytoplasmic genes also regulate various traits linked to photosynthetic efficiency, herbicide resistance, and abiotic stresses that are being crucial threat of sustainable agriculture due to climate change.

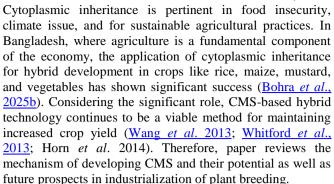
Cytoplasmic inheritance was frequently disregarded in the initial breeding; but it has now attained as asset in commercial breeding, particularly because maternal genes influence a range of agronomic traits that are essential for crop productivity and adaptation. One of the most significant applications of cytoplasmic inheritance is observed in the creation and use of CMS systems (Seli et al., 2019; Gautam et al., 2023). Consequently, CMS systems provide new

opportunities for plant breeders. One of the most thoroughly researched and applied aspects of cytoplasmic inheritance is its function in inducing male sterility, a characteristic that is crucial for hybrid production. Hybrid varieties frequently display heterosis, resulting in enhanced production, pest and disease resistance, and increased stress tolerance (Seli et al. 2019). CMS allows for the generation of hybrids without the necessity for the manual removal of anthers, thus promoting efficient, large-scale hybrid seed production. This technology is playing vital role in enhancing yields and crop uniformity in various species such as rice, sorghum, maize, sunflower, cotton, and brassica crops (Bohra et al., 2016).

CMS plays major role in commercial production of seed without removal of male parts. Sterility of CMS can be overcome by nuclear restorer (Rf) genes, which enable breeders to restore fertility in F₁ hybrids (Kim and Zhang, 2018; Bhattacharya et al., 2024; Bohra et al., 2025b). The prospects for cytoplasmic inheritance in the enhancement of plants are being further broadened through advancements in molecular biology, genomics, and plant transformation These innovations techniques. have created opportunities for the identification, manipulation, and transfer of advantageous cytoplasmic traits. Despite facing obstacles, such cytoplasmic-nuclear certain as incompatibilities and the limited methods available for transforming organellar genomes, ongoing research is progressively addressing these challenges (Zhang et al., 2014; Poornima et al., 2020).

CMS systems are identified in more than 140 plants and are regularly used in hybrid breeding of maize, rice, sorghum, sunflower, and various vegetables. Hybrid varieties, recognized for their yield stability and adaptability, are increasingly regarded as a viable solution. The application of CMS systems provides a genetically stable, economically feasible, and environmentally sustainable method for big amount hybrid seed production (Gopinath, 2024). In commercial breeding, cytoplasmic inheritance has become a significant tool for the development of crop varieties. For example, CMS, a trait governed by mitochondrial DNA, is extensively utilized in hybrid seed production to facilitate cross-pollination and boost hybrid vigor (Schnable and Wise, 1998).

Moreover, progress in genetic engineering and CRISPR/Cas9 gene editing has broadened the possibilities for utilizing cytoplasmic inheritance in crops that do not possess natural cytoplasmic male sterility (CMS) systems (Bohra et al., 2025b). Consequently, it is essential to comprehend the mechanisms, benefits, and limitations of cytoplasmic inheritance for contemporary plant breeding initiatives. In addition to traditional breeding methods, cytoplasmic inheritance offers further potential. The CRISPR/Cas9 technology is now capable of altering the genomes of mitochondria and chloroplasts, thereby creating new avenues for the introduction of desirable traits into crops (Levings and Brown, 1989). A thorough comprehension of the CMS/Rf system, facilitated by omics technologies, significantly enhances the capacity to utilize hybrid for boosting field crop's productivity (Bohra et al., 2016). However, there are specific challenges associated with the application of cytoplasmic inheritance in breeding. Major hurdles include a lack of genetic diversity, possible adverse effects on fitness, and technical difficulties in modifying cytoplasmic DNA (Greiner and Bock 2013; Gómez-Tatay et al., 2017; Hill et al., 2019; Bohra et al., 2025b).



History of cytoplasmic inheritance

Genes found in eukaryotic organisms are confined in nucleus. These genes are transmitted to future generations via meiosis, which entails a rigorous segregation. Eukaryotic cells also harbor smaller genomes located in mitochondria, chloroplast. The concept of cytoplasmic inheritance, also known as extranuclear or non-Mendelian inheritance, refers to the transfer of genetic traits through cellular components that exist outside the nucleus, primarily within the cytoplasm. The notions of extrachromosomal, organellar, or cytoplasmic inheritance relate to the non-nuclear elements found in the cytoplasm that affect the phenotypic characteristics of the offspring. Nevertheless, eukaryotic cells also include smaller genomes, such as those from symbiotic organisms, mitochondrial DNA, and chloroplast DNA, which are located in cytoplasm (Camus et al., 2022).

The earliest recorded evidence of this phenomenon can be traced back to Carl Correns', where described the non-Mendelian genetics of Mirabilis jalapa leaf color (Correns Importantly, cytoplasmic genetic components demonstrate markedly different patterns of inheritance than Mendelian nuclear genes. The inheritance was solely maternal: a seed that arose from the ovule of non-green stem produced non-green progeny rather than the colour of pollen source. In 1943, Sonneborn discovered cytoplasmic inheritance of kappa particles in Paramecium. Over the years, numerous researchers highlighted the essential role of cytoplasm in genetic inheritance. By 1952, the evidence supporting different types of cytoplasmic elements were grown to unify the genetics of organelles (Lederberg 1952). Variability in genetic patterns (whether paternal or biparental) was described across a wide taxa (Birky and William, 2001). CMS may generate spontaneously in breeding lines due to mutation, hybridization or inter species exchanges of cytoplasmic and nuclear genes (Dalvi et al., 2010; Islam et al., 2014). A notably successful cross was recorded between two distinct CMS-inducing cytoplasm of species, (Schnable and Wise, 1998). Helianthus Consequently, it can be concluded that interspecific hybridization and backcrosses lead to the emergence of CMS.

Types of cytoplasmic inheritance

Maternal inheritance

In cytoplasmic inheritance, the traits of offspring are determined exclusively by the cytoplasm of the mother, rather than by nuclear genes. During the process of fertilization, the egg provides the majority of the cytoplasm



to the zygote, while the sperm primarily contributes nuclear DNA. For instance, in *Mirabilis jalapa*, the leaf color (green, white, variegated) is inherited solely from the female parent. Mitochondrial disorders, such as Leber's hereditary optic neuropathy, are transmitted from the mother to all offspring, but only daughters are able to pass the trait on further. Recent research has offered in depth insights of vertically cytoplasmic genomes transmission, indicating binary classification: uniparental and biparental inheritance. Maternal; maternal inheritance of transmission were identified, which represent leakage of paternal and maternal and biparental inheritance (Figure 1) (Birky and William 2001; Camus et al., 2022). No fixed mechanism involves in cytoplasmic genome transmission. Rather, different species employ different processes to influence their inheritance. These transmission mechanisms are different from Mendelian genetics.

Organellar inheritance

The transmission of traits is governed by genes situated in organelles such as mitochondria and chloroplasts. Mitochondria are present in almost all eukaryotic organisms and play a crucial role in respiration. Chloroplasts, on the other hand, are found in plants and algae and are essential for photosynthesis. For instance, in yeast, petite mutants arise from mitochondrial mutations that result in slow-growing colonies due to impaired respiration. In maize, chloroplast inheritance leads to the emergence of albino or variegated seedlings due to mutations in chloroplast DNA. The inheritance mode could be paternal, biparental or maternal varying by species (Figure 1). Organellar genomes are characterized by their small, circular structure and their ability to replicate independently of nuclear DNA. Unlike nuclear chromosomes, organellar inheritance does not exhibit recombination.

In 1976, Birky described the principles of cytoplasmic genomes inheritance. Among these two distinct processes significantly influence cytoplasmic inheritance, such as vegetative separation and uniparental inheritance across species in different kingdoms. Importantly, these two processes address critical events of cytoplasmic inheritance: i) during cell division, process of distributing the cytoplasmic genomes among daughter cells ii) process of passing cytoplasmic genomes to offspring during reproduction?

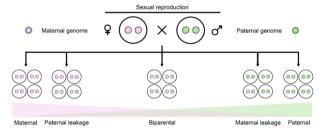


Figure 1: Various species shows unique perpendicular passing of cytoplasm. Although uniparental genetics was historically regarded as norm, research indicates that deviation happen frequently. Figure sourced from Chung (2025).

CMS controlling mechanisms

The mechanisms underlying sterility and corresponding fertility restorer genes were thoroughly investigated across plants, leading to the proposal of several theories. Interaction between gene of anther specific products and CMS genes somehow leads to mitochondrial dysfunction. Furthermore, it is proposed that this limitation could develop from the natural selection (Chase, 2007). Mitochondrial mutations influence the female parts by eliminating fertility of hermaphrodite flowers. Conversely, a mutation of the male reproductive system impacts to future generations (Chase and Gabay-Laughnan, 2004). CMS can spontaneously develop due to mutagenesis and cross pass of genes from nucleus to cytoplasm or vice-versa (Dalvi et al., 2010; Islam et al., 2014).

Maize T-cytoplasm contributes to develop standard CMS lines (Dewey et al., 1987). Cytoplasm remains generation by generation until the loss of fertility restoring gene. The processes of backcrossing and inter species cross may develop CMS inducing cytoplasm. A particularly hybridization was found in Sunflower, leading to development of CMS (Schnable and Wise, 1998). CMS mechanism are described in the: energy deficiency model, cytotoxicity model, aberrant programmed cell death (PCD) model, and retrograde regulation model (Chen et al., 2023).

CMS resulting lack of anther's energy

In 1978, Warmke and Lee proposed the energy deficiency model, where mitochondrial functions are modified by CMS genes and make barrier in pollen development. A significant amount of energy is required for developing sporophytic and gametophytic cells in anther. This energy requirement meets by enhancing mitochondrial functions and/or increasing number of mitochondria in the cells. A swift mitochondrial change was recorded in case of CMS in maize, which leads inactivation of mitochondria and causes limited ATP for anther maturation (Dewey et al., 1987). This theory is endorsed by analyzing structure of CMS proteins corroborated that are transmembrane and play a role in ATP synthesis. In oilseed rape, enhanced deposition of reactive oxygen species was found due to co-transcription of nad3 and rp212 genes with orf346. As a result, ATP levels are reduced and led to dysfunction of mitochondria, which finally causes pollen abortion.

Cytotoxicity model of CMS

Proteins that are associated with CMSs can eliminate cells with cytotoxic characteristics. Sequencing analyses revealed that the molecular weight varies from 10-35 kDa of the CMS encodes proteins (Kim and Zhang 2018). Research uncovered the existence of CMS products at inner mitochondrial membrane, of which marked transmembrane domains (Levings and Brown, 1989). This domain leads to mitochondrial malfunction and causes abortion of male organ. The proteins cluster of membrane polymers resulting electrolyte leakage, which illustrates their cytotoxic effects on E. coli and yeast (Huang 2022). Similar mechanism found in maize URF13 protein, which produces a pore-forming receptor.



Aberrant programmed cell death model

The aberrant programmed cell death (PCD) model shows the relationship of tapetal cell of gametophyte and sporophyte. Male sterility arises from late PCD of tapetal cells. The cytoplasm of *A. kotschyi* and *Ae. juvenalis* showed PCD of anther tapetal cells, which stopped microspore genesis in alloplasmic male-sterile wheat (Bhattacharya et al., 2024). The polima-CMS system found in oilseed rape, where orf224 induces sterility due to the premature PCD of sporogenous cells and abnormal division of the tapetum as well as microspore mother cells (Wang et al., 2013).

Retrograde regulation model of CMS

Retrograde model of CMS focuses on RETROGRADE-REGULATED MALE STERILITY (RMS) proteins, which are mitochondrial components encoded by nuclear fertility restorer (Rf) genes and are regulated by signals that originate from the mitochondria. These non-PPR proteins are believed to inhibit pollen germination, resulting in sterility, a phenomenon that is emphasized by the coevolution of CMS and Rf genes in various crops. A prominent example is the Rf17 gene in rice, where a decrease in expression leads to restored fertility, while overexpression results in pollen lethality. Although RMS proteins do not alter CMSassociated RNAs, their loss of function enhances fertility, a conclusion supported by CRISPR/Cas9-induced mutations in the RMS gene that restored fertility without impacting PPR2 (Suketomo et al., 2020). This research underscores the potential of targeting RMS genes for restorer line development.

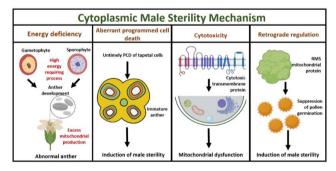


Figure 2: Mechanisms of CMS; (i) anther energy deficiency, (ii) programmed cell death, (iii) cytotoxic in the cells, and (iv) retrograde regulation model (Bhattacharya *et al.* 2024).

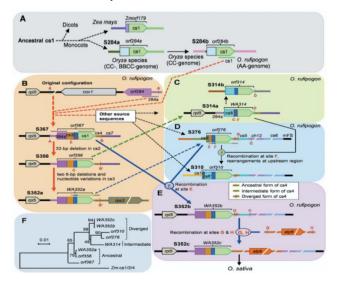
Molecular basis of CMS

Tang et al. (2017) studied expression patterns of CMS genes of O. sativa L. ssp. japonica, had recessive rf3 and rf4-j alleles. Expression of these genes is not influenced due to absence of restorer genes (Luo et al., 2013; Tang et al., 2014). The orf314 which was marked as orf288 by sequencing mistake previously (Notsu et al., 2002) cannot cause CMS. This is despite the fact that its ORF sequence closely resembles that of WA314, exhibiting 13 amino acid variations between the encoded proteins.

Mitochondrial genes are often initiate transcription in different mRNA species. Every mRNA species initiates transcription in different promoter's controlled sites (Zhang and Liu, 2006). For instance, a dicistronic transcript accomplished with *rpl5* and *WA352c* ORF and other two monocistronic transcripts are produced by *WA352c* (Luo et

al., 2013). The proposed orf284 features a 5'-promoter segment which play role in CMS-related ORF formation. Therefore, the local orf284-derived promoter offered an additional promoter of rpl5 acts as CMS and CMS-like genes. Although structure and expression of orf367 exhibit capabilities as CMS, but it depends on different factors. A high nucleotide similarity of S284a and the maize Zmorf179 with 94% possess identical cs1/downstream sequences. This indicates that they probably evolved from a shared ancestral cs1-containing sequence. The divergence in sequences between \$284a and its homologs is believed to have taken place in *Oryza* species from other plant species (Figure 3A). S284b has developed from rearrangement of S284a ORF of CC-genome species and has been inherited to O. rufipogon (AA-genome) and O. officinalis (CC-genome). The cs1 fragment present in S284b acts as primary source of CMS genes in O. rufipogon.

The rpl5/cox1/orf284 complex (Figure 3B) contain nine out of the ten mitochondrial sequence, without CMS-WA line of O. rufipogon (Bentolila and Stefanov 2012; Igarashi et al., 2013). The rpl5/cox1/orf284 complex confirmed the ancestral makeup of AA-genome in wild rice (Tang et al., 2017). CMS gene probably emerged from the area downstream of rpl5, which is a result of recombination between orf284 and its promoter region of mitochondrial genome (Figure 3A and 3B). The evolutionary relationships among were established after the formation of S284a and S284b with multiple nucleotide variations. Sequences of S367, S356, and S352a showed homology to reference sequences. In contrast, the sequences of S276, S310, S352b, and S352c were more divergent. While conserved and divergent sites was identified in S314a (Figure 3B-E). It is probable that S367, S356, and S352a had the primitive sequences, where S314a was act as the precursor of S276, S310, S352b, and S352c. The nucleotides of S367 align with the outgroup and found different structure indicates that S367 is most closely related to S284b.



Source: (Tang et al. 2017).

Figure 3: Evolutionary pathway of CMS-related genes in wild rice. Features in *O. rufipogon* were deduced from their contents and sequence homology. A-H indicate the sites of repetition that enhance chance of recombination between source and donor sequences, resulted new features. Solid line represents straight forward rearrangements through one or two recombination, while dotted line represent intricate changes. (A) S284a and S284b are originated from *cs1* by



various recombination. (B) rpl5/cox1/orf284 located at downstream of rpl5, where recombinant S367 was generated from S356. The red arrows depict the primary evolutionary direction leading to development of proto-genes (orf367 and orf356) with intermediate CMS (WA352a). (C) S314a was formed the translocation of fragment of S356 by alternations. (D) S276 has arisen from rearrangement of S352a, in combination with cs5, ch12/cs6/mFS, and cs9. (E) S352b derived from recombination of S367 and S276, followed by incorporation of ATP6-containing sequence, resulting the formation of S352c. This indicates the latest evolutionary pathway of the functional CMS genes WA352b and WA352c. S352c in O. sativa during the domestication. Additionally, S352c from O. rufipogon and O. sativa employed as donors of CMS-WA lines (Luo et al., 2013). (F) A phylogenetic tree contains cs1, cs2, and cs4 sequences identified in wild rice and maize, constructed by neighborjoining method.

Use of cytoplasmic inheritance in commercial plant breeding

Heterosis is a concept, shows enhanced criteria in F_1 produces from crossing between two parents (<u>Birchler</u>, 2015). Hybrid crops can produce yields that are 15–50% higher than those of inbred varieties. The economic benefits associated with heterosis have greatly improved global crop production. Utilizing heterosis is a vital approach to enhance yield and expand the adaptability. This concept is widely used in different crops, including maize, rice, cotton, rapeseed, tomato, bell pepper, cucumber, watermelon, and melon (Bohra *et al.*, 2025a).

The practical aspect of using heterosis is the large-scale production of hybrid seeds. Maize has separate male and female parts on the same plant. Hybrid can be produced by pollinating the ear by the pollen of male parent following detasseling. Maize was the inaugural hybrid crop to be brought to market, owing to the comparative ease and practicality of producing hybrid seeds (Duvick, 2001). The majority of monoecious gourd crops, including pumpkins and cucumbers, as well as dioecious crops characterized by substantial floral structures, such as cotton, tomatoes, and undergo manual emasculation. emasculation is not economically viable for large scale production of hybrid with small reproductive structures, like rice, wheat, and Brassica (Longin et al., 2012). To generate hybrid seeds from self-pollinating plants, it is crucial to perform emasculation to stop selfing. Prior to 20th century, emasculation dependent hybrid seed production hangs on labor, machinery, high costs, inefficiency, and environmental constrains. Therefore, searching for male-sterile lines was in prime need.

Rice is essential cereal crop worldwide. Research indicates that the significant hybrid vigor found in rice can lead to an estimated yield enhancement of 20% in the F_1 hybrid than parents (Ma and Yuan, 2015). Since the 1970s, rice hybrid was introduced to the market in China, resulting in a considerable influence on rice production globally (Li and Yuan 1999). Now a days, two technologies are utilized in rice hybrid: the three-line and two-line methods. In three-line method, CMS is used as seed parent, this method known as first-generation. In contrast, the two-line technique is known as second-generation method using EGM as seed parent (Wang and Deng, 2018).

In 3-line method, a CMS line (A-line), a maintainer line (Bline), and a restorer line (R-line) are pre-requisite (Chen and Liu, 2014). A cytotoxic gene present in the CMS, which hinders the development of fertile pollen. CMS genes are chimeric in nature evolved through insertion, and/or deletion within genes present in the mitochondria (Tang et al., 2017). CMS is sterile, which has no capacity of perpetuation without pollen from B or R lines (Figure 4A). The B line is a sister line of CMS but having fertile cytoplasmic gene, which leads to its pollen being typically fertile. The CMS lines are maintained by crossing them with B line (Figure 4A). The R line has fertile nuclear gene called restorer (Rf) gene(s) which has capability to stop function of CMS gene. A robust hybrid is produced by crossing R line the CMS line, which gives vigor in F₁ (Figure 4A). At the moment, there are eight CMS types are characterized in rice (Chen and Liu 2014). Among them, CMS-WA was isolated from wild rice (Oryza rufipogon) and widely used in rice hybrid production (Bai et al., 2018).

EGMS gene plays vital role in two-line rice hybrid seed production. A recessive EGMS line is used as seed parent and a parental line with different nuclear gene rather than EGMS is used as pollen parent (Zhang et al., 2014). EGMS line plays dual role as maintainer and/or male-sterile line based on environmental status (Figure 4B). Under favorable conditions with long day length, high temperature with low humidity, EGMS lines demonstrate male sterility. In contrast, under unfavorable conditions with short day length, low temperature, and high humidity-EGMS lines become fertile and produce seed by selfing (Figure 4B). The two-line system provides numerous benefits compared to 3-line system, like improved synchronization flexibility, use of diverse resources, more effective breeding, and shorter breeding cycles in EGMS, easy maintenance of male-sterile line (Ashraf et al., 2020). In 2022, two-line hybrid rice covered 4.59 million hectares, accounting for 48.4% of the overall land used for hybrid rice cultivation in China (Zhang et al., 2023). The predominant technique utilized for leveraging heterosis in rice is the two-line approach (Pak et *al.*, 2021).

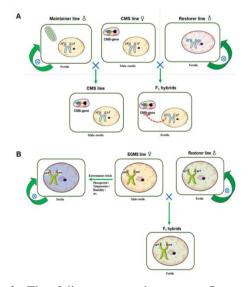


Figure 4: The 3-line system, known as first-generation system, and the two-line system, representing 2-generation, are employed in rice hybrid breeding. (A) 3-line system includes A-line (CMS) due to presence of the mitochondrial CMS gene; without nuclear restorer gene (*Rf*). This line maintained by crossing with B-line. *Rf* genes stop expression



of CMS gene and restores fertility of the F_1 . (B) 2-line system includes an EGMS with recessive nuclear gene (mt). The restorer carries dominant (Mt) gene. EGMS line shows male sterility and can be produced F_1 hybrid seeds through crossing with restorer line; Figure adopted from (Chen et al., 2023).

Future challenges and opportunity in hybrid seed production

First and second generations of hybrid technologies have enhanced global rice production since their adoption. However, first two generations reach almost in peak, therefore land allocation for hybrid rice cultivation has steadily declined from 65% to 45% in 2019 (Huang, 2022). The main reasons are yield plateau, high labor cost in seed production, and substandard cooking quality of many varieties, which bring many challenges in hybrid rice farming. The limitations of conventional male-sterile systems pose challenges to develop new hybrid varieties. Technical innovations are required for addressing these challenges and overcome the limitations of conventional technologies.

Introduction of TGHRT represents a great breakthrough in rice hybrid breeding. TGHRT enables the selection of a wider germplasms as parent for creating hybrids with improved heterosis. The sterility remains constant without influenced by environmental factors, help to by-pass the risks of unpredictable climate change effect in hybrid seed production. This system offers numerous benefits compared to the conventional systems in hybrid rice production. This serves as an example of progress in genetic engineering for alleviating certain challenges in breeding. Similar technologies may be created for a range of other crops, like wheat, sorghum, soybean, rapeseed, etc. *CRISPR/Cas9* technology is becoming more practical for TGHRT in other crops.

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