

Advancements in Wheat Hybridization: Overcoming Biological Barriers

Feng Huang ✉, Xiaoyu Du, Shaokui Zou, Lina Wang, Yulin Han

Zhoukou Academy of Agricultural Sciences, Zhoukou, 466001, China

✉ Corresponding email: huangfeng0714@163.com

Bioscience Evidence, 2024, Vol.14, No.5 doi: [10.5376/be.2024.14.0021](https://doi.org/10.5376/be.2024.14.0021)

Received: 22 Jul., 2024

Accepted: 27 Aug., 2024

Published: 08 Sep., 2024

Copyright © 2024 Huang et al., This is an open access article published under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Preferred citation for this article:

Huang F., Du X.Y., Zou S.K., Wang L., and Han Y.L., 2024, Advancements in wheat hybridization: overcoming biological barriers, Bioscience Evidence, 14(5): 195-205 (doi: [10.5376/be.2024.14.0021](https://doi.org/10.5376/be.2024.14.0021))

Abstract Wheat hybrid breeding is a key approach to improving global wheat productivity and ensuring food security. However, reproductive barriers between different wheat species, difficulties in chromosome pairing, and sterility issues in hybrid seed production have limited the widespread adoption of hybrid wheat varieties. To overcome these biological barriers, scientists have developed various advanced technologies and methods, facilitating progress in wheat hybrid breeding. This study reviews the latest technological advancements in overcoming biological barriers in wheat hybrid breeding, focusing on the application of male sterility systems, embryo rescue techniques, and gene editing. It also analyzes the progress in genomic and molecular tools. The research finds that male sterility systems, embryo rescue techniques, and gene editing technologies have successfully addressed some of the biological barriers in wheat hybrid breeding. Successful cases of hybrid wheat demonstrate that these technologies not only improve hybridization success rates but also enhance crop disease resistance and yield potential. Additionally, genomic tools have significantly accelerated the hybrid breeding process and optimized breeding efficiency. Overcoming biological barriers not only improves the efficiency of hybrid wheat breeding but also aids in the development of hybrid varieties with higher yields and enhanced disease resistance under adverse environmental conditions. This is of great significance for ensuring global food security.

Keywords Wheat; Hybrid breeding; Reproductive barriers; Gene editing; Male sterility system

1 Introduction

Wheat is a staple crop that plays a crucial role in global food security. However, the increasing demand for wheat, coupled with the challenges posed by climate change, evolving pathogens, and pests, necessitates innovative approaches to enhance wheat production. One promising avenue is wheat hybridization, which has the potential to significantly improve yield and stress resistance. Wheat hybridization involves the crossing of different wheat varieties to combine desirable traits from both parents. Traditional breeding methods, such as direct hybridization and backcrossing, have been employed to introduce traits like disease resistance, abiotic stress tolerance, and improved grain yield into wheat varieties (Rauf et al., 2015; Mondal et al., 2016). However, these methods are often time-consuming and limited by the complexities of screening and selecting for multiple desirable traits simultaneously (Mondal et al., 2016). Recent advancements in genomic technologies, such as high-throughput phenotyping, genome sequencing, and genomic selection, offer new opportunities to accelerate the breeding process and enhance the genetic gains in wheat (Zhao et al., 2015; Mondal et al., 2016; Thudi et al., 2020).

Hybrid wheat has the potential to deliver substantial improvements in yield and stress resistance. The exploitation of hybrid vigor, or heterosis, can result in higher grain yields and greater resilience to environmental stresses compared to pure-line varieties (Zhao et al., 2015; Alotaibi et al., 2020). For instance, the development of high-yielding heterotic patterns through genomic prediction and selection has shown promise in boosting wheat yields and stability (Zhao et al., 2015). Additionally, hybrid wheat can incorporate traits that enhance tolerance to abiotic stresses, such as drought and heat, as well as resistance to biotic stresses, including diseases and pests.

Despite the potential benefits, several biological barriers impede the successful development of hybrid wheat. One major challenge is the self-pollinating nature of wheat, which complicates the production of hybrid seeds. Techniques such as male sterility and modifications in floral architecture are being explored to facilitate outcrossing and improve hybrid seed production (Whitford et al., 2013; Alotaibi et al., 2020). Moreover, the

limited genetic diversity within the wheat gene pool poses a bottleneck for breeding programs. Utilizing genetic resources from wild relatives and other Triticeae species can help overcome this limitation and introduce new alleles for stress resistance and yield improvement (Mondal et al., 2016; Ali et al., 2020).

This study provides a comprehensive overview of the advancements in wheat hybrid breeding and the strategies to overcome biological barriers. It summarizes the current state of wheat hybridization techniques and their application in breeding programs, evaluates the potential of hybrid wheat in improving yield and stress resistance, identifies the key biological barriers in hybrid wheat development, and proposes innovative approaches to address these challenges. Furthermore, it highlights the future prospects and research directions for hybrid wheat breeding. By addressing these objectives, the study contributes to the ongoing efforts to tackle current challenges, enhance wheat production, and ensure global food security.

2 Biological Obstacles Challenges in Wheat Hybridization

2.1 Reproductive barriers

Reproductive barriers are significant challenges in wheat hybridization, often manifesting as incompatibility between different wheat species and sterility issues in hybrids. These barriers can be prezygotic, such as pollen-pistil incompatibility, or postzygotic, including hybrid sterility and inviability. For instance, hybrid sterility is a common issue when crossing hexaploid bread wheat (*Triticum aestivum*) with tetraploid durum wheat (*Triticum turgidum*), leading to pentaploid hybrids that frequently exhibit sterility and poor seed set (Padmanaban et al., 2017). This sterility is often due to genetic incompatibilities that disrupt normal meiotic processes, resulting in unviable gametes (Forsdyke, 2018).

Moreover, hybrid sterility can be exacerbated by epistatic interactions between divergent loci from the parent species. These interactions can lead to dysfunctional gene networks, further reducing hybrid fertility. For example, in the case of Solanum species, it was found that hybrid sterility often results from complex genetic interactions rather than simple pairwise incompatibilities, indicating a similar potential mechanism in wheat hybrids (Guerrero et al., 2016). Overcoming these reproductive barriers requires careful selection of parental genotypes and advanced breeding techniques to ensure compatibility and fertility in the resulting hybrids.

2.2 Chromosomal differences

Chromosomal differences pose another significant challenge in wheat hybridization, particularly due to the difficulty in successful chromosome pairing between species with different ploidy levels. Hexaploid wheat (*Triticum aestivum*, $2n=6x=42$) and tetraploid wheat (*Triticum turgidum*, $2n=4x=28$) have different numbers of chromosome sets, complicating meiosis and leading to issues such as unbalanced gametes and reduced fertility (Padmanaban et al., 2017). The presence of homeologous chromosomes, which are similar but not identical, further complicates pairing during meiosis, often resulting in meiotic instability and chromosomal rearrangements (Parisod and Badaeva, 2020).

Interspecific hybridization can lead to significant chromosomal restructuring, as observed in wild wheat species. These structural changes can include chromosomal fusions, fissions, and translocations, which can disrupt normal genetic function and lead to hybrid sterility or inviability (Parisod and Badaeva, 2020). Additionally, the phenomenon of "genome shock" in synthetic allotetraploid wheat, where newly formed hybrids exhibit extensive karyotype variation and meiotic irregularities, highlights the challenges posed by chromosomal differences in hybridization efforts (Sha et al., 2023). Addressing these challenges requires advanced cytogenetic techniques and a deep understanding of the genetic and chromosomal architecture of the parent species.

2.3 Hybrid seed production challenges

Hybrid seed production in wheat is often hindered by the limitations of male sterility systems, which are crucial for preventing self-pollination and ensuring cross-pollination. One of the primary bottlenecks in hybrid wheat breeding is the lack of an efficient and practical sterility system. Traditional male sterility systems, such as cytoplasmic male sterility (CMS), have limitations, including incomplete sterility and the need for fertility restorers, which complicate breeding programs (Kempe et al., 2014).

Recent advancements have introduced genetic systems for pollination control, such as the split-gene system, which relies on the expression of a phytotoxic barnase to induce male sterility. This system allows for the maintenance of male-sterile lines and the production of hybrid seeds without the need for fertility restorers (Kempe et al., 2014). However, these systems still face challenges, including the potential for incomplete sterility and the need for precise genetic manipulation. Overcoming these limitations requires continued innovation in genetic engineering and breeding techniques to develop more reliable and efficient male sterility systems for hybrid wheat production.

3 Technological Advances in Overcoming Hybridization Barriers

3.1 Cytoplasmic and nuclear male sterility

Cytoplasmic male sterility (CMS) systems have been a cornerstone in the development of hybrid wheat varieties. CMS is a maternally inherited trait that results in the inability of plants to produce functional pollen, thus facilitating cross-pollination. The S type of CMS in wheat, derived from *Aegilops* species, has been extensively studied and utilized. However, practical application has faced challenges such as limited restoration resources and lower germination rates (Wang et al., 2013). Recent advancements have identified specific genes, such as *Rf1* and *Rf3*, which can restore fertility in CMS lines by binding to mitochondrial transcripts and preventing the expression of the sterility trait (Figure 1) (Melonek et al., 2021). This genetic understanding is crucial for developing more efficient CMS-based hybridization systems.

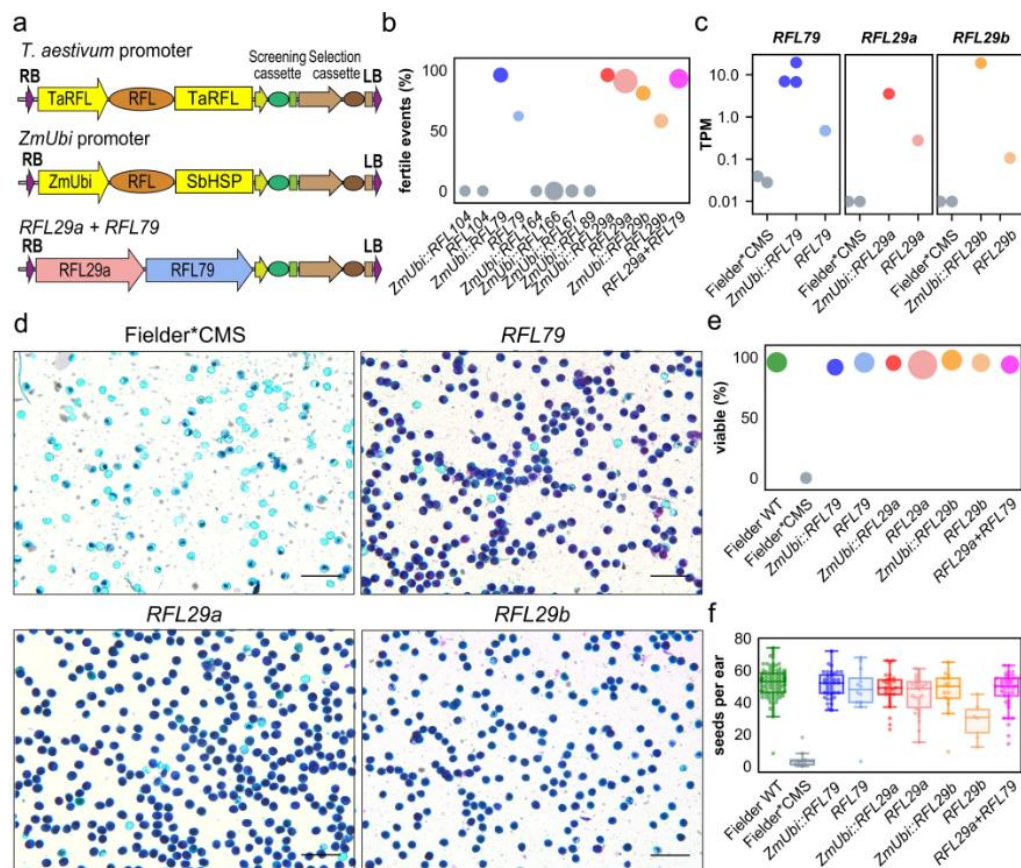


Figure 1 Evaluation of fertility restoration by *Rf1* and *Rf3* genes in Fielder*CMS lines (Adapted from Melonek et al., 2021)

Image caption: A: Design of constructs used in the transgenic experiment, covering wheat candidate restorer genes (*Rf1* and *Rf3*) and their expression regulatory elements; B: Evaluation of fertility restoration rates in T0 plants restored with different gene constructs; C: Transgenic expression levels obtained through RNA-Seq (TPM); D: Pollen morphology of restored transgenic plants shown through Alexander staining; E: Pollen viability statistics; F: Assessment of the number of seeds per spike in transgenic plants (Adapted from Melonek et al., 2021)

In the study by Melonek et al. (2021), the fertility restoration effect was evaluated by introducing the restorer genes *Rf1* and *Rf3*, either individually or in combination, into the CMS wheat sterile line Fielder*. The transgenic lines successfully expressed the restorer genes and exhibited significant improvements in pollen morphology, viability, and the number of seeds per spike. The results indicated that *Rf79* made a considerable contribution to fertility restoration, either alone or in combination with other genes.

Nuclear male sterility (NMS) systems offer an alternative to CMS by using nuclear genes to control male fertility. For instance, the barnase gene, when expressed under tapetum-specific promoters, can induce male sterility in wheat (Block et al., 1997). This method allows for precise control over male fertility and can be integrated into hybrid breeding programs. The development of NMS systems, such as those involving the *Ms1*, *Ms5*, *TaMs26*, and *TaMs45* genes, has shown promise in creating stable and efficient hybridization platforms (Singh et al., 2021). These systems can potentially lower the cost of hybrid seed production and enhance the commercial viability of hybrid wheat varieties.

3.2 Embryo rescue techniques

Embryo rescue is a critical technique in overcoming post-fertilization barriers in wheat hybridization. This method involves the *in vitro* culture of embryos that would otherwise abort due to incompatibilities between the parental genomes. Embryo rescue has been successfully used to produce hybrids between wheat and its wild relatives, thereby introducing beneficial traits such as disease resistance and abiotic stress tolerance into cultivated wheat varieties.

The technique has evolved with advancements in tissue culture and molecular biology. For example, the optimization of culture media and growth conditions has significantly improved the success rates of embryo rescue. Additionally, the use of molecular markers to select viable embryos at an early stage has streamlined the process, making it more efficient and reliable. These improvements have expanded the potential of embryo rescue in wheat breeding programs, enabling the incorporation of a wider range of genetic diversity into commercial wheat varieties.

3.3 Gene editing (CRISPR/Cas9)

Gene editing technologies, particularly CRISPR/Cas9, have revolutionized the field of plant breeding by enabling precise modifications to the genome. In wheat, CRISPR/Cas9 has been used to target genes associated with male sterility and fertility restoration, thereby facilitating hybridization (Ma and Cai, 2024). For instance, the targeted mutagenesis of genes such as *Ms1* and *TaMs45* has been shown to induce male sterility, which is essential for hybrid seed production (Singh et al., 2021).

CRISPR/Cas9 offers several advantages over traditional breeding methods. It allows for the introduction of specific genetic changes without the need for extensive backcrossing, thereby accelerating the breeding process. Moreover, the ability to multiplex CRISPR/Cas9, i.e., target multiple genes simultaneously, provides a powerful tool for manipulating complex traits such as male fertility. This technology holds great promise for overcoming biological barriers in wheat hybridization and enhancing the efficiency and precision of hybrid breeding programs.

4 Application and Progress of Genomic and Molecular Tools in Wheat Hybridization

4.1 Marker-assisted selection (MAS)

Marker-Assisted Selection (MAS) has revolutionized wheat breeding by enabling the precise selection of desirable traits through the use of DNA markers. This technique allows breeders to identify and select plants carrying specific genes associated with beneficial traits, thereby accelerating the breeding process and improving the efficiency of developing hybrid wheat varieties (Wu, 2024). MAS has been particularly effective in incorporating traits such as disease resistance, yield potential, and quality characteristics into new wheat hybrids. The development of high-density genetic maps and the identification of quantitative trait loci (QTLs) have been instrumental in the success of MAS in wheat breeding programs (Collard et al., 2005; Paux et al., 2012; Rathan et al., 2023).

4.2 Quantitative trait locus (QTL) mapping

QTL mapping is a powerful tool used to identify genomic regions associated with important agronomic traits in wheat. By analyzing the genetic composition and phenotypic characteristics of wheat populations, researchers can pinpoint specific loci that contribute to heterosis and yield potential. Recent studies have identified stable QTLs for yield-related traits such as thousand kernel weight (TKW), plant height (PH), and spike length (SL) across multiple environments, providing valuable targets for breeding programs (Guan et al., 2018; Ma et al., 2023; Rathan et al., 2023). The integration of QTL mapping with other genomic tools, such as meta-QTL analysis, has further refined the identification of key genomic regions, enhancing the precision of marker-assisted selection and facilitating the development of high-yielding hybrid wheat varieties (Figure 2) (Shariatipour et al., 2021; Li et al., 2023).

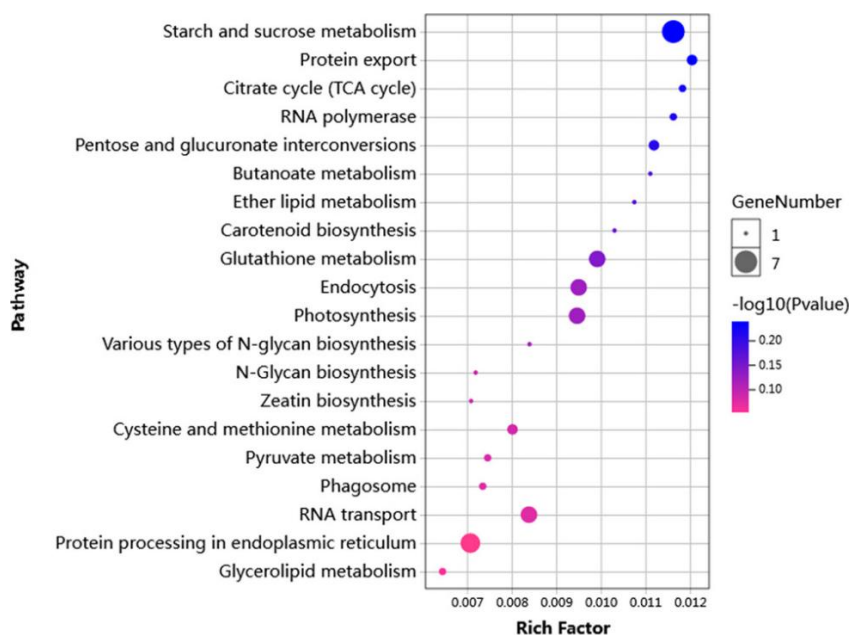


Figure 2 KEGG pathway enrichment analysis of all genes in the MQTL region (Adapted from Li et al., 2023)

Image caption: The x-axis represents the enrichment factor, and the y-axis shows the pathway names. The different colored circles represent p-values, with colors ranging from magenta to blue, indicating decreasing p-values and increasing enrichment levels. The size of the circles represents the number of genes enriched in each pathway (Adapted from Li et al., 2023)

Li et al. (2023) analyzed the enrichment of genes extracted from the MQTL (meta-QTL) regions in the top 20 KEGG pathways. The enrichment analysis revealed significant enrichment of genes involved in key metabolic pathways such as starch and sucrose metabolism, protein export, and the TCA cycle, suggesting that these pathways may play crucial roles in controlling growth, yield, and stress resistance in crops like wheat. The enrichment of genes related to carbohydrate, lipid metabolism, and antioxidant metabolism also highlights the importance of these metabolic pathways in crop adaptation to environmental stresses. This figure provides insights into the functions of genes in complex traits, offering guidance for molecular breeding.

4.3 Utilization of genomic selection (GS)

Genomic Selection (GS) leverages genome-wide marker data to predict the performance of wheat hybrids, streamlining the breeding process by selecting the best candidates for further development. Unlike traditional breeding methods, which rely on phenotypic selection, GS uses statistical models to estimate the genetic potential of individuals based on their genomic profiles. This approach has been shown to significantly reduce the time and cost associated with developing new wheat hybrids while maintaining or even improving genetic gains (Paux et al., 2012; Raj and Nadarajah, 2022). The application of GS in wheat breeding has been facilitated by advances in next-generation sequencing technologies and the availability of comprehensive genomic resources, enabling breeders to make more informed decisions and accelerate the development of superior hybrid wheat varieties (Gao et al., 2015).

5 Case Studies of Successful Hybrid Wheat Breeding

5.1 Hybridization between bread and durum wheat

Hybridization between bread wheat (*Triticum aestivum* L.) and durum wheat (*Triticum turgidum* spp. *durum* Desf.) has led to the development of pentaploid hybrids with unique chromosomal constitutions. These hybrids can improve the genetic background of either parent by transferring traits of interest, such as disease resistance, abiotic tolerance, and grain quality. However, challenges such as low pollen compatibility, poor seed set, and frequent sterility in F1 hybrids have been noted. Careful selection of parental genotypes and using the higher ploidy level genotype as the maternal parent can overcome most of these barriers (Padmanaban et al., 2017).

In another study, durum wheat was proposed as the female progenitor of bread wheat. Crosses between a durum wheat cultivar carrying a gene for meiotic restitution and *Aegilops tauschii* produced highly fertile triploid F1 hybrids without the need for embryo rescue techniques. These hybrids spontaneously set hexaploid F2 seeds, demonstrating high fertility and vigorous growth habits, which supports the theory of durum wheat being a progenitor of bread wheat (Matsuoka and Nasuda, 2004).

5.2 Overcoming hybrid lethality using embryo culture: breaking wheat-rye reproductive barriers

Hybrid lethality is a significant barrier in wheat-rye hybridization, often resulting from the interaction of incompatible genes. In situ embryo rescue techniques have been employed to overcome this barrier. By culturing immature embryos via callus induction, researchers have successfully regenerated plantlets from abnormal embryos. This method has shown that the reproductive barrier in wheat-rye hybrids may have an epigenetic origin, which can be mitigated through in vitro culture methods. Despite the success in overcoming embryo lethality, challenges such as pollen and embryo sac sterility remain, affecting both male and female gametophytes (Tikhenko et al., 2017).

Further analysis of hybrid lethality in F1 wheat-rye hybrid embryos revealed that the Embryo lethality mutant (Eml) of rye arrests the formation of the shoot meristem but does not affect the root meristem. This lethality could not be overcome by direct regeneration on Kruse medium, indicating the need for alternative approaches to address gene expression variations during hybrid formation (Tikhenko et al., 2008).

Wide hybridization experiments have also been conducted with cereals, including wheat, barley, and rye, using various species of the Poaceae and Panicoideae families. Embryo formation was achieved with several species, and new embryo culture techniques have enabled these embryos to grow into plants, demonstrating the potential for overcoming hybridization barriers in cereals.

6 Applications of Hybrid Wheat in Modern Agriculture

6.1 Enhancing yield in marginal environments

Hybrid wheat has shown significant potential in improving yield potential in stress-prone environments. The development of hybrid wheat varieties can address the challenges posed by abiotic stresses such as drought, heat, and poor soil conditions. For instance, hybrid wheat cultivars have demonstrated higher stress resistance and better performance under drought conditions compared to traditional line cultivars (Prey et al., 2019). Additionally, the use of innovative breeding strategies and genetic diversity has been essential in developing wheat varieties that can thrive in marginal environments, thereby enhancing productivity and food security (Mondal, 2016; Tshikunde et al., 2019).

Prey et al. (2019) revealed the yield potential of hybrid wheat in marginal environments, particularly showing significant hybrid vigor in traits such as grain yield, nitrogen uptake efficiency, and biomass accumulation compared to inbred lines. The hybrid vigor for some traits exhibited considerable variation across different years, indicating that environmental factors play an important role in the trait performance of hybrid wheat. Although certain traits may display negative hybrid vigor in marginal environments, the overall trend demonstrates the potential of hybrid varieties for yield improvement and enhanced nitrogen use efficiency, providing strong evidence for the development of high-yielding hybrid wheat in challenging environments (Figure 3).

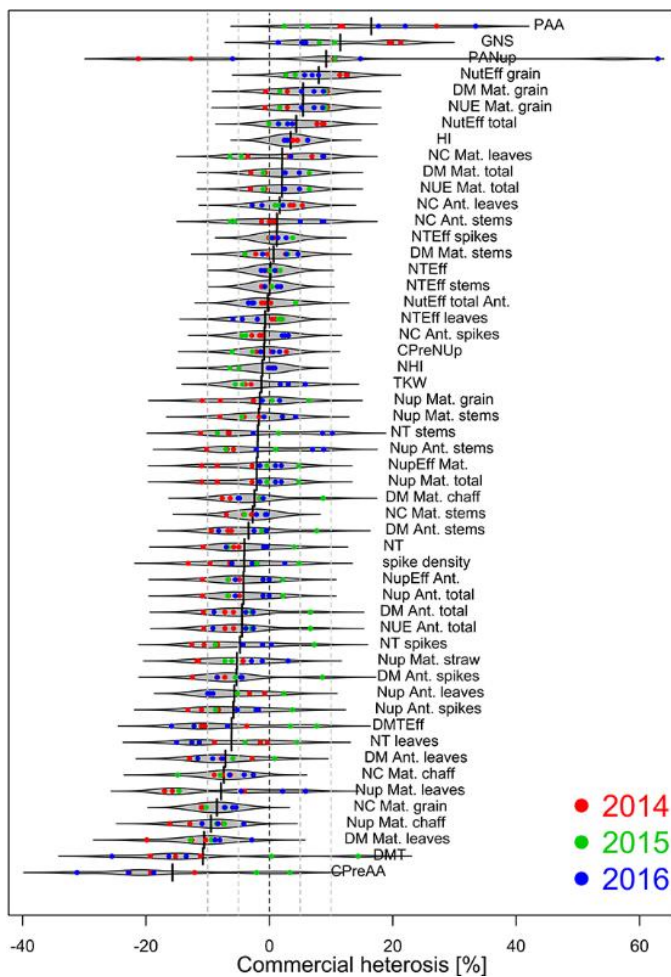


Figure 3 Percentage of Hybrid vigor for different traits in commercial wheat hybrids over the years (Adapted from Prey et al., 2019)
 Image caption: Hybrid vigor was calculated based on marginal means for each year and nitrogen fertilizer level combination (n=8). Negative values indicate poorer performance of the hybrid compared to the parent, while positive values indicate superior hybrid traits compared to the parent. The dashed lines represent 0%, $\pm 5\%$, and $\pm 10\%$ hybrid vigor values (Adapted from Prey et al., 2019)

6.2 Developing disease-resistant hybrids

Hybrid wheat plays a crucial role in developing disease-resistant varieties. The genetic variability introduced through hybridization can improve resistance to a wide range of pests and pathogens. For example, pentaploid wheat hybrids, which are developed through interspecific hybridization, have shown potential in enhancing disease resistance and abiotic tolerance (Padmanaban et al., 2017). Moreover, the introgression of resistance genes from wild relatives into hybrid wheat has been a successful strategy to combat new and emerging diseases, thereby ensuring crop resilience and sustainability (Wulff and Moscou, 2014).

6.3 Economic viability of hybrid wheat

The economic viability of hybrid wheat adoption involves a careful analysis of costs and benefits. While hybrid wheat can offer higher yields and better stress resistance, the initial costs associated with hybrid seed production and purchase can be higher. However, studies have shown that hybrid wheat can lead to significant yield increases, which can offset the higher seed costs. For instance, hybrid wheat cultivars in Europe have demonstrated a yield advantage of 5.5% over line cultivars, which can contribute to higher profitability for farmers (Prey et al., 2019). Additionally, the adoption of heat-tolerant hybrid maize in Nepal has shown that hybrids can increase yields and income, suggesting similar economic benefits for hybrid wheat in stress-prone environments (Kulkarni et al., 2023).

7 Future Directions in Wheat Hybridization

7.1 Expanding genetic resources

Expanding the genetic resources available for wheat hybridization is crucial for enhancing grain yield potential and ensuring food security. More than half a million wheat genetic resources are stored in gene banks worldwide, yet their potential remains largely untapped. Recent advances in hybrid wheat technology can help unlock the hidden favorable genetic diversity within these resources. By gathering phenotypic information, researchers can make targeted choices of accessions with high value for pre-breeding, moving away from traditional allele mining towards genome-wide selection. This paradigm shift is essential for bridging the yield gap between genetic resources and elite breeding pools (Longin and Reif, 2014).

Moreover, the integration of novel male sterility systems and the identification of key fertility genes, such as *Msl*, can significantly enhance the efficiency of hybrid wheat breeding. The *Msl* gene, for instance, has been identified as crucial for pollen exine development and can be used for large-scale, low-cost production of male-sterile female lines necessary for hybrid seed production. This represents a key step towards developing a robust hybridization platform in wheat, enabling the exploitation of genetic resources more effectively (Tucker et al., 2017).

7.2 Integrating omics data in hybrid wheat

The integration of omics data, including genomics, transcriptomics, proteomics, and metabolomics, holds great promise for advancing hybrid wheat breeding. These technologies provide a comprehensive understanding of the molecular mechanisms underlying various stress factors and yield traits. For instance, the use of next-generation sequencing (NGS), RNA sequencing, and CRISPR/Cas9 genome editing can help identify and manipulate genes associated with stress resilience and yield improvement. However, the challenge lies in the effective interpretation and integration of the vast amounts of data generated by these technologies (Alotaibi et al., 2020).

Recent studies have demonstrated the potential of combining genomic data with other omics predictors to improve hybrid prediction accuracy. For example, in maize, the integration of transcriptomic data with genomic information has led to higher success rates in predicting untested hybrid combinations. This approach can be extended to wheat, where the use of downstream omics data can capture physiological epistasis and provide valuable insights for selecting superior hybrid candidates. By leveraging the power of omics technologies, researchers can enhance the efficiency of hybrid wheat breeding and achieve significant yield gains (Westhues et al., 2017).

7.3 Enhancing hybrid fertility

Enhancing hybrid fertility is a critical aspect of successful hybrid wheat breeding. One of the major challenges in this area is the development of efficient sterility systems to prevent self-pollination and promote outcrossing. Recent advancements in molecular biology have led to the identification of novel male sterility systems, such as the split-gene system, which relies on the expression of a phytotoxic barnase to induce male sterility. This system allows for the growth and maintenance of male-sterile female crossing partners while ensuring full restoration of fertility in the hybrid wheat seed (Kempe et al., 2014).

Additionally, the use of CRISPR/Cas9 technology has enabled the rapid generation of male-sterile hexaploid wheat lines by introducing targeted mutations in the *Msl* gene. This approach has shown great potential for producing non-transgenic male-sterile lines, which are essential for commercial hybrid seed production. By overcoming the biological barriers associated with hybrid fertility, these innovative technologies pave the way for the large-scale adoption of hybrid wheat, ultimately leading to higher yields and improved food security (Okada et al., 2019).

8 Concluding Remarks

Recent advancements in wheat hybridization have focused on overcoming the biological barriers that have historically impeded the development of hybrid wheat. One of the primary challenges has been the inbreeding nature of wheat, which necessitates effective methods to enforce outcrossing. Technological innovations such as

the development of male sterility systems, including the use of cytoplasmic male sterility (CMS) and chemical hybridizing agents (CHA), have been pivotal. For instance, the split-gene system for hybrid wheat seed production has shown promise by enabling the generation and maintenance of male-sterile parents and ensuring full fertility restoration in hybrids. Additionally, the barnase-barstar system and other transgenic approaches have been developed to facilitate male sterility without the need for fertility restorers.

Advances in genomic resources and technologies have also played a crucial role. The explosion in genome sequencing and the development of high-throughput genotyping and phenotyping tools have provided new opportunities to enhance hybrid wheat production systems. These technologies help in identifying and utilizing genetic diversity, which is essential for breeding programs aimed at improving yield, disease resistance, and climate resilience. Moreover, genome editing technologies, such as CRISPR/Cas9, have been employed to make precise genetic modifications, further aiding in the development of elite wheat cultivars.

The future potential of hybrid wheat in increasing global wheat production and ensuring food security is substantial. Hybrid wheat varieties have demonstrated superior yield and growth characteristics compared to their homozygous counterparts, which could significantly boost global wheat production. The implementation of hybrid wheat on a commercial scale could lead to a major lift in yield, addressing the growing demand for wheat driven by population growth and changing consumption patterns.

Furthermore, hybrid wheat can contribute to food security by enhancing the resilience of wheat production systems. The ability to incorporate traits such as disease resistance, drought tolerance, and improved nutrient use efficiency through hybridization and advanced breeding techniques can mitigate the impacts of climate change and reduce the reliance on chemical inputs. This is particularly important in the context of sustainable agriculture, where the goal is to increase productivity without exacerbating environmental degradation.

Acknowledgments

We would like to thank the anonymous peer reviewers for their valuable guidance and feedback on revisions.

Funding

This study was funded by the Henan Modern Agricultural Industry Technology System Construction Special Project (HARS-22-1-Z7).

Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

References

- Ali N., Rahman I., Badakshi F., Tariq M., and Mujeeb-Kazi A., 2020, Ensuring sustainable food security: exploiting alien genetic diversity in wheat breeding for adaptation to emerging stresses, In: Ozturk M., and Gul A., eds., *Climate Change and Food Security with Emphasis on Wheat*, Academic Press, pp.31-42.
<https://doi.org/10.1016/b978-0-12-819527-7.00002-9>
- Alotaibi F., Alharbi S., Alotaibi M., Mosallam M., Motawei M., and Alrajhi A., 2020, Wheat omics: classical breeding to new breeding technologies, *Saudi Journal of Biological Sciences*, 28: 1433-1444.
<https://doi.org/10.1016/j.sjbs.2020.11.083>
- Block M., Debrouwer D., and Moens T., 1997, The development of a nuclear male sterility system in wheat, expression of the barnase gene under the control of tapetum specific promoters, *Theoretical and Applied Genetics*, 95: 125-131.
<https://doi.org/10.1007/s001220050540>
- Collard B., Collard B., Jahufer M., Brouwer J., and Pang E., 2005, An introduction to markers, quantitative trait loci (QTL) mapping and marker-assisted selection for crop improvement: the basic concepts, *Euphytica*, 142: 169-196.
<https://doi.org/10.1007/s10681-005-1681-5>
- Forsdyke D., 2018, When acting as a reproductive barrier for sympatric speciation, hybrid sterility can only be primary, *Biological Journal of the Linnean Society*, 128(4): 779-788.
<https://doi.org/10.1093/biolinnean/blz135>

- Gao F., Wen W., Liu J., Rasheed A., Yin G., Xia X., Wu X., and He Z., 2015, Genome-wide linkage mapping of QTL for yield components, plant height and yield-related physiological traits in the chinese wheat cross zhou 8425B/Chinese spring, *Frontiers in Plant Science*, 6: 1099.
<https://doi.org/10.3389/fpls.2015.01099>
- Guan P., Lu L., Jia L., Kabir M., Zhang J., Lan T., Zhao Y., Xin M., Hu Z., Yao Y., Ni Z., Sun Q., and Peng H., 2018, Global QTL analysis identifies genomic regions on chromosomes 4A and 4B harboring stable loci for yield-related traits across different environments in wheat (*Triticum aestivum* L.), *Frontiers in Plant Science*, 9: 529.
<https://doi.org/10.3389/fpls.2018.00529>
- Guerrero R., Muir C., Josway S., and Moyle L., 2016, Pervasive antagonistic interactions among hybrid incompatibility loci, *PLoS Genetics*, 13(6): e1006817.
<https://doi.org/10.1101/090886>
- Kempe K., Rubtsova M., and Gils M., 2014, Split-gene system for hybrid wheat seed production, *Proceedings of the National Academy of Sciences*, 111: 9097-9102.
<https://doi.org/10.1073/pnas.1402836111>
- Kulkarni A., Tripathi M., Gautam D., Koirala K., Kandel M., Regmi D., Sapkota S., and Zaidi P., 2023, Impact of adoption of heat-stress tolerant maize hybrid on yield and profitability: evidence from Terai region of Nepal. *Front. Sustain. Food Syst.*, 7: 1101717.
<https://doi.org/10.3389/fsufs.2023.1101717>
- Li N., Miao Y., Ma J., Zhang P., Chen T., Liu Y., Che Z., Shahinnia F., and Yang D., 2023, Consensus genomic regions for grain quality traits in wheat revealed by Meta-QTL analysis and in silico transcriptome integration, *The Plant Genome*, 16(2): e20336.
<https://doi.org/10.1002/tpg2.20336>
- Longin C., and Reif J., 2014, Redesigning the exploitation of wheat genetic resources, *Trends in Plant Science*, 19(10): 631-636.
<https://doi.org/10.1016/j.tplants.2014.06.012>
- Ma Z.Q., and Cai R.X., 2024, The significance of wide hybridization for wheat genetic improvement, *Triticeae Genomics and Genetics*, 15(2): 100-110.
<https://doi.org/10.5376/tgg.2024.15.0010>
- Ma F., Xu Y., Wang R., Tong Y., Zhang A., Liu D., and An D., 2023, Identification of major QTLs for yield-related traits with improved genetic map in wheat, *Frontiers in Plant Science*, 14: 1138696.
<https://doi.org/10.3389/fpls.2023.1138696>
- Matsuoka Y., and Nasuda S., 2004, Durum wheat as a candidate for the unknown female progenitor of bread wheat: an empirical study with a highly fertile F1 hybrid with *Aegilops tauschii* Coss, *Theoretical and Applied Genetics*, 109: 1710-1717.
<https://doi.org/10.1007/s00122-004-1806-6>
- Melonek J., Duarte J., Martin J., Beuf L., Murigneux A., Varenne P., Comadran J., Spelcer S., Levadoux S., Bernath-Levin K., Torney F., Pichon J., Perez P., and Small I., 2021, The genetic basis of cytoplasmic male sterility and fertility restoration in wheat, *Nature Communications*, 12: 1036.
<https://doi.org/10.1038/s41467-021-21225-0>
- Mondal S., Rutkoski J., Velu G., Singh P., Crespo-Herrera L., Guzmán C., Bhavani S., Lan C., He X., and Singh R., 2016, Harnessing diversity in wheat to enhance grain yield, climate resilience, disease and insect pest resistance and nutrition through conventional and modern breeding approaches, *Frontiers in Plant Science*, 7: 991.
<https://doi.org/10.3389/fpls.2016.00991>
- Okada A., Arndell T., Borisjuk N., Sharma N., Watson-Haigh N., Tucker E., Baumann U., Langridge P., and Whitford R., 2019, CRISPR/Cas9-mediated knockout of Msl enables the rapid generation of male-sterile hexaploid wheat lines for use in hybrid seed production, *Plant Biotechnology Journal*, 17: 1905-1913.
<https://doi.org/10.1111/pbi.13106>
- Padmanaban S., Zhang P., Hare R., Sutherland M., and Martin A., 2017, Pentaploid wheat hybrids: applications, characterisation, and challenges, *Frontiers in Plant Science*, 8: 358.
<https://doi.org/10.3389/fpls.2017.00358>
- Parisod C., and Badaeva E., 2020, Chromosome restructuring among hybridizing wild wheats, *The New phytologist*, 226(5):1263-1273.
<https://doi.org/10.1111/nph.16415>
- Paux E., Sourdille P., Mackay I., and Feuillet C., 2012, Sequence-based marker development in wheat: advances and applications to breeding, *Biotechnology Advances*, 30(5): 1071-1088.
<https://doi.org/10.1016/j.biotechadv.2011.09.015>
- Prey L., Kipp S., Hu Y., and Schmidhalter U., 2019, Nitrogen use efficiency and carbon traits of high-yielding european hybrid vs. line winter wheat cultivars: potentials and limitations, *Frontiers in Plant Science*, 9: 1988.
<https://doi.org/10.3389/fpls.2018.01988>
- Raj S., and Nadarajah K., 2022, QTL and candidate genes: techniques and advancement in abiotic stress resistance breeding of major cereals, *International Journal of Molecular Sciences*, 24(1): 6.
<https://doi.org/10.3390/ijms24010006>
- Rathan N., Krishnappa G., Singh A., and Govindan V., 2023, Mapping QTL for phenological and grain-related traits in a mapping population derived from high-zinc-biofortified wheat, *Plants*, 12(1): 220.
<https://doi.org/10.3390/plants12010220>

- Rauf S., Zaharieva M., Warburton M., Zhang P., Al-Sadi A., Khalil F., Kozak M., and Tariq S., 2015, Breaking wheat yield barriers requires integrated efforts in developing countries, *Journal of Integrative Agriculture*, 14: 1447-1474.
[https://doi.org/10.1016/S2095-3119\(15\)61035-8](https://doi.org/10.1016/S2095-3119(15)61035-8)
- Sha Y., Li Y., Zhang D., Lv R., Wang H., Wang R., Ji H., Li S., Gong L., Li N., and Liu B., 2023, Genome shock in a synthetic allotetraploid wheat invokes subgenome-partitioned gene regulation, meiotic instability and karyotype variation, *Journal of Experimental Botany*, 74(18): 5547-5563.
<https://doi.org/10.1093/jxb/erad247>
- Shariatipour N., Heidari B., Tahmasebi A., and Richards C., 2021, Comparative genomic analysis of quantitative trait loci associated with micronutrient contents, grain quality, and agronomic traits in wheat (*Triticum aestivum* L.), *Frontiers in Plant Science*, 12: 709817.
<https://doi.org/10.3389/fpls.2021.709817>
- Singh M., Albertsen M., and Cigan A., 2021, Male fertility genes in bread wheat (*Triticum aestivum* L.) and their utilization for hybrid seed production, *International Journal of Molecular Sciences*, 22(15): 8157.
<https://doi.org/10.3390/ijms22158157>
- Thudi M., Palakurthi R., Schnable J., Chitikineni A., Dreisigacker S., Mace E., Srivastava R., Satyavathi C., Odeny D., Tiwari V., Lam H., Hong Y., Singh V., Li G., Xu Y., Chen X., Kaila S., Nguyen H., Sivasankar S., Jackson S., Close T., Shubo W., and Varshney R., 2020, Genomic resources in plant breeding for sustainable agriculture, *Journal of Plant Physiology*, 257: 153351.
<https://doi.org/10.1016/j.jplph.2020.153351>
- Tikhenko N., Rutten T., Senula A., Rubtsova M., Keller E., and Börner A., 2017, The changes in the reproductive barrier between hexaploid wheat (*Triticum aestivum* L.) and rye (*Secale cereale* L.): different states lead to different fates, *Planta*, 246: 377-388.
<https://doi.org/10.1007/s00425-017-2694-8>
- Tikhenko N., Rutten T., Voylokov A., and Houben A., 2008, Analysis of hybrid lethality in F1 wheat-rye hybrid embryos, *Euphytica*, 159: 367-375.
<https://doi.org/10.1007/s10681-007-9528-x>
- Tshikunde N., Mashilo J., Shimelis H., and Odindo A., 2019, Agronomic and physiological traits, and associated quantitative trait loci (QTL) affecting yield response in wheat (*Triticum aestivum* L.): a review, *Frontiers in Plant Science*, 10: 1428.
<https://doi.org/10.3389/fpls.2019.01428>
- Tucker E., Baumann U., Kouidri A., Suchecki R., Baes M., Garcia M., Okada T., Dong C., Wu Y., Sandhu A., Singh M., Langridge P., Wolters P., Albertsen M., Cigan A., and Whitford R., 2017, Molecular identification of the wheat male fertility gene *Msl* and its prospects for hybrid breeding, *Nature Communications*, 8(1): 869.
<https://doi.org/10.1038/s41467-017-00945-2>
- Wang J., Wang X., Xu H., Tang H., Zhang G., and Liu Y., 2013, Structural and expressional variation analyses of mitochondrial genomes reveal candidate transcripts for the S(V) cytoplasmic male sterility in wheat (*Triticum aestivum* L.), *Journal of Genetics And Genomics=Yi Chuan Xue Bao*, 40(8): 437-439.
<https://doi.org/10.1016/j.jgg.2013.03.004>
- Westhues M., Schrag T.A., Heuer C., Thaller G., Utz H.F., Schipprack W., Thiemann A., Seifert F., Ehret A., Schlereth A., Stitt M., Nikoloski Z., Willmitzer L., Schön C.C., Scholten S., and Melchinger A.E., 2017, Omics-based hybrid prediction in maize, *Theoretical and Applied Genetics*, 130: 1927-1939.
<https://doi.org/10.1007/s00122-017-2934-0>
- Whitford R., Fleury D., Reif J., Garcia M., Okada T., Korzun V., and Langridge P., 2013, Hybrid breeding in wheat: technologies to improve hybrid wheat seed production, *Journal of Experimental Botany*, 64(18): 5411-5428.
<https://doi.org/10.1093/jxb/ert333>
- Wu W.C., 2024, Genetic diversity and molecular marker discovery of adaptive traits in Triticeae crops, *Triticeae Genomics and Genetics*, 15(1): 10-18.
<https://doi.org/10.5376/tgg.2024.15.0002>
- Wulff B., and Moscou M., 2014, Strategies for transferring resistance into wheat: from wide crosses to GM cassettes, *Frontiers in Plant Science*, 5: 692.
<https://doi.org/10.3389/fpls.2014.00692>
- Zhao Y., Li Z., Liu G., Jiang Y., Maurer H., Würschum T., Mock H., Matros A., Ebmeyer E., Schachschneider R., Kazman E., Schacht J., Gowda M., Longin C., and Reif J., 2015, Genome-based establishment of a high-yielding heterotic pattern for hybrid wheat breeding, *Proceedings of the National Academy of Sciences*, 112: 15624-15629.
<https://doi.org/10.1073/pnas.1514547112>

Disclaimer/Publisher's Note

The statements, opinions, and data contained in all publications are solely those of the individual authors and contributors and do not represent the views of the publishing house and/or its editors. The publisher and/or its editors disclaim all responsibility for any harm or damage to persons or property that may result from the application of ideas, methods, instructions, or products discussed in the content. Publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.