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The Significance of Wide Hybridization for Wheat Genetic Improvement

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Abstract Wide hybridization has emerged as a pivotal strategy for the genetic improvement of wheat, offering a means to introduce novel genetic variation and enhance key agronomic traits. This study explores the significance of wide hybridization in wheat breeding, highlighting its potential to improve grain quality, yield, and hybrid seed production. Studies have demonstrated that hybridization with wild relatives and underutilized varieties can significantly expand the genetic diversity of wheat, leading to improvements in grain hardness, gluten quality, and nutritional content. Additionally, the integration of genome-wide association studies (GWAS) and genomic selection has facilitated the identification of key genomic regions and candidate genes associated with important traits, thereby enhancing the efficiency of hybrid breeding programs. The development of hybrid wheat varieties through reciprocal recurrent genomic selection and the optimization of floral traits for better cross-pollination have shown promising results in increasing hybrid seed set and overall yield potential. This study underscores the transformative impact of wide hybridization on wheat genetic improvement and its critical role in meeting future food security challenges.

Keywords Wide hybridization; Wheat genetic improvement; Hybrid breeding; Genome-wide association studies (GWAS); Genetic diversity

1 Introducion

Wheat (*Triticum aestivum* L.) is a fundamental staple food crop globally, playing a crucial role in food security and agricultural economies. The continuous improvement of wheat yield and quality is essential to meet the demands of a growing global population and to address challenges such as climate change, water scarcity, and environmental sustainability (Pang et al., 2020; Li et al., 2021; Patil et al., 2023). Traditional breeding methods have significantly contributed to wheat improvement; however, the complex polyploid genome of wheat presents challenges for genetic research and precision breeding (Li et al., 2021; Bhalla et al., 2017). Recent advancements in genomic technologies, such as genome-wide association studies (GWAS), high-throughput genotyping, and genome editing, have opened new avenues for enhancing wheat traits (Bhalla et al., 2017; Pang et al., 2020; Li et al., 2021).

Wide hybridization refers to the crossing of wheat with distant relatives or other species to introduce novel genetic variations that are not present within the primary gene pool of wheat. This technique is pivotal for incorporating beneficial traits such as disease resistance, abiotic stress tolerance, and yield improvement (Whitford et al., 2013). The process involves overcoming reproductive barriers and ensuring the stable integration of desirable traits into wheat cultivars. Wide hybridization has the potential to significantly enhance genetic diversity and provide new opportunities for wheat improvement, which are crucial for developing resilient and high-yielding wheat varieties (Whitford et al., 2013).

The main purpose of this study was to evaluate the importance of wide hybridization in genetic improvement of wheat. The channels for genetic improvement of wheat and the challenges faced by traditional breeding methods are summarized. Broad hybridization is also defined and its importance in introducing new genetic variation is discussed. While studying the technological advances and methods that promote broad hybridization in wheat, an effective assessment of the impact of broad hybridization on wheat yield, quality and stress tolerance is made, and the future prospects and potential for utilizing broad hybridization in wheat breeding programs are identified research direction. By synthesizing recent research findings, this study aims to provide a comprehensive understanding of the role of hybridization in advancing wheat genetic improvement and highlight its potential in addressing global food security challenges.

2 Historical Perspectives on Wide Hybridization

2.1 Early studies and milestones

The concept of wide hybridization, which involves crossing different species or genera to introduce new genetic variations, has been a cornerstone in plant breeding for many decades. Early studies focused on the potential of wide hybridization to enhance crop traits such as yield, disease resistance, and stress tolerance. One of the pioneering efforts in this field was the exploration of hybridization between wheat and its wild relatives, which aimed to introduce beneficial traits from wild species into cultivated wheat varieties (Alvarez and Guzmán, 2018). These initial experiments laid the groundwork for understanding the genetic and phenotypic outcomes of wide hybridization.

2.2 Evolution of techniques and approaches

Over the years, the techniques and approaches for wide hybridization have evolved significantly. Early methods primarily relied on conventional crossing techniques, which often faced challenges such as prezygotic and postzygotic barriers. To overcome these barriers, several advanced techniques have been developed, including chromosome doubling, bridging species, protoplast fusion, and embryo rescue (Anushma et al., 2021). These methods have proven highly beneficial in recovering fertile progenies from wide crosses, thereby enhancing the success rate of wide hybridization efforts.

In recent times, the integration of genomic tools has further revolutionized wide hybridization. Genomic prediction and genome-wide association studies have enabled breeders to identify and select for desirable traits more efficiently. For instance, a three-step strategy involving genomic prediction has been developed to establish high-yielding heterotic patterns in hybrid wheat breeding (Zhao et al., 2015). This approach has shown promise in boosting grain yield and stability by exploiting heterosis, thereby marking a significant advancement in the field.

2.3 Case studies of successful wide hybrids

Several case studies highlight the success of wide hybridization in wheat genetic improvement. One notable example is the hybridization between wheat and various species of the Poaceae and Panicoideae families, which resulted in the formation of both haploid and diploid embryos. These hybrids have demonstrated the potential to introduce new genetic variations that can be harnessed for crop improvement.

Another successful case is the use of wild relatives and old varieties to enhance wheat grain quality. Hybridization events with these sources have been shown to enlarge the genetic variability for traits such as grain hardness, gluten quality, and nutritional components like vitamins and micronutrients (Alvarez and Guzmán, 2018). This approach has not only improved the technological and nutritional quality of wheat but also expanded the range of traits available for breeding programs.

The historical perspectives on wide hybridization underscore its significance in wheat genetic improvement. From early studies and milestones to the evolution of advanced techniques and successful case studies, wide hybridization continues to be a vital tool in the quest for enhanced wheat varieties.

3 Mechanisms of Wide Hybridization

3.1 Genetic and genomic compatibility

Wide hybridization involves crossing wheat with its wild or distantly related species to introduce new genetic diversity and desirable traits. The genetic compatibility between wheat and its relatives is crucial for successful hybridization. For instance, the genetic control of compatibility in crosses between wheat and its wild or cultivated relatives has been extensively studied, revealing that the genetic background of both the recipient and donor varieties significantly influences crossability (Laugerotte et al., 2022). Additionally, the use of wild relatives and old varieties has been shown to enhance wheat quality by introducing novel genetic variations

(Alvarez and Guzmán, 2018). The development of high-throughput genotyping arrays and improved methods of gene discovery have further facilitated the identification of useful genetic variations in wild relatives, which can be integrated into wheat breeding programs (Rasheed et al., 2018).

3.2 Cytogenetic barriers and solutions

Cytogenetic barriers, such as chromosome elimination and non-disjunction, often pose significant challenges in wide hybridization. For example, in crosses between wheat and pearl millet, non-wheat chromosomes are frequently eliminated during embryogenesis, leading to hybrid instability (Ishii et al., 2010). However, innovative approaches have been developed to overcome these barriers. The creation of stable amphiploids and the strategic use of known genes have shown promise in developing perennial grain crops that combine the desirable traits of both parents (Curwen-McAdams and Jones, 2017). Moreover, the development of compensating wheat/barley Robertsonian translocation lines has successfully transferred favorable traits, such as salt tolerance and elevated β-glucan content, into a stable genetic background (Türkösi et al., 2018).

3.3 Molecular techniques for enhancing hybridization

Advances in molecular techniques have significantly enhanced the efficiency of wide hybridization. Genomic in situ hybridization (GISH) and fluorescence in situ hybridization (FISH) are powerful tools for tracing and identifying wheat and non-wheat chromatin in hybrid embryos, facilitating the monitoring of chromosome dynamics and stability (Türkösi et al., 2018). Additionally, the integration of genomics-assisted selection and gene editing technologies has accelerated the exploitation of exotic genes, increasing the rate of genetic gain in wheat breeding programs (Rasheed et al., 2018). These molecular techniques, coupled with phenotypic recurrent selection and genome-wide prediction approaches, have shown potential in improving traits such as anther extrusion and hybrid seed set, which are critical for hybrid wheat breeding (Boeven et al., 2016; Boeven et al., 2018).

Wide hybridization offers a valuable strategy for wheat genetic improvement by introducing new genetic diversity and desirable traits from wild and distantly related species. Overcoming genetic and cytogenetic barriers through advanced molecular techniques and strategic breeding approaches can significantly enhance the success and stability of wide hybrids, contributing to the development of improved wheat cultivars with enhanced quality, stress resistance, and yield potential.

4 Contributions to Wheat Breeding

4.1 Introduction of novel traits

Wide hybridization has played a crucial role in introducing novel traits into wheat, significantly enhancing its genetic diversity. For instance, the hybridization between wheat and tall wheatgrass (*Thinopyrum ponticum*) has led to the development of wheat cultivars such as Xiaoyan 4, Xiaoyan 5, Xiaoyan 6, Xiaoyan 54, Xiaoyan 60, and Xiaoyan 81, which exhibit multiple disease resistances and adaptability to various environments (Li et al., 2015). Additionally, the utilization of wild relatives of wheat has provided valuable sources of allelic diversity, contributing to the introduction of novel traits such as resistance to stripe rust and Karnal bunt (Shafqat et al., 2021).

4.2 Improvement of disease resistance

Wide hybridization has been instrumental in improving disease resistance in wheat. The introgression of resistance genes from wild relatives has significantly enhanced wheat's ability to withstand various diseases. For example, resistance has been successfully introgressed from at least 52 species from 13 genera, demonstrating the remarkable plasticity of the wheat genome (Wulff and Moscou, 2014). Moreover, the development of wheat-Thinopyrum bessarabicum genetic stock has provided novel sources of resistance to stripe rust and Karnal bunt, which are critical for sustainable crop production (Shafqat et al., 2021). The Xiaoyan series of wheat cultivars also exhibit multiple disease resistances, likely derived from tall wheatgrass (Li et al., 2015).

4.3 Enhancement of abiotic stress tolerance

Abiotic stress tolerance is another area where wide hybridization has made significant contributions. The introduction of genetic diversity from wild relatives has enhanced wheat's tolerance to various abiotic stresses such as drought, salinity, and extreme temperatures. For instance, the development of synthetic hexaploid, hybrid, and transgenic wheats has expanded genetic variability and improved stress resistance (Rauf et al., 2015). Genetic engineering techniques, including transgenesis and genome editing, have further enhanced wheat's tolerance to environmental stresses, ensuring high yields without increasing cultivated land (Figure3) (Trono and Pecchioni, 2022).

4.4 Yield and quality improvement

Wide hybridization has also contributed to yield and quality improvements in wheat. The integration of novel genetic diversity has led to the development of high-yielding and high-quality wheat varieties. For example, the BREEDWHEAT project has provided new molecular tools to breeders, enabling the efficient analysis and structuring of genetic diversity, which is crucial for developing high-yielding varieties (Paux et al., 2022). Additionally, the use of high-throughput phenotyping, genome sequencing, and genomic selection has accelerated genetic gains, resulting in more productive wheat varieties (Mondal et al., 2016). The Xiaoyan series of wheat cultivars, developed through wide hybridization, also exhibit good adaptability and high yield potential (Li et al., 2015).

Wide hybridization has significantly contributed to wheat breeding by introducing novel traits, improving disease resistance, enhancing abiotic stress tolerance, and improving yield and quality. These advancements are crucial for meeting the global demand for wheat in the face of increasing environmental challenges and population growth.

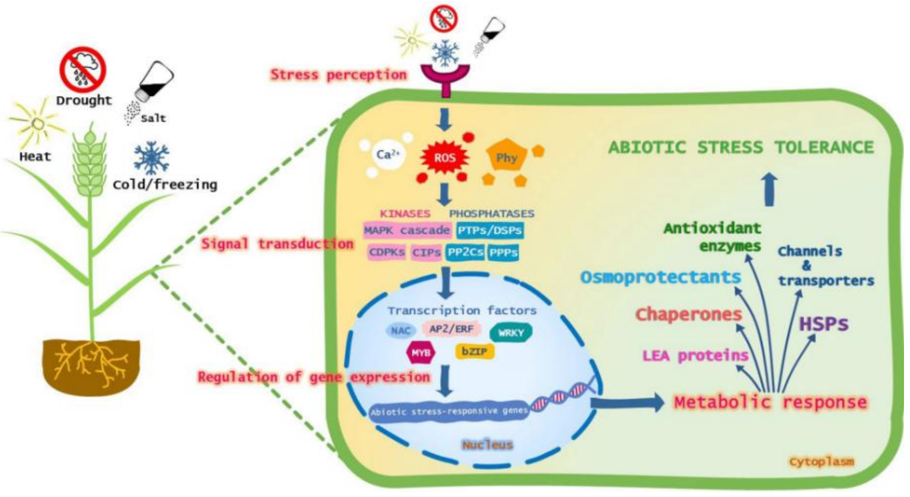

Figure 1 Schematic representation of the signalling pathway leading to the plant response to abiotic stresses (Adopted from Trono and Pecchioni, 2022)

Image caption: Specific receptors in the plasma membrane perceive the external stress signal and transmit the signal intracellularly through phytohormones and secondary messengers, such as calcium (Ca^{2+}) and reactive oxygen species (ROS); The second messengers activate different classes of protein kinases, including mitogen-activated protein kinase (MAPK) cascade, calcium-dependent protein kinases (CDPKs), and calcineurin-B-like proteins-interacting protein kinases (CIPKs), and protein phosphatases, such as protein tyrosine phosphatases/dual-specificity phosphatases (PTPs/DSPs), protein phosphatases 2C (PP2Cs), and serine/threonine-specific protein phosphatases (PPPs); Subsequently, the protein kinases and phosphatases catalyze the phosphorylation/dephosphorylation of transcription factors, including APETALA2/ethylene response element-binding factors (AP2/ERF), the large NAC family, basic leucine zipper (bZIP), WRKY, and MYB; These finally regulate the expression of abiotic stress-responsive genes encoding heat shock proteins (HSPs) and other chaperones, late embryogenesis abundant (LEA) proteins, enzymes involved in the biosynthesis of osmolytes, antioxidant enzymes and enzymes involved in the biosynthesis of small antioxidant molecules, aquaporins and ion transporters, which contribute to the tolerance of wheat to abiotic stresses (Adopted from Trono and Pecchioni, 2022)

5 Methodologies in Wide Hybridization

5.1 Cross-breeding techniques

Cross-breeding techniques are fundamental in wide hybridization, allowing the combination of desirable traits from different parental taxa. This process can be categorized into sexual and somatic hybridization. Sexual hybridization involves the pollination of plants from different species, either naturally or through induction, to combine their genomes. This method has been instrumental in introducing genetic variability and enhancing traits such as yield and disease resistance in wheat (Mwangangi et al., 2019). Somatic hybridization, on the other hand, involves the fusion of somatic cells rather than gametes, which requires the successful differentiation of protoplasts into whole plants in vitro. This technique is particularly useful for overcoming species barriers that are not easily crossed through sexual hybridization (Mwangangi et al., 2019).

5.2 Use of molecular markers

Molecular markers play a crucial role in the identification and selection of hybrids. Techniques such as genomic selection use whole-genome markers to predict the performance of potential hybrids. This method has been successfully applied in crops like rice, where it has significantly increased the efficiency of selecting superior hybrids with desirable traits(Cui et al., 2019). The use of molecular markers allows for the precise identification of genetic variations and the tracking of desirable traits through generations, thereby enhancing the effectiveness of hybrid breeding programs (Mwangangi et al., 2019).

5.3 Biotechnological tools and innovations

Biotechnological tools and innovations have revolutionized the field of wide hybridization. Techniques such as chromosome doubling, the use of hormones like 2,4-Dichlorophenoxyacetic acid (2,4-D), and embryo rescue are employed to overcome challenges such as sterility, arrested growth of pollen tubes, and embryo abortion in hybrids (Mwangangi et al., 2019). Additionally, advanced genomic tools like genomic best linear unbiased prediction (GBLUP) have been used to predict hybrid performance, thereby reducing the costs and time associated with field evaluations (Cui et al., 2019). These biotechnological advancements have significantly improved the success rates of wide hybridization and the development of superior wheat cultivars.

The methodologies in wide hybridization, including cross-breeding techniques, the use of molecular markers, and biotechnological tools, have greatly contributed to the genetic improvement of wheat. These approaches have enabled the introduction of desirable traits from diverse genetic backgrounds, thereby enhancing the overall productivity and resilience of wheat cultivars.

6 Challenges and Limitations

6.1 Genetic incompatibility issues

Genetic incompatibility is a significant challenge in wide hybridization for wheat genetic improvement. The primary barriers include prezygotic and postzygotic incompatibilities. Prezygotic barriers, such as those determined by Kr genes, prevent successful fertilization between wheat and its wild relatives, like rye (Pershina and Trubacheeva, 2017). Postzygotic incompatibilities often result in hybrid seed lethality due to uniparental chromosome elimination and abnormal endosperm development, which are critical during the early stages of hybrid seed development (Pershina and Trubacheeva, 2017). These genetic barriers limit the success rate of wide hybridization and necessitate the development of advanced techniques to overcome them.

6.2 Fertility and viability of hybrids

The fertility and viability of hybrids produced through wide hybridization are often compromised. Hybrid sterility is a common issue, which can be attributed to nuclear-cytoplasmic interactions and the structural and functional variability of nuclear and organelle genomes (Pershina and Trubacheeva, 2017). Additionally, hybrid depression, characterized by hybrid necrosis, chlorosis, and dwarfness, further reduces the viability of hybrids (Pershina and Trubacheeva, 2017). These factors collectively hinder the practical application of wide hybridization in wheat breeding programs.

6.3 Regulatory and ethical considerations

Regulatory and ethical considerations also pose significant challenges to the application of wide hybridization in wheat genetic improvement. The introduction of genes from wild relatives into cultivated wheat varieties raises concerns about biosafety and the potential impact on ecosystems. Regulatory frameworks often require extensive testing and evaluation to ensure that new hybrids do not pose risks to human health or the environment. Ethical considerations include the potential for unintended consequences, such as the loss of genetic diversity in wild populations and the ethical implications of manipulating plant genomes (Pershina and Trubacheeva, 2017; Alvarez and Guzmán, 2018). These considerations necessitate a careful and balanced approach to the use of wide hybridization in wheat breeding.

7 Case Studies of Wide Hybridization in Wheat

7.1 Successful examples in wheat breeding programs

Wide hybridization has been an essential tool for introducing new genetic variations and improving various agronomic traits in wheat breeding programs. By crossing with wild relatives and old varieties, wheat quality traits such as grain hardness, gluten quality, and starch content have been improved. This approach has also expanded the nutritional quality of wheat by introducing vitamins, fibers, and micronutrients (Alvarez and Guzmán, 2018).

A large-scale GWAS involving 768 wheat varieties identified 395 quantitative trait loci (QTL) for 12 traits. This study highlighted the potential of wide hybridization in identifying candidate genes to improve key traits such as spikelet number and grain size, which are crucial for increasing yield (Figure 2) (Pang et al., 2020).

Experiments involving 15 different species from the Poaceae and Panicoideae families demonstrated the feasibility of wide hybridization among wheat, barley, and rye. Successful embryo formation with species such as Agropyron and maize showed the potential for creating new genetic combinations. Studies on wheat hybrid seed set exhibited significant genetic variation and high heritability. By selecting male floral traits such as anther extrusion, breeders can indirectly improve hybrid seed set, thus enhancing the efficiency of hybrid wheat breeding programs (Boeven et al., 2018). A three-step strategy was developed to identify heterotic patterns for high-yield hybrid wheat breeding. This method, which includes genomic prediction and simulated annealing algorithms, showed promise in improving grain yield and stability by leveraging heterosis (Zhao et al., 2015).

7.2 Comparative analysis of different methods

Various methods have been explored in wide hybridization of wheat, proving to be very effective in introducing new quality traits and nutritional components. However, careful selection of parental species is required to ensure compatibility and successful hybridization (Alvarez and Guzmán, 2018). GWAS provides a high-resolution method for identifying QTL and candidate genes associated with important agronomic traits. This approach is data-intensive, requiring large populations and high marker density for accurate results (Pang et al., 2020). Wide hybridization experiments demonstrated that embryo culture techniques could facilitate the growth of haploid and diploid embryos from multiple species. This method is crucial for overcoming hybridization barriers and ensuring the development of viable plants. Indirect selection of traits such as anther extrusion can improve hybrid seed set, making this a practical method for enhancing the efficiency of hybrid wheat breeding. However, it requires a deep understanding of the genetic architecture of these traits (Boeven et al., 2018). The three-step strategy for identifying heterotic patterns combines genomic prediction and advanced algorithms to optimize hybrid performance. This method is highly effective but requires substantial computational resources and expertise in genomics (Zhao et al., 2015).

7.3 Lessons learned and best practices

Utilizing a broad genetic base, including wild relatives and old varieties, can significantly enhance the genetic diversity and quality traits of wheat (Alvarez and Guzmán, 2018). Employing high-resolution mapping techniques such as GWAS can identify key QTL and candidate genes, facilitating targeted breeding efforts (Figure 3) (Pang et al., 2020). Developing and refining embryo culture techniques are crucial for the success of wide hybridization, especially when dealing with distant species. Focusing on indirect traits related to desired outcomes, such as anther extrusion for hybrid seed set, can simplify the breeding process and improve efficiency (Boeven et al., 2018). Implementing structured approaches to identify and exploit heterotic patterns can maximize the benefits of heterosis and enhance yield stability (Zhao et al., 2015). By integrating these best practices, wheat breeding programs can effectively utilize wide hybridization to achieve significant genetic improvements and meet the growing demands for food security.

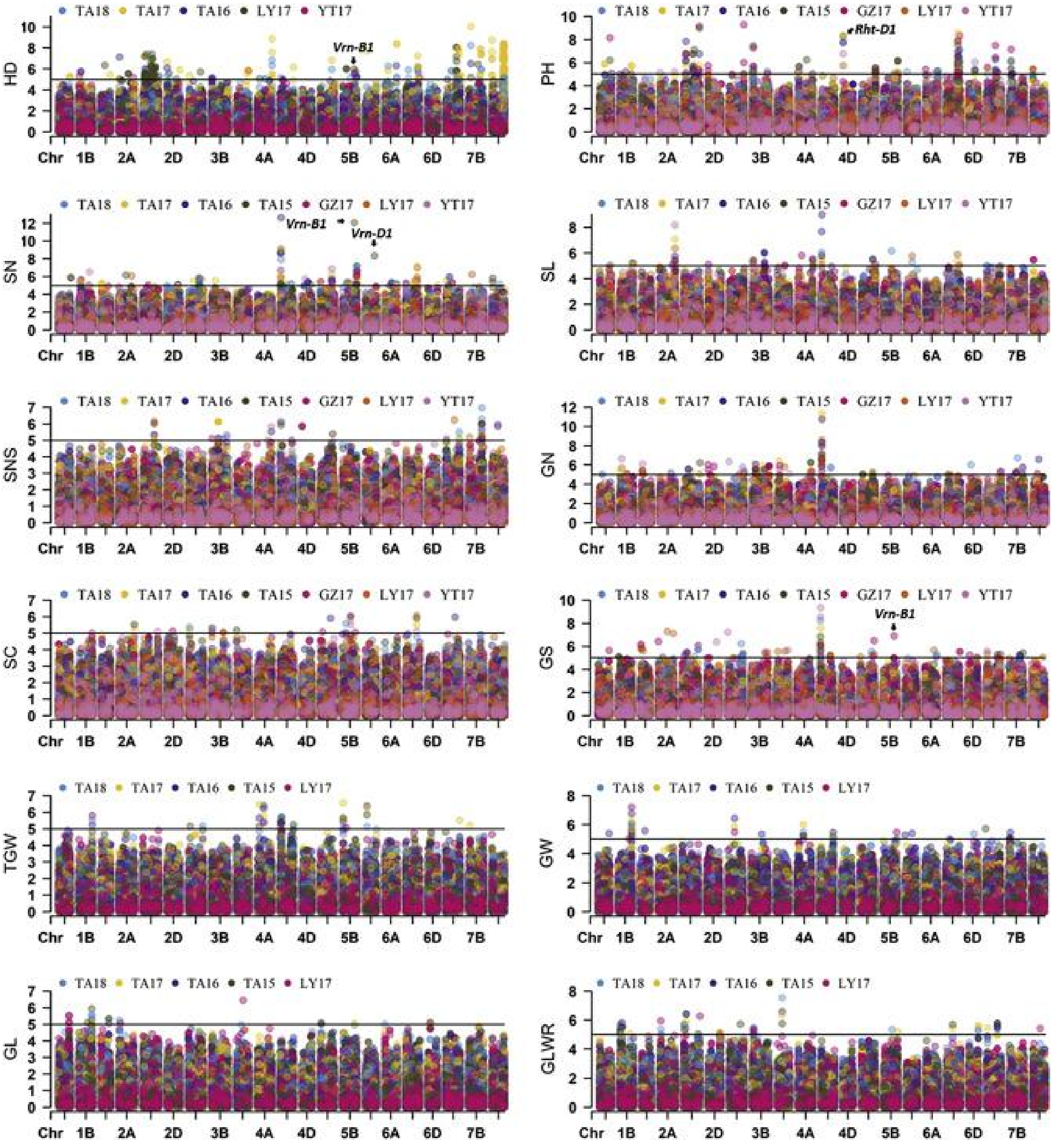

Figure 2 Manhattan plots for all traits under multiple environments from GWAS (Adopted from Pang et al., 2020)

Image caption: The y axis refers to −log10(p) for different traits, and the colors of dots refer to different environments. HD: heading date; PH, plant height; SN: spike number; SL: spike length; SNS: spikelet number per spike; GN: grain number; GS, grain setting; SC: spike compactness; TGW: thousand-grain weight; GL: grain length; GW: grain width; GLWR: grain length to width ratio (Adopted from Pang et al., 2020)

8 Future Directions and Prospects

8.1 Emerging technologies and innovations

The future of wheat genetic improvement through wide hybridization is promising, particularly with the advent of emerging technologies and innovations. Recent advances in genome sequencing and sequence assembly have produced high-quality genome sequences for wheat, which can significantly accelerate the progress in wheat biology and breeding programs (Li et al., 2020). High-throughput phenotyping and genomic selection are also promising approaches that can maximize progeny screening and selection, thereby accelerating genetic gains in breeding more productive varieties (Mondal et al., 2016). Additionally, the integration of genomic prediction and simulated annealing algorithms has been shown to effectively identify high-yielding heterotic patterns, which can boost grain yield through the exploitation of heterosis (Zhao et al., 2015). These technological advancements are pivotal in uncovering the hidden favorable genetic diversity in wheat genetic resources, thus enabling a targeted choice of accessions with high value for pre-breeding (Longin and Reif, 2014).

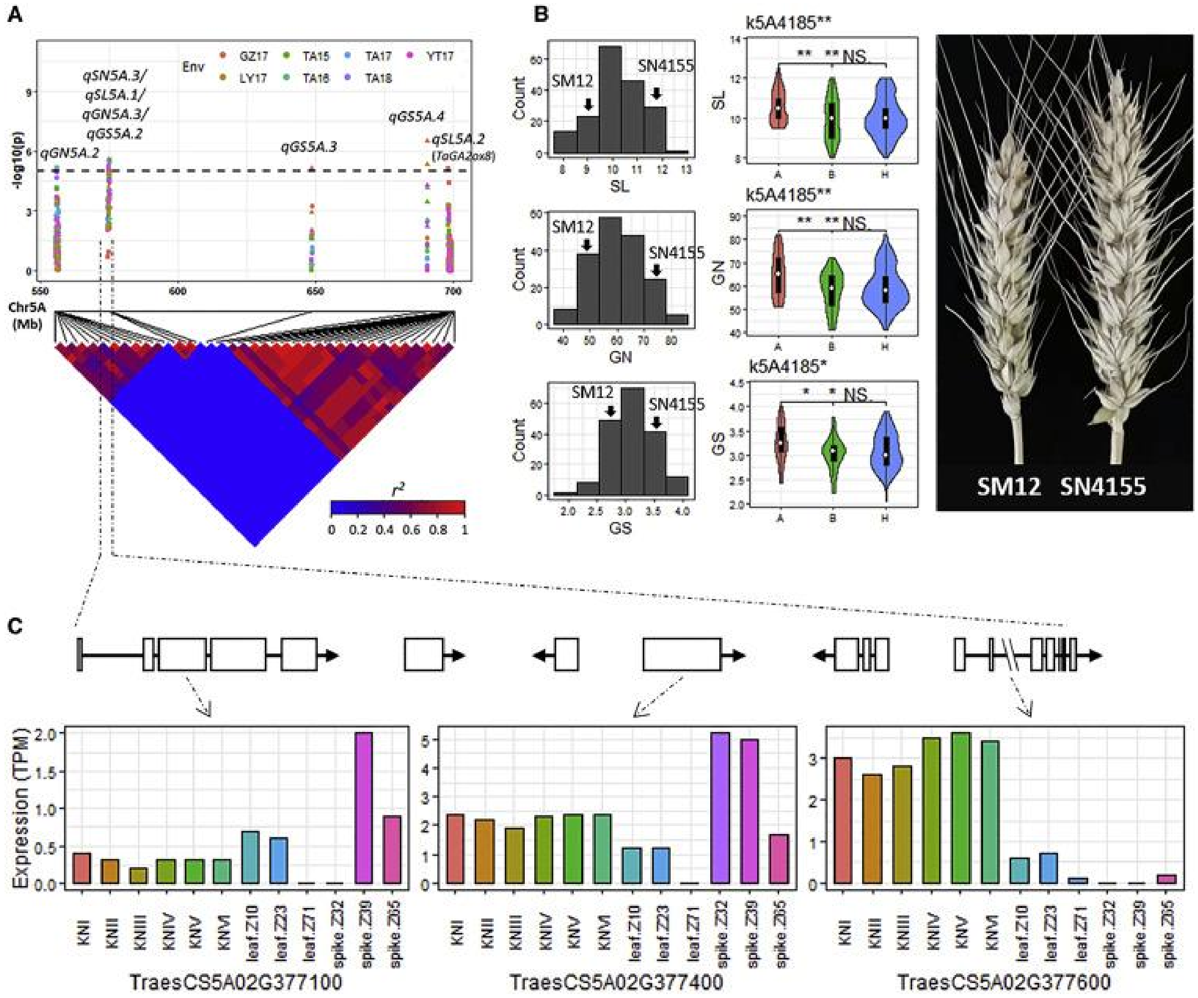

Figure 3 Validation of candidate genes of the qSN5A.3/qSL5A.1/qGN5A.3/qGS5A.2 QTL for spike traits on chromosome 5A (Adopted from Pang et al., 2020)

Image caption: A: LD: Local Manhattan plot and linkage disequilibrium; SL: heatmap of QTLs for spike length; GN: grain number and; GS: grain setting identified on 5AL; Only SNPs within the peak of the LD block of each QTL are shown; B: Frequency distributions of SL, GN, and GS traits for individuals in the F_2 population with their parents Shimai 12 (SM12) and Shannong 4155 (SN4155) (left and right), and comparison of phenotypes between contrasting alleles at the qSN5A.3/qSL5A.1/qGN5A.3/qGS5A.2 QTL for SL, GN, and GS traits in the SM12/SN4155 population based on the KASP marker k5A4185 (middle); A is the allele from SN4155, B is the allele from SM12, and H refers to the heterozygote; C: The six annotated genes in the qSN5A.3/qSL5A.1/qGN5A.3/qGS5A.2 QTL region (top) and the three genes that are expressed in leaves and spikes at different developmental stages (bottom); KNI, KNII, KNIII, KNIV, KNV, and KNVI refer to the six early spike development stages in wheat variety Kenong 9204. Leaf.Z10, leaf.Z23, leaf.Z71, spike.Z32, spike.Z39, and spike.Z65 refer to three leaf and spike developmental Zodac stages of Chinese Spring (Adopted from Pang et al., 2020)

8.2 Potential for sustainable agriculture

Wide hybridization holds significant potential for promoting sustainable agriculture. By harnessing the genetic diversity present in both wild and cultivated relatives of wheat, it is possible to develop wheat varieties that are more resilient to biotic and abiotic stresses (Ali et al., 2020). This is crucial for ensuring food security in the face of climate change and the increasing global population. The integration of alien genetic diversity into wheat breeding programs can help in developing varieties that are better adapted to emerging stresses, thereby supporting sustainable food production systems (Ali et al., 2020). Moreover, the use of cisgenic techniques to transfer beneficial alleles within related species offers great promise for achieving durable resistance to diseases such as rust, further contributing to sustainable agricultural practices (Mondal et al., 2016).

8.3 Strategies for overcoming current challenges

Despite the potential benefits, several challenges need to be addressed to fully realize the advantages of wide hybridization in wheat genetic improvement. One of the primary challenges is the complexity and enormous size of the wheat genome, which has historically impeded progress in wheat genetics and functional genomics (Li et al., 2020). To overcome this, it is essential to adopt innovative breeding strategies and novel tools that can efficiently utilize genetic diversity for new genes and alleles (Mondal et al., 2016). Additionally, the development of a high-yielding heterotic pattern through a systematic three-step strategy can help in overcoming the stagnation in yield growths observed in selfing species like wheat (Zhao et al., 2015). Efforts should also be directed towards transforming and reorienting agricultural systems to integrate food security and climatic change concerns, thereby addressing both biotic and abiotic stress resistances/tolerances in crops (Ali et al., 2020). By focusing on these strategies, it is possible to bridge the yield gap between genetic resources and elite breeding pools, ultimately enhancing grain yield potential and ensuring sustainable wheat production (Longin and Reif, 2014).

The future of wheat genetic improvement through wide hybridization is bright, with emerging technologies and innovations playing a crucial role. By harnessing genetic diversity and adopting innovative strategies, it is possible to overcome current challenges and promote sustainable agriculture, thereby ensuring food security for the growing global population.

9 Concluding Remarks

Wide hybridization has emerged as a pivotal strategy for enhancing wheat genetic improvement. The integration of wild relatives and underutilized wheat varieties has significantly expanded the genetic variability available for wheat breeding, particularly in terms of grain quality, disease resistance, and yield stability. The use of advanced genomic tools, such as non-denaturing fluorescence in situ hybridization (ND-FISH), has facilitated the identification and utilization of genetic diversity within wheat germplasm. Moreover, the application of both conventional and modern breeding approaches has successfully introgressed desirable traits, including climate resilience and nutritional quality, into wheat varieties.

Future research should focus on overcoming the barriers to wide hybridization, such as genetic incompatibility and sterility issues, to further enhance the efficiency of this breeding strategy. The integration of high-throughput phenotyping, genome sequencing, and genomic selection will be crucial in accelerating the genetic gains in wheat breeding programs. Additionally, exploring the potential of hybrid wheat breeding, which involves the development of lines with favorable male floral characteristics, could significantly boost grain yield and yield stability. There is also a need to reassess and redesign pre-breeding strategies to unlock the hidden genetic potential of wheat genetic resources stored in gene banks worldwide.

Wide hybridization stands as a cornerstone for the future of wheat genetic improvement. By tapping into the vast genetic diversity of wild relatives and neglected wheat varieties, breeders can introduce novel traits that enhance grain quality, disease resistance, and yield stability. The continuous advancements in genomic technologies and breeding methodologies promise to overcome existing challenges and unlock new opportunities for wheat improvement. Ultimately, wide hybridization not only contributes to the sustainability and resilience of wheat production but also plays a critical role in ensuring global food security in the face of growing population demands and climate change.

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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.

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