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Cytoplasmic Male Sterility in Wheat Hybrid Breeding: Advances, Mechanisms and Applications

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ABSTRACT

Wheat (Triticum aestivum L.) sustains more than one-third of the world's population, yet its self-pollinating floral biology has restricted the commercial exploitation of heterosis. Cytoplasmic male sterility (CMS) remains the most robust genetic platform for producing hybrid wheat seed. This review integrates classical breeding progress with recent molecular insights into T. timopheevii- (T-), Aegilops kotschyi- (K-) and Ae. crassa- (D-) based CMS systems, the discovery of the chimeric mitochondrial gene orf279 and its nuclear restorers Rf1 and Rf3, and emerging CRISPR-mediated male-sterility platforms such as Ms1 knockout. Applications in three-line and two-line hybrid pipelines, current adoption bottlenecks and future directions in genomic selection, pentatricopeptide-repeat engineering and climate-resilient hybrid design are discussed to guide the next generation of hybrid wheat cultivars.

Keywords: *Cytoplasmic male sterility; Hybrid wheat; Fertility restoration; CRISPR-Cas9.*

INTRODUCTION

Bread wheat (*Triticum aestivum* L., 2n = 6x = 42) supplies roughly 20 % of global calories and protein and is cultivated on more than 220 million hectares worldwide. Meeting the projected demand for a 60 % increase in wheat production by 2050, under a warming climate and shrinking arable base, will require breeding strategies that go beyond the incremental gains achievable from pure-line cultivars. Hybrid breeding, which systematically captures heterosis, has transformed maize, rice, sorghum and pearl millet, yet hybrid wheat still accounts for less than 1 % of the global sown area (Longin et al., 2012; & Whitford et al., 2013).

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The key obstacle is wheat's cleistogamous floral biology: perfect, self-pollinating florets in which the anthers dehisce inside the closed lemma and palea before the stigma is exposed. To force outcrossing on a field scale, breeders must render the seed parent completely and reliably male-sterile while retaining full female fertility. Among the biological options — genetic male sterility (GMS), environment-sensitive male sterility (EGMS), chemical hybridizing agents (CHAs) and cytoplasmic male sterility (CMS) — CMS remains the most stable, heritable and economical route for large-scale hybrid seed production (Adugna et al., 2004; & Singh et al., 2015).

CMS is a maternally inherited trait caused by aberrant mitochondrial genomes that fail to produce functional pollen but leave female fertility intact (Chen & Liu, 2014). Fertility can be restored in the F1 generation through nuclear restorer-of-fertility (Rf) genes carried by the pollen parent, an elegant biological switch that has underpinned commercial hybrid seed industries in many crops. This chapter reviews the historical trajectory, the molecular architecture and the contemporary applications of CMS in wheat, and evaluates how genomics-assisted and genome-editing tools are reshaping the pathway to viable hybrid wheat cultivars.

The economic argument for hybrid wheat rests on the magnitude and reliability of heterosis. Mid-parent heterosis for grain yield in bread wheat averages 8–12 %, with high-parent heterosis of 3.5–15 % achievable in the best crosses (Boeven et al., 2020). Heterosis is consistently accompanied by improvements in yield stability, biomass accumulation, nitrogen-use efficiency and tolerance to abiotic stress, traits that pure-line breeding alone cannot easily deliver. In a climate-change scenario in which yield variance is expected to rise, hybrids offer a strategic hedge against sudden losses in single-genotype crops. This chapter therefore treats CMS not as an isolated genetic phenomenon but as the central pillar of a system for capturing and delivering heterosis at farm scale, and examines each of the biological, molecular and technological components on which that system depends.

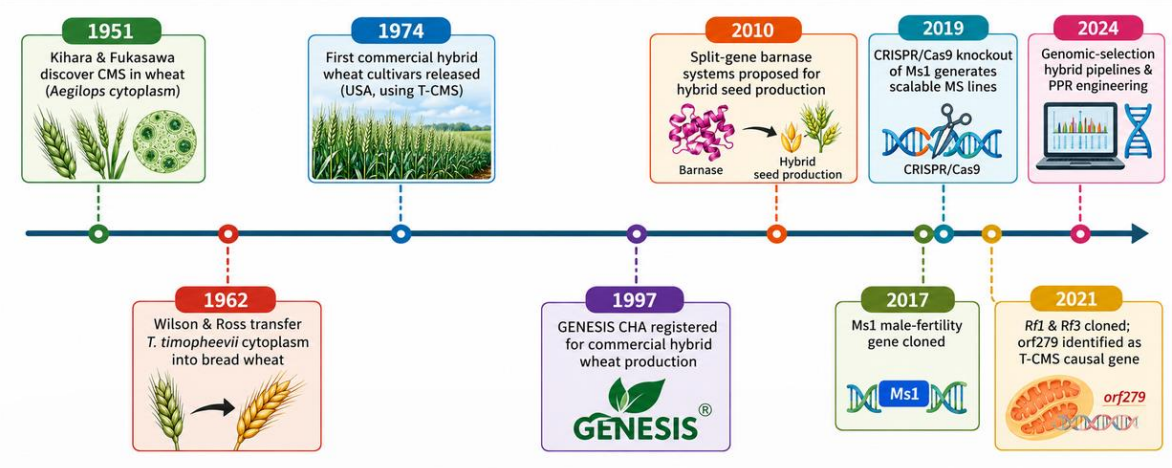

Figure1. Key milestones in CMS-based hybrid wheat breeding, from the discovery of alien-cytoplasm sterility in the 1950s to genome editing and genomic-selection-guided pipelines in the 2020s

2. Historical Development of CMS in Wheat

CMS was first observed in wheat by Kihara and Fukasawa in 1951, when backcrossing bread wheat as a recurrent male parent into Aegilops caudata cytoplasm produced completely male-sterile progeny (Kihara, 1951). The breakthrough that catalysed hybrid wheat research came in 1962, when Wilson and Ross transferred the cytoplasm of tetraploid T. timopheevii into hexaploid wheat

and identified nuclear restorers in the recurrent parent (Wilson & Ross, 1962). The resulting T-CMS system supported the release of the first commercial hybrid wheats in the United States and parts of Europe during the 1970s (Cisar & Cooper, 2002).

Enthusiasm cooled during the 1980s because seed yields on the A-line were low, restoration in North-American germplasm was unstable and chemical hybridizing agents offered an apparently simpler route. Yet the CMS platform never disappeared. In China, breeders systematically developed alternative alien-cytoplasm systems using Ae. kotschyi (K-CMS) and Ae. crassa (D-CMS), and in Europe programmes at Saaten-Union and INRA continued to release T-CMS-based hybrids at a small commercial scale (Singh et al., 2015). Recent renewed interest is driven by the convergence of hybrid seed technology with high-throughput genotyping and gene editing, which together promise to solve the historic limitations of the three-line system.

A second impetus for revisiting CMS-based wheat hybrids has come from parallel work in other cereals. The demonstration of stable heterosis in hybrid rice using both three-line and two-line systems, and the more recent commercialisation of hybrid barley in Germany and the United Kingdom using T. timopheevii-derived cytoplasm, has shown that hybrid technology can succeed even in strictly self-pollinating cereals (Longin et al., 2012). These successes have encouraged both public and private wheat programmes to reinvest in CMS pipelines and to accept the long developmental timelines that CMS-based breeding inevitably requires.

3. Molecular Mechanisms of CMS and Fertility Restoration

3.1 Origin of the sterility factor

CMS phenotypes almost invariably originate from mitochondrial genome rearrangement. Recombination between short repeat sequences produces chimeric open reading frames (ORFs) whose protein products interfere with electron transport and ATP synthesis in the inner mitochondrial membrane, disproportionately affecting the highly energy-demanding tapetum and microsporogenesis (Chen & Liu, 2014; & Melonek et al., 2021). In wheat, the AL-type (from Aegilops longissima) CMS phenotype was shown by Liu et al. (2021) to co-segregate with a novel chimeric ORF, orf279, which produces sterility when expressed in Arabidopsis, confirming its causal role.

The same orf279 transcript was identified in T. timopheevii-derived T-CMS lines by Melonek et al. (2021). Its protein interferes with mitochondrial function during meiosis, causing tapetal degeneration, collapsed microspores and abortive pollen. Because mitochondria are maternally inherited, every seed produced on the female-sterile plant will inherit the same defective cytoplasm — the basis of stable, heritable maternal sterility.

3.2 Restorer-of-fertility genes

Fertility restoration in the F1 is mediated by nuclear Rf genes, most of which encode pentatricopeptide-repeat (PPR) proteins that bind specific mitochondrial transcripts and either cleave or destabilise them (Dahan & Mireau, 2013). In wheat, nine Rf loci (Rf1–Rf9) have been reported to restore T-CMS to varying degrees. Melonek et al. (2021) used a combination of high-resolution mapping and comparative sequence analysis to clone Rf1 (chromosome 1A) and Rf3 (chromosome 1B) and demonstrated that both encode PPR proteins that bind the orf279 transcript in vitro and induce its cleavage in planta, restoring normal pollen development. Additional loci such as Rf8 on chromosome 2A and Rf9 on chromosome 6B contribute complementary or additive restoration and are increasingly deployed in marker-assisted breeding (Sinha et al., 2013; & Shahinnia et al., 2020).

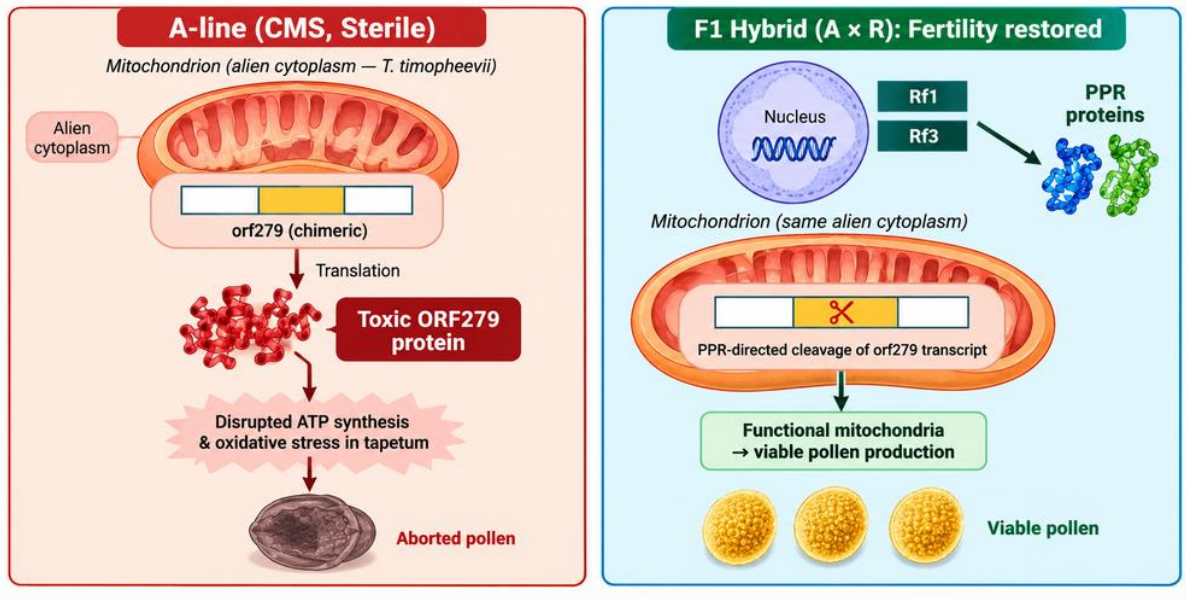

Figure2. Molecular basis of CMS and fertility restoration in wheat In the A-line, the chimeric mitochondrial gene orf279 produces a toxic protein that disrupts ATP synthesis in the tapetum, leading to pollen abortion. In the F1 hybrid, nuclear Rf1 and Rf3 PPR proteins bind and cleave the orf279 transcript, restoring functional mitochondria and viable pollen

3.3 Retrograde signalling and metabolic consequences

Beyond direct disruption of oxidative phosphorylation, CMS triggers retrograde signals from the dysfunctional mitochondrion to the nucleus that reprogram anther transcriptomes. Transcriptomic and metabolomic studies of K-CMS lines under permissive and restrictive temperatures have revealed differentially expressed genes in flavonoid biosynthesis, programmed cell death and cell-wall remodelling — pathways essential for tapetal function and pollen wall formation (Ye et al., 2015; & Liu et al., 2023). These findings help explain why apparently minor mitochondrial lesions produce complete sterility, and they point to new candidate genes for engineered restoration.

An important corollary is that CMS phenotypes are quantitative in nature, modulated by the nuclear background, developmental stage and environment. Low nitrogen supply, cold snaps during meiosis and drought stress can each partially destabilise sterility in genotypes carrying weak restoration alleles, producing self-set seed contamination in commercial fields. Understanding the interaction between nuclear modifiers and mitochondrial gene expression is therefore critical for the design of A-lines that maintain complete sterility across the climatic range in which the eventual hybrid will be grown.

4. Major CMS Systems Used in Hybrid Wheat

4.1 T-CMS (Triticum timopheevii cytoplasm)

The T-CMS system is the most widely deployed in commercial hybrid wheat programmes. Sterility is stable across environments, and a growing collection of restorer lines and molecular markers — particularly for Rf1, Rf3 and Rf8 — permits efficient breeding (Melonek et al., 2021). Historic drawbacks such as reduced seed set on the A-line and susceptibility to some fungal diseases have been partially overcome by introducing modifier alleles and screening for cytoplasmic-nuclear compatibility (Longin et al., 2012).

4.2 K-CMS (Aegilops kotschyi cytoplasm)

The K-CMS system, developed extensively in China, is thermo-sensitive: lines are completely male-sterile at temperatures below approximately 18 °C during Zadoks stages 45–52 and partially fertile at higher temperatures, permitting self-multiplication of the maintainer without a separate B-line (Ye et al., 2015; & Bhullar et al., 2023). Transcriptomic dissection

has identified a core K-CMS regulatory network centred on tapetal programmed cell death and pollen-coat biosynthesis, and candidate restorer genes such as TaEXPB5 have recently been implicated (Liu et al., 2023).

4.3 D-CMS and photoperiod-sensitive systems

The Ae. crassa D-type cytoplasm confers photoperiod-sensitive CMS (PCMS): lines are male-sterile under long-day conditions (≥ 15 h photoperiod) and fertile under short days (Murai, 2023). This trait enables a two-line system, avoiding the maintenance costs of a separate B-line. Field trials at latitudes above 35°N have demonstrated stable long-day sterility, and Japanese programmes have released experimental PCMS-based hybrids. The critical breeding challenge is stabilising the sterility switch against year-to-year weather variation.

4.4 Other alien-cytoplasm systems

Additional cytoplasms from Aegilops caudata, Ae. longissima, Ae. variabilis, Ae. juvenalis and Triticum araraticum have been transferred to bread wheat and evaluated for CMS induction. Each combines slightly different levels of sterility stability, cytoplasm-nuclear compatibility and pleiotropic effects on plant vigour, tiller number and disease resistance. Building a portfolio of complementary cytoplasms is strategically important: it broadens the mitochondrial genetic base of the crop, reduces the risk of a maize-1970-type cytoplasm-specific disease epidemic, and gives breeders room to select the cytoplasm best matched to a target production environment.

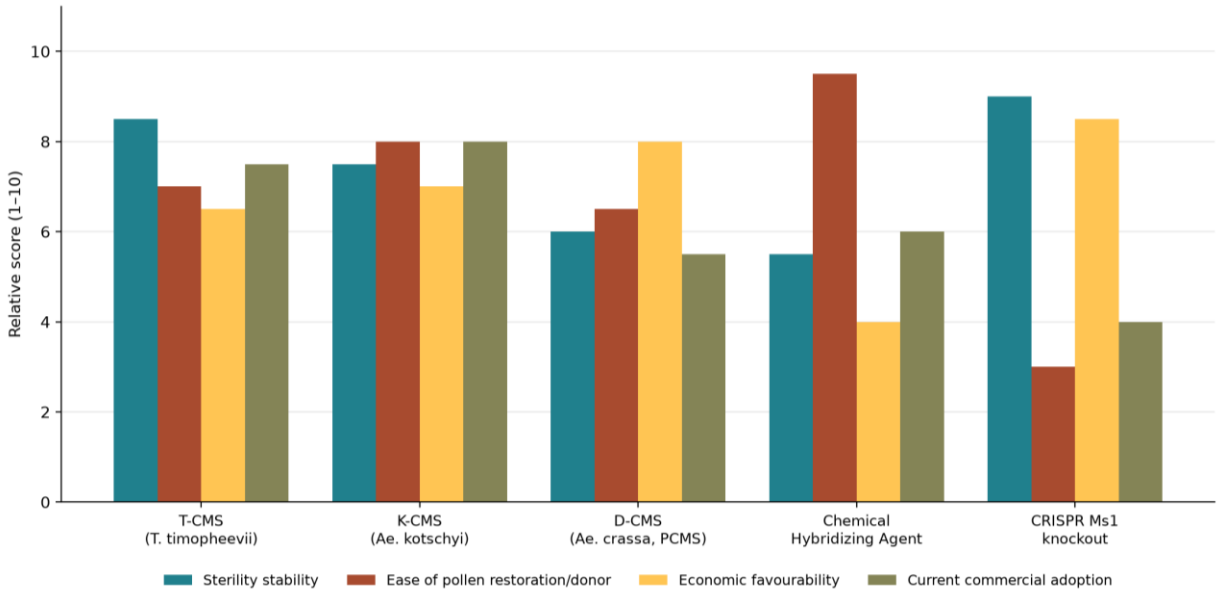

Figure3. Comparative evaluation of five male-sterility platforms currently used or explored for hybrid wheat, scored on sterility stability, ease of pollen-donor identification, economic favourability and current commercial adoption T-CMS combines high stability with mature adoption, while CRISPR Ms1-based systems offer the strongest genetic control but require established restoration workflows

5. Recent Advances

5.1 Cloning of causal genes

The 2021 cloning of Rf1, Rf3 and orf279 provided the first complete molecular description of a CMS–Rf system in wheat and enabled the design of diagnostic KASP and CAPS markers now used in dozens of public and private breeding programmes (Melonek et al., 2021; & Shahinnia et al., 2020). Parallel work identified additional PPR candidates for Rf8 and Rf9 through RNA-seq and paralogue analysis (Melonek et al., 2019, & 2021), further enriching the toolkit for stacking restoration.

5.2 Genome editing for male sterility

A complementary route to CMS is the induction of nuclear recessive male sterility through gene editing. Wang et al. (2017) and

Ni et al. (2017) cloned Ms1, an anther-expressed lipid-transfer protein essential for pollen coat formation. Okada et al. (2019) used CRISPR/Cas9 to knock out Ms1 in three elite bread-wheat backgrounds within a single generation, generating stable, non-transgenic male-sterile lines suitable for maintainer-free hybrid production. TALEN-based mitochondrial genome editing has also been shown to "cure" CMS in rapeseed and rice, offering a proof-of-concept for directly targeting mitochondrial ORFs in wheat (Kazama et al., 2019).

5.3 Genomic selection and heterotic pools

Predicting F1 performance from parental genotype is essential to make hybrid pipelines economically competitive. Genomic-selection models trained on European winter wheat populations have delivered prediction accuracies of 0.4–0.7 for grain yield in test-cross hybrids, and their combination with mid-parent heterosis estimates is now guiding the definition of heterotic pools analogous to those used in maize (Zhao et al., 2015; & Boeven et al., 2020). Establishing complementary male-sterile and restorer heterotic groups is arguably the most important strategic advance since the cloning of Rf1.

5.4 Transcriptomic dissection of sterility and restoration

High-throughput RNA-sequencing of anthers at sequential developmental stages has begun to place CMS in a systems-biology framework. Comparative transcriptomics of BS-type photo-thermo-sensitive male-sterile lines has identified conserved heat-shock, ROS-scavenging and lipid-metabolism modules that maintain sterility under fluctuating temperatures. Analogous studies in T-CMS and K-CMS lines have converged on tapetal programmed cell death, callose degradation and sporopollenin biosynthesis as the pathways most sensitive to mitochondrial dysfunction. These conserved signatures allow breeders to screen restorer candidates with transcript-level assays and to prioritise crosses that are likely to yield stable, high-restoration hybrids.

6. Applications in Hybrid Seed Production

The classical three-line (A/B/R) scheme remains the backbone of CMS-based hybrid wheat production. The male-sterile A-line is multiplied by alternating strips with an isogenic maintainer B-line that shares the same nuclear genotype but a normal cytoplasm. Commercial F1 seed is produced by planting the A-line with a restorer R-line as the pollen donor (Figure 4). Because wheat is only weakly outcrossing, seed yields on the female strips typically reach 40–60 % of a self-pollinated crop, and pollen-carrying capacity of the restorer is often the yield-limiting factor (Whitford et al., 2013).

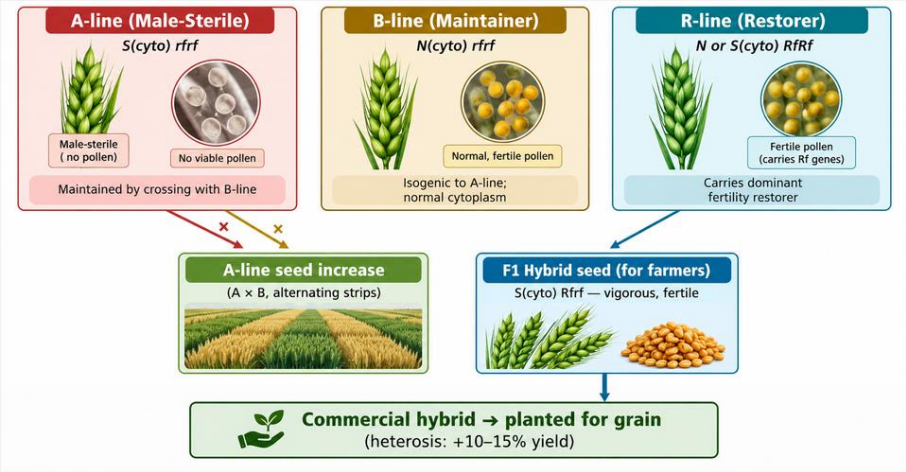

Figure4. The three-line (A/B/R) system for CMS-based hybrid wheat seed production. The male-sterile A-line is maintained by crossing with the isogenic B-line, and commercial F1 hybrid seed is produced by crossing the A-line with a nuclear-restorer R-line. The resulting F1 combines sterile cytoplasm with a heterozygous Rf/rf nuclear background, yielding fully fertile, vigorous plants

Recent field studies confirm mid-parent heterosis for grain yield of roughly 10 % in European winter wheat, with the best hybrids exceeding the highest-yielding pure lines by 3.5–15 % (Boeven et al., 2020; & Rembe et al., 2019). Hybrids also show improved nitrogen-use efficiency and yield stability under drought and heat, largely because a longer grain-filling period increases thousand-kernel weight (Gowda et al., 2013; & Nguyen et al., 2019). Chemical hybridizing agents such as GENESIS and Croisor 100 continue to provide an alternative genetic-free route, but they are expensive, weather-dependent and rarely achieve the complete sterility offered by CMS.

Two-line PCMS-based schemes offer a simpler production model when the sterility switch can be tied to a reliable environmental cue. In such systems, the A-line is self-multiplied under fertility-permissive conditions and used as the female parent under sterility-inducing conditions, dispensing with a separate maintainer. Chinese and Japanese programmes have released two-line hybrids based on K-TCMS (thermo-sensitive) and D-PCMS (photoperiod-sensitive) cytoplasms, respectively (Ye et al., 2015; & Murai, 2023). The main operational risk is that unusual weather during meiosis can compromise sterility, an issue that climate change is likely to exacerbate.

Practical hybrid seed production also depends on optimising the floral biology of the parental lines. Breeders now select A-line candidates for larger anthers, greater pollen shed, protracted stigma receptivity and improved floret gaping, all of which raise cross-pollination efficiency. The addition of rye chromosome 4R to bread wheat has been shown to increase anther length and pollen grain number, offering an attractive route to enhance restorer performance (Nguyen et al., 2019). On the agronomic side, the ratio of female to male strips, planting date synchronisation to match anthesis, and the use of growth regulators to align flowering across parents are refined every season and directly determine the profitability of a hybrid seed enterprise.

7. Challenges and Constraints

Four challenges continue to limit the wider adoption of CMS-based hybrid wheat. First, wheat's floral architecture — small, cleistogamous florets with limited stigma exsertion and short-lived pollen — restricts cross-pollination efficiency. Selection for larger anthers, protracted stigma receptivity and improved floret opening is essential (Whitford et al., 2013). Second, restoration in globally elite germplasm is genetically narrow: many high-yielding cultivars lack functional Rf1 or Rf3 alleles and require conversion. Third, cytoplasmic-nuclear interactions can impose a yield penalty on the A-line and, in some backgrounds, alter disease susceptibility. Finally, the cost of hybrid seed — typically two to three times that of pure-line seed — must be offset by a reliable yield premium, which requires strong, reproducible heterotic groups (Longin et al., 2012).

A further, often under-appreciated constraint is the narrow cytoplasmic base of most CMS programmes. Over-reliance on a single alien cytoplasm across large production areas exposes the crop to potentially devastating cytoplasm-specific disease susceptibility, as illustrated historically by the Bipolaris maydis Southern corn leaf blight epidemic of 1970 that targeted the T-cytoplasm of maize. Diversifying wheat CMS platforms — for example by combining T-CMS with K- or D-cytoplasm hybrids and by adding non-CMS options such as CRISPR Ms1 lines — is therefore both an economic and a biosecurity priority (Adugna et al., 2004; & Bhullar et al., 2023). Regulatory and intellectual-property considerations, particularly around gene-edited male-sterile lines, will further shape which technologies reach commercial scale in different jurisdictions.

8. Future Prospects

The next decade will see CMS-based hybrid wheat converge with three complementary technologies. Pangenome resources for wheat and its wild relatives are cataloguing structural variation in Rf loci, enabling the discovery and pyramiding of stronger and more reliable

restorers (Walkowiak et al., 2020). Precise editing of PPR-binding specificities could permit the engineering of custom restorers matched to any chimeric mitochondrial ORF, decoupling restorer availability from germplasm history. In parallel, non-CMS platforms such as CRISPR-based Ms1/Ms26 male-sterile systems and split-gene barnase constructs offer maintainer-free alternatives that may complement, rather than replace, CMS for specific market segments (Kempe et al., 2014; & Okada et al., 2019). Integration with high-throughput phenotyping, genomic selection and speed-breeding will compress the time from parental-line development to commercial hybrid release from more than a decade to under five years.

A second strategic priority is the deliberate construction of heterotic pools. In maize, more than eight decades of divergent selection between the Reid Yellow Dent and Lancaster Sure Crop groups produced the yield advantage that made hybrid maize dominant. Wheat has no such history, and current elite germplasm forms a single, weakly structured pool. Rembe et al. (2019) showed that reciprocal recurrent genomic selection can accelerate the formation of complementary female (CMS-carrying) and male (restorer-carrying) pools within a decade, delivering compounding gains in mid-parent heterosis and hybrid grain yield. Coupled with marker-assisted introgression of Rf1, Rf3 and Rf8 into elite pollen parents, this pool-based approach could raise commercial heterosis in wheat to levels comparable with hybrid rye.

Finally, hybrid wheat will need to demonstrate not only a yield premium but also improved climate resilience, end-use quality and low-input performance, which are the traits farmers and consumers increasingly value. Multi-environment trials that include drought, heat and reduced nitrogen regimes will therefore be as important as classical yield testing. Public–private consortia in Europe, Australia and India are beginning to embed such testing into their hybrid pipelines, and the data they generate will determine whether CMS-based hybrid wheat finally achieves the market share long predicted for it.

CONCLUSION

Cytoplasmic male sterility has moved from a curiosity of wide hybridisation to a molecularly defined breeding platform. The cloning of the causal mitochondrial gene orf279 and its nuclear restorers Rf1 and Rf3, complemented by advances in CRISPR-mediated nuclear male sterility, genomic selection and heterotic-pool design, has removed many of the fundamental biological uncertainties that historically constrained hybrid wheat. Remaining challenges are now largely engineering and economic: improving pollen-donor performance, widening the pool of elite restorers, and demonstrating a consistent yield premium under farmer conditions. As climate variability tightens the genetic-gain bottleneck, CMS-based hybrid wheat is well positioned to deliver the yield stability and resource-use efficiency needed to keep pace with global food demand. Sustained investment in public–private partnerships, molecular-marker infrastructure and farmer-participatory evaluation will determine how quickly the promise of hybrid wheat translates into on-farm impact.

Looking forward, the integration of CMS with gene-editing platforms, pangenome-informed marker design and quantitative-genetic prediction provides a coherent roadmap for the next generation of hybrid wheat cultivars. If breeders can combine stable CMS-based sterility with strong, easily deployed restorers and clearly defined heterotic pools, hybrid wheat could finally realise the yield and stability advantages that have long been predicted for it. Achieving this outcome will require close collaboration among molecular geneticists, quantitative breeders, seed-industry agronomists and policy-makers, but the scientific foundations laid over the past seven decades — and particularly the transformative discoveries of the past five years — suggest that this collaborative effort is both feasible and increasingly urgent.

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Author Contribution:
All authors have participated in critically revising of the entire manuscript and approval of the final manuscript.

REFERENCES

Adugna, A., Nanda, G. S., Singh, K., & Bains, N. S. (2004). A comparison of cytoplasmic and chemically-induced male sterility systems for hybrid seed production in wheat (*Triticum aestivum* L.). *Euphytica, 135*(3), 297–304.

Bhullar, R., Bansal, M., Bhatt, R., & Yaqoob, M. (2023). Male sterility systems in wheat: An overview of hybrid seed production strategies. *Journal of Cereal Research, 15*(2), 118–131.

Boeven, P. H. G., Zhao, Y., Thorwarth, P., Liu, F., Maurer, H. P., Gils, M., & Longin, C. F. H. (2020). Negative dominance and dominance-by-dominance epistatic effects reduce grain-yield heterosis in wide crosses in wheat. *Science Advances, 6*(24), eaay4897.

Chen, L., & Liu, Y. G. (2014). Male sterility and fertility restoration in crops. *Annual Review of Plant Biology, 65*, 579–606.

Cisar, G., & Cooper, D. B. (2002). Hybrid wheat. In B. C. Curtis, S. Rajaram, & H. Gómez Macpherson (Eds.), Bread wheat: Improvement and production (FAO Plant Production and Protection Series No. 30). Rome: *Food and Agriculture Organization of the United Nations*.

Dahan, J., & Mireau, H. (2013). The Rf and Rf-like PPR in higher plants: A fast-evolving subclass of PPR genes. *RNA Biology, 10*(9), 1469–1476.

Gowda, M., Longin, C. F. H., Lein, V., & Reif, J. C. (2013). Relevance of specific versus general combining ability in winter wheat. *Crop Science, 53*(4), 1477–1485.

Kazama, T., Okuno, M., Watari, Y., Yanase, S., Koizuka, C., Tsuruta, M., & Toriyama, K. (2019). Curing cytoplasmic male sterility via TALEN-mediated mitochondrial genome editing. *Nature Plants, 5*(7), 722–730.

Kempe, K., Rubtsova, M., & Gils, M. (2014). Split-gene system for hybrid wheat seed production. *Proceedings of the National Academy of Sciences of the United States of America, 111*(25), 9097–9102.

Kihara, H. (1951). Substitution of nucleus and its effects on genome manifestations. *Cytologia, 16*, 177–193.

Liu, S., Xu, S., Wang, J., Zhang, L., & Ye, J. (2023). Transcriptomics reveals a core transcriptional network of K-type cytoplasmic male sterility in wheat. *BMC Plant Biology, 23*, 590.

Liu, W., Wang, X., Song, Q., & Chen, F. (2021). Characterization of the mitochondrial genome of a wheat AL-type male-sterility line and the candidate CMS gene. *International Journal of Molecular Sciences, 22*(12), 6388.

Longin, C. F. H., Mühleisen, J., Maurer, H. P., Zhang, H., Gowda, M., & Reif, J. C. (2012). Hybrid breeding in autogamous cereals. *Theoretical and Applied Genetics, 125*(6), 1087–1096.

Melonek, J., Duarte, J., Martin, J., Beuf, L., Murigneux, A., Varenne, P., & Small, I. (2021). The genetic basis of cytoplasmic male sterility and fertility restoration in wheat. *Nature Communications, 12*, 1036.

Melonek, J., Zhou, R., Bayer, P. E., Edwards, D., Stein, N., & Small, I. (2019). High intraspecific diversity of Restorer-of-fertility-like genes in barley. *The Plant Journal, 97*(2), 281–295.

Murai, K. (2023). Hybrid wheat breeding using photoperiod-sensitive cytoplasmic male sterility (PCMS) caused by Aegilops crassa cytoplasm. *Cytologia*, *88*(3), 191–197.

Nguyen, V., Fleury, D., Timmins, A., Laga, H., Hayden, M., Mather, D., & Okamoto, M. (2019). Addition of rye chromosome 4R to wheat increases anther length and pollen grain number. *Theoretical and Applied Genetics*, *132*(11), 3125–3133.

Ni, F., Qi, J., Hao, Q., Lyu, B., Luo, M. C., Wang, Y., & Fu, D. (2017). Wheat Ms2 encodes for an orphan protein that confers male sterility in grass species. *Nature Communications*, *8*, 15121.

Okada, A., Arndell, T., Borisjuk, N., Sharma, N., Watson-Haigh, N. S., Tucker, E. J., & Whitford, R. (2019). CRISPR/Cas9-mediated knockout of Ms1 enables the rapid generation of male-sterile hexaploid wheat lines for use in hybrid seed production. *Plant Biotechnology Journal*, *17*(10), 1905–1913.

Rembe, M., Zhao, Y., Jiang, Y., & Reif, J. C. (2019). Reciprocal recurrent genomic selection: An attractive tool to leverage hybrid wheat breeding. *Theoretical and Applied Genetics*, *132*(3), 687–698.

Shahinnia, F., Geyer, M., Schürmann, F., Rudolphi, S., Holzapfel, J., Kempf, H., & Hartl, L. (2020). Genetic association of frost tolerance QTL with Rf3 fertility restoration on chromosome 1BS in wheat. *Theoretical and Applied Genetics*, *133*(6), 1975–1988.

Singh, S. K., Chatrath, R., & Mishra, B. (2015). Perspective of hybrid wheat research: A review. *Indian Journal of Agricultural Sciences*, *80*(12), 1013–1027.

Sinha, P., Tomar, S. M. S., Vinod, Singh, V. K., & Balyan, H. S. (2013). Genetic analysis and molecular mapping of a new fertility restorer gene Rf8 for Triticum timopheevii cytoplasm in wheat (*Triticum aestivum* L.) using SSR markers. *Genetica*, *141*(10–12), 431–441.

Walkowiak, S., Gao, L., Monat, C., Haberer, G., Kassa, M. T., Brinton, J., & Pozniak, C. J. (2020). Multiple wheat genomes reveal global variation in modern breeding. *Nature*, *588*(7837), 277–283.

Wang, Z., Li, J., Chen, S., Heng, Y., Chen, Z., Yang, J., & Zhang, D. (2017). Poaceae-specific MS1 encodes a phospholipid-binding protein for male fertility in bread wheat. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(47), 12614–12619.

Whitford, R., Fleury, D., Reif, J. C., Garcia, M., Okada, T., Korzun, V., & Langridge, P. (2013). Hybrid breeding in wheat: Technologies to improve hybrid wheat seed production. *Journal of Experimental Botany*, *64*(18), 5411–5428.

Wilson, J. A., & Ross, W. M. (1962). Male sterility interaction of the *Triticum aestivum* nucleus and Triticum timopheevi cytoplasm. *Wheat Information Service*, *14*, 29–30.

Ye, J., Duan, Y., Hu, G., Geng, X., Zhang, G., Yan, P., & Ma, W. (2015). Identification of candidate genes and biosynthesis pathways related to fertility conversion by wheat KTM3315A transcriptome profiling. *Frontiers in Plant Science*, *6*, 691.

Zhao, Y., Mette, M. F., Gowda, M., Longin, C. F. H., & Reif, J. C. (2015). Bridging the gap between marker-assisted and genomic selection of heading time and plant height in hybrid wheat. *Heredity*, *112*(6), 638–645.