Received: 21 May 2025 | Accepted: 26 November 2025

DOI: 10.1002/tpg2.70176

The Plant Genome

REVIEW

Genomics in wheat improvement: Progress and perspectives

Shaoshuai Liu[1,2] | **Shuaifeng Geng**[1] | **Susanne Dreisigacker**[2]

[1]State Key Laboratory of Crop Gene Resources and Breeding and National Key Facility for Crop Resources and Genetic Improvement, Institute of Crop Science, Chinese Academy of Agricultural Sciences, Beijing, China

[2]International Maize and Wheat Improvement Center (CIMMYT), Carretera Mex-Veracruz, Texcoco, Mexico

Correspondence
Shaoshuai Liu, State Key Laboratory of Crop Gene Resources and Breeding and National Key Facility for Crop Resources and Genetic Improvement, Institute of Crop Science, Chinese Academy of Agricultural Sciences, Beijing, 100081, China. Email: liushaoshuai@caas.cn

Assigned to Associate Editor Manuel Spannagl.

Funding information
National Natural Science Foundation of China, Grant/Award Number: 32201878; Key R&D Program of Shandong Province, China, Grant/Award Number: 2024SFGC0404; Biological Breeding-National Science and Technology Major Project, Grant/Award Number: 2023ZD0406802; China Scholarship Council (CSC), Grant/Award Number: 202403250025

Abstract

Bread wheat (*Triticum aestivum*) remains a major source of food and calories globally, yet its vast genome, polyploidy, and high number of repetitive sequences make genomic research challenging in this crop. In this review, we discuss the progress and future perspectives of genome research in wheat. Current efforts focus on the establishment of genome assemblies, advances in functional genomics, advances in epigenetics, translational genetics, and CRISPR-Cas9 genome editing offers a powerful tool for site-specific genome editing for wheat improvement and functional genetic analysis. These approaches have elucidated the genetic basis of many important agronomic traits such as grain yield, biotic and abiotic stress, and wheat quality. Future aims are expected to expand to pan-genomics, the mechanism of wheat domestication, funnel the outputs of functional genomics for deployment in wheat breeding, multi-omics studies facilitate genetic dissection, and the era of big data: creation, integration and utilization, and artificial intelligence breeding.

Plain Language Summary

Wheat feeds billions worldwide, but its genome is very large and complex, which makes genetic research hard. This review summarizes what scientists have learned about wheat's genome and what they expect to explore next. We survey recent literature on wheat genome sequencing, assembly, and annotation to evaluate how the genome's size, polyploidy, and repetitive content shape current methods. The goal is to identify methodological gaps and propose directions that will accelerate genome-enabled wheat breeding and biology. A major finding of this review is that coordinated advances across genome assembly, functional genomics, epigenetics, translational genetics, and CRISPR-Cas9 editing are enabling the identification of genetic bases for key bread wheat traits, paving the way for more precise breeding and functional validation. However, the wheat genome's size, polyploidy, and high repetitive content continue to constrain comprehensive knowledge, underscoring the

Abbreviations: AI, artificial intelligence; ATAC-seq, assay for transposase-accessible chromatin using sequencing; BSA, bulk-segregant analysis; CUT&Tag, cleavage under targets & tagmentation; GWAS, genome-wide association studies; QTL, quantitative trait loci; RNA-seq, RNA sequencing; scRNA-seq, single-cell RNA sequencing; SNP, single nucleotide polymorphism; ST, spatiotemporal transcriptomics; WGS, whole genome sequencing.

Shaoshuai Liu and Shuaifeng Geng contributed equally to this work.

urgency of pan-genomics, multi-omics integration, and AI-driven breeding to fully unlock genome-enabled improvement.

1 | INTRODUCTION

Bread wheat (*Triticum aestivum*) is the most important staple crop worldwide. It accounts for 17% (one-sixth) of all crop acreage and provides 20% (one-fifth) of all food calories and protein needed for human nutrition However, to meet the world's food demand by 2050, agricultural production must rise by 50% (Senapati et al., 2022), despite facing severe challenges, such as climate change (temperature, heat, and drought), degrading soil health (type of soil and organic composition), and the overuse of pesticides and fertilizers (Bibi & Rahman, 2023; Wan et al., 2022).

Wheat was one of the first crops grown in the Fertile Crescent during the agricultural revolution 10,000 years ago (Gutaker & Purugganan, 2024). Bread wheat contains three related sub-genomes. The diploid progenitors of the A and D sub-genomes have been identified, while the origin of the B genome has been a long-standing subject of debate (Levy & Feldman, 2022). Given its complex evolution, several types of wheat species exist: bread wheat (hexaploid, *T. aestivum*, AABBDD, $2n = 6x = 42$), tetraploid wheat (*Triticum turgidum*, AABB, $2n = 4x = 28$), and einkorn wheat (*Triticum monococcum*, AA, $2n = 14$). For a long time, genome research in wheat has lagged other staple crops (e.g., rice and maize), due to its large and highly repetitive genome (C. Wang & Han, 2022; N. Yang & Yan, 2021). However, over the past decades, sustained efforts have led to significant advancements, generating a wealth of knowledge and resources that have been leveraged to improve the crops' yields, grain quality, and stress tolerance (X. Huang et al., 2022; Yao et al., 2025).

In this review, we describe areas of recent progress and future perspectives of genome research in wheat. The establishment of a reference genome along with advancements in functional genomics, epigenomics, and molecular genetics have laid a solid foundation for future research in these fields such as pan-genomics, multi-omics, "big data" analysis, and artificial intelligence (AI) breeding.

2 | MAJOR ADVANCES IN WHEAT GENOME RESEARCH

2.1 | The establishment of genome assemblies

During the last two to three decades, multiple efforts have been made to create new resources for wheat genome research. The sequencing of different sub-genomes of wheat and its relatives has been completed (Figure 1). The International Wheat Genome Sequencing Consortium (IWGSC), established in 2005, was the first to publish the physical map and reference sequence of chromosome 3B in bread wheat, which provided guidance for deciphering the sequence of the other chromosomes in wheat (Choulet et al., 2014). Using first- and second-generation technologies has facilitated the assembly of numerous plant genomes. The initially fragmented assemblies created from short reads have been significantly enhanced by long-read sequencing, streamlining the process and improving the generation of chromosome-level assemblies while reducing costs and improving quality (Tiwari et al., 2024). *Triticum urartu* (diploid, AA) was confirmed as the progenitor of the A sub-genome of wheat. Ling et al. (2018) thus completed the first draft of the A subgenome and a high-resolution reference genome for this species. To verify the D sub-genome progenitor, *Aegilops tauschii* accession AL8/78 was first sequenced (M. Luo et al., 2017; G. Zhao et al., 2017). To date, a number of high-quality reference genomes of *A. tauschii* have been constructed (Cavalet-Giorsa et al., 2024; Gaurav et al., 2022; L. Wang et al., 2021; Y. Zhou et al., 2021). The species consists of three lineages distinguished by subtle phenotypic variations. Lineage 1, *A. tauschii* spp. *tauschii*, is distributed throughout the native range of *A. tauschii*, whereas Lineage 2, *A. tauschii* spp. *strangulata*, is predominantly located near the Caspian Sea in Iran and Azerbaijan. Lineage 3 has not yet been assigned a name from the historical subspecies classifications. Lineage 2 is recognized as the main contributor of the D sub-genome in wheat (Delorean et al., 2021). Although the exact progenitor of the wheat B genome is unknown, the genomes of several related Sitopsis species have been explored, for example, *Aegilops speltoides*, *Aegilops bicornis*, *Aegilops searsii*, *Aegilops longissimi*, and *Aegilops sharonensis* (L. Li, Zhang, et al., 2022; Y. Yang et al., 2023). The long-held belief that *A. speltoides* was the origin of the B sub-genome of wheat has been refuted by a comparison of these species' genomes with the B sub-genome of polyploid wheat. As a result, scientists generally agree that the origin of the B sub-genome is either undiscovered or extinct.

Tetraploid wild emmer wheat (*T. turgidum* ssp. *dicoccoides*) followed by domesticated emmer wheat (*T. turgidum* ssp. *dicoccum*) are known as the progenitors of durum wheat (*T. turgidum* ssp. *durum*) (Figure 1). Wild emmer accession Zavitan, derived from Israel's Zavitan nature reserve, was sequenced in 2017 (Avni et al., 2017). A 10.45 Gb reference

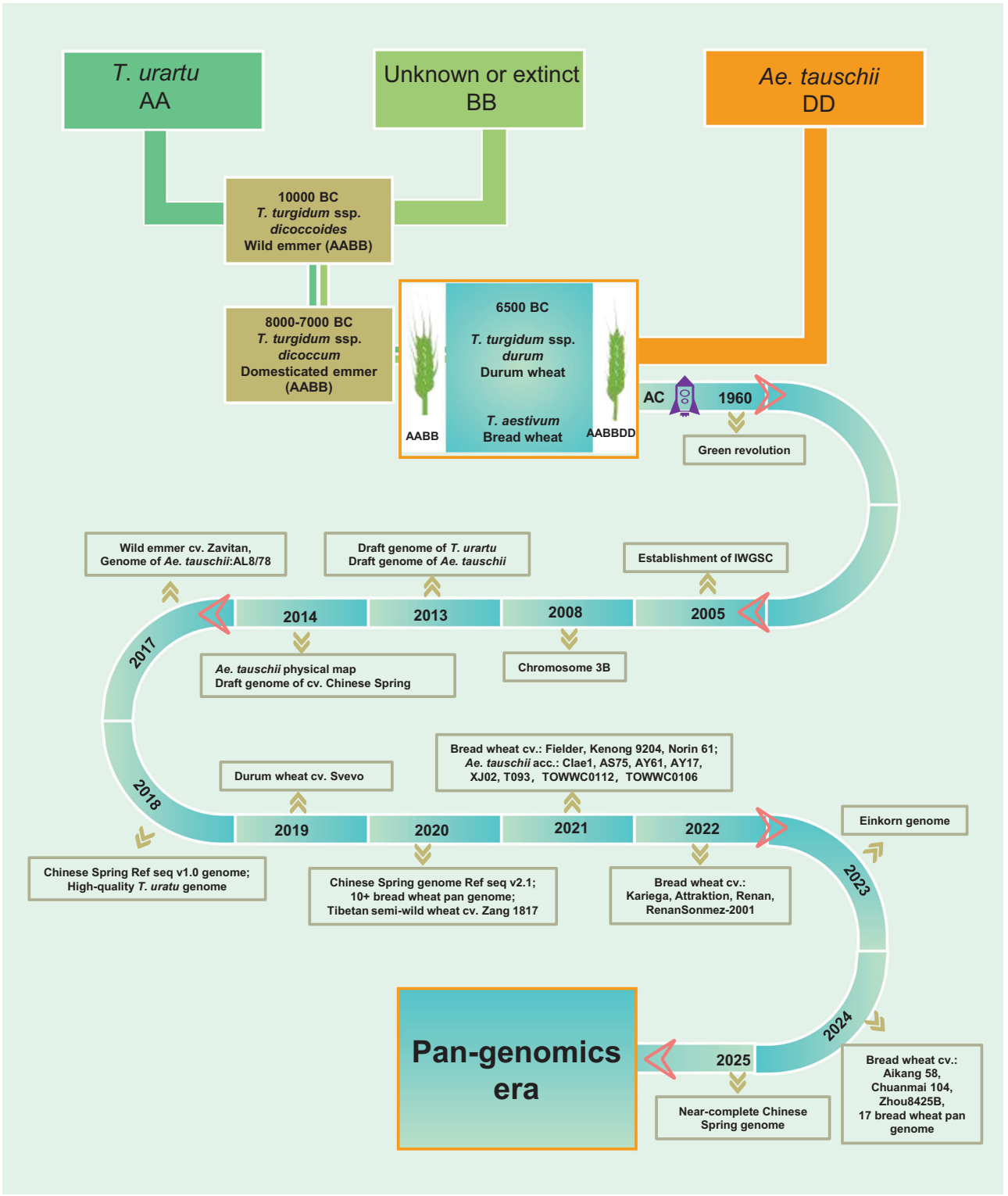

FIGURE 1 Phylogenetic representation of wheat evolution and important milestones in genomics. Wheat evolution is shown starting from a progenitor that gave rise to the A and B subgenomes merged to form emmer wheat, then fused D subgenome to generate bread wheat. With the development of sequencing technology, several wheat genomes have been produced. IWGSC, International Wheat Genome Sequencing Consortium; *T. dicoccoides*, *Triticum turgidum* ssp. *dicoccoides*; *T. dicoccum*, *T. turgidum* ssp. *dicoccum*.

genome of the durum wheat variety Svevo was subsequently generated (Maccaferri et al., 2019). As expected, comparative studies revealed substantial synteny between the genomes of Zavitan and Svevo, with high similarity in the number of high confidence genes, chromosome structure, and content of transposable elements, These are attributed to their short-term evolutionary, making them conserved evolutionary relationships.

In 2018, the IWGSC finalized and published the cultivar Chinese Spring v1.0 chromosome-scale pseudomolecule sequences (~16 Gb), later updated to v2.1 currently representing the gold standard reference sequence of hexaploid wheat (IWGSC, 2018; Zhu et al., 2021). Recently, near-complete assembly of the CS-CAU and telomere-to-telomere gap-free CS-IAAS genomes were finished to support wheat breeding and functional research (S. Liu et al., 2025; Z. Wang et al., 2025). It is worth mentioning that Walkowiak et al. (2020) released the first pan-genome, which included eight spring and seven winter varieties representing different regions and breeding programs. Beside, pan-genomes were constructed from 17 common cultivars, and researchers discovered a considerable number of structural variations, encompassing presence-absence variations (PAVs), translocations, and inversions. By comparing PAV frequencies across cultivars from various decades, they revealed the incorporation of European germplasm into contemporary Chinese wheat breeding (Jiao et al., 2024). To date, many additional wheat genomes from around the world have been assembled (Table 1), which greatly accelerate research in the following key areas (Figure 2): (i) structural and functional genomics, (ii) epigenomics, (iii) and molecular genetics.

2.2 | Advances in functional genomics

High-resolution genome assemblies have unlocked functional genomics studies and allowed precise mapping and cloning of genes, and quantitative trait loci (QTLs) for yield and stress tolerance. Functional genomics has been greatly facilitated with the advent of wheat genome sequencing (Mao et al., 2018). The challenge lies in determining the functions of large volumes of genome sequences and understanding surrounding regulatory networks that control key traits for optimal crop growth. These traits include those related to grain yield and its components, resistance to biotic and abiotic stresses, as well as traits related to grain end use and nutritional quality (Figure 2). Researchers can unravel the genetic basis of traits and improve wheat breeding programs by integrating genomic data. This knowledge is crucial for developing resilient wheat varieties that can withstand climate change and meet global food demands.

2.2.1 | Grain yield contributing traits

Higher grain yield is the most considered trait for meeting the objective of feeding an increasing population. Grain size, grain number, and spike number per unit area are three components that make up the complex quantitative feature of grain yield. The post-anthesis phase includes cell proliferation, grain filling, and grain desiccation until grain maturity. Under extreme weather conditions, grain size may be directly or indirectly influenced by post-anthesis variables (Brinton & Uauy, 2019; Gasparis & Miłoszewski, 2023; Ugarte et al., 2007). The negative balance between grain size and grain number has posed a challenge to increasing grain productivity. Grain yield-related genes were successfully isolated, including the *CYTOKININ OXIDASE/DEHYDROGENASE* gene *TaCKX2-1* (Z. Zhang et al., 2019), *TaGW2* (W. Wang et al., 2018), the *FLOWERING LOCUS T* (*FT*) (Sakuma & Schnurbusch, 2020), and the wheat ortholog of the rice *ABNORMAL CYTOKININ RESPONSE1 REPRESSOR1* (*TaARE1*) (J. Zhang et al., 2021), all of which control grain size and weight. Grain yield in transgenic plants has shown to be increased when the dominant *TaCol-B5* allele is constitutively overexpressed in a common wheat cultivar, by generating additional tillers and spikes and increases the number of spikelet nodes per spike (X. Zhang et al., 2022). The *WHEAT ORTHOLOG OF APO1* gene (*TaWAPO1*) was isolated from wheat chromosome 7AL and natural alleles were observed, which increases the number of spikelets per spike (Wittern et al., 2022). The transcription factor *LEAFY* (*LFY*) interacts both genetically and physically with *WAPO1* to control the number of spikelets per spike and the growth of the florets (Paraiso et al., 2024). The discovery of these genes offers enormous potential for increasing yields.

2.2.2 | Biotic and abiotic stress

Fluctuating climates increase wheat's vulnerability to biotic (e.g., pests and pathogens) and abiotic stresses (e.g., heat, drought, and salt). Understanding the function of stress-related genes is therefore crucial for developing wheat varieties that can thrive under challenging conditions.

NLR (nucleotide-binding leucine-rich repeat) genes are a class of genes that play a crucial role in plant immune responses. The isolation of NLR has been an important aspect of plant molecular breeding and functional genomics. With advancements in high-throughput sequencing technologies and bioinformatics tools, researchers are able to identify and characterize these genes in plant genomes efficiently. The MutRenSeq (combines chemical mutagenesis with exome capture and sequencing) and AgRenSeq (association

TABLE 1 A list and description of wheat and related species with availability of genome assemblies.

Species	Varieties/accession	Ploidy	Contig N50	Gene count	Type	Genome size (Gb)	References
Triticum urartu	PI428198	$2n = 2x = 14$	344 kb	41,507	AA	4.94	(Ling et al., 2018)
Aegilops tauschii	AL8/78	$2n = 2x = 14$	4.5/2170/50.3 kb	~40,000	DD	4.36/4.31	(Jia et al., 2013; M. Luo et al., 2017; Zhao et al., 2017)
	Aet v5.0: CIae1, AS75	$2n = 2x = 14$	1.72/1.12 Mb	39,635	DD	4.29/4.69	(L. Wang et al., 2021)
	AY61, AY17, XJ02, T093	$2n = 2x = 14$	2.2/1.9/0.5/0.5 Mb	~44,513	DD	~4.4	(Y. Zhou et al., 2021)
Triticum turgidum ssp. *dicoccoides*	Wild emmer cv. Zavitan	$2n = 4x = 28$	57 kb	110,544	AABB	12	(Avni et al., 2017)
T. turgidum ssp. *durum*	Durum wheat cv. Svevo	$2n = 4x = 28$	6 Mb	66,559	AABB	10.45	(Maccaferri et al., 2019)
	Durum wheat cv. Kronos	$2n = 4x = 28$	NA	NA	AABB		(Seong et al., 2023)
Triticum aestivum	Chinese spring CS-CAS, CS-IAAS	$2n = 6x = 42$	55.01/180.14/ 723.78 Mb	~163,329	AABBDD	~15	(IWGSC, 2014, 2018; S. Liu et al., 2025; Z. Wang et al., 2025; Zhu et al., 2021)
	Norin 61	$2n = 6x = 42$	96 kb	118,734	AABBDD	15	(Shimizu et al., 2020)
	Mace, LongReach Lancer, CDC Stanley, CDC Landmark, Julius, Norin 61, ArinaLrFor, PI190962 (spelt wheat), Jagger, SY Mattis, Cadenza, Paragon, Robigus, Claire, Weebill 1	$2n = 6x = 42$	>48 kb	~107,000	AABBDD	~14.5	(Walkowiak et al., 2020)
	Fielder	$2n = 6x = 42$	NA	116,480	AABBDD	15	(Sato et al., 2021)
	Kenong 9204	$2n = 6x = 42$	366 kb	105,692	AABBDD	14.77	(X. Shi et al., 2022)
	Renan	$2n = 6x = 42$	2.2 Mb	109,552	AABBDD	14.26	(Aury et al., 2022)
	Attraktion	$2n = 6x = 42$	17.3 Mb	NA	AABBDD	14.7	(Kale et al., 2022)
	Sonmez	$2n = 6x = 42$	427 bp	NA	AABBDD	13.3	(Akpinar et al., 2022)
	Kariega	$2n = 6x = 42$	30.22 Mb	110,383	AABBDD	14.7	(Athiyannan et al., 2022)
	Aikang 58	$2n = 6x = 42$	237.2 kb	119,448	AABBDD	14.75	(Jia et al., 2023)
	Synthetic hexaploid wheat-derived cv. Chuanmai 104	$2n = 6x = 42$	58.25 Mb	136,431	AABBDD	14.81	(Z. Liu, Yang, et al., 2024)
	Zhou8425B	$2n = 6x = 42$	70.94 Mb	106,940	AABBDD	14.75	(G. Li et al., 2024)
	BJ8, MZM, XN6028, Abo, NC4, YM158, XY6, AMN, JM47, S4185, CM42, JM22, KF11, ZM366, ZM16, ZM22, HD6172	$2n = 6x = 42$	27.36 Mb	~153,077	$2n = 6x = 42$	~14.86	(Jiao et al., 2024)

(Continues)

TABLE 1 (Continued)

Species	Varieties/accession	Ploidy	Contig N50	Gene count	Type	Genome size (Gb)	References
T. aestivum ssp. *tibetanum*	Tibetan semi-wild wheat cv. Zang 1817	$2n = 6x = 42$	66 kb	118,078	AABBDD	14.71	(W. Guo et al., 2020)
Aegilops speltoides	Sitopsis, close to B-genome	$2n = 2x = 14$	3.1 Mb	36,928	SS	5.13	(Avni et al., 2022; L. Li, Zhang, et al., 2022)
Triticum monococcum	Einkorn, A genome, cv. TA10622, TA299, and PI 306540	$2n = 2x = 14$	344 kb	41,507	A^mA^m	5.2	(Ahmed et al., 2023; X. Wang et al., 2024)
Aegilops sharonensis	Sitopsis, close to B-genome	$2n = 2x = 14$	12.4 Mb	68,797	SS	6.7	(Avni et al., 2022)
Aegilops longissima	Sitopsis, close to B-genome	$2n = 2x = 14$	3.7 Mb	68,093	SS	6.7	(Avni et al., 2022)
Aegilops bicornis, *A. longissima*, *Aegilops searsii*, *A. sharonensis*, *A. speltoides*	Sitopsis, close to B-genome	$2n = 2x = 14$	9.16/1.05/0.56/ 1.01/1.78 Mb	~61,000	SS	~4–6	(L. Li, Zhang, et al., 2022)
Secale cereale	Wild relative	$2n = 2x = 14$	480.35 kb	45,596	RR	7.9	(G. Li et al., 2021)
Thinopyrum elongatum	Wild relative	$2n = 2x = 14$	2.15 Mb	44,474	EE	4.63	(H. Wang et al., 2020)

genetics with *R* gene enrichment sequencing) strategies are applied to rapidly clone *R* genes. Using these methods, the stem rust resistance genes *Sr22*, *Sr33*, and *Sr45* were successfully cloned (Arora et al., 2019; Steuernagel et al., 2016).

Related to abiotic stress, the *dehydration-responsive element binding* (*DREB*) transcription factor gene (*TaDTG6-B*) detected through genome-wide association studies (GWAS) has shown proven effects for drought tolerance. Overexpression and introgression of $TaDTG6\text{-}B^{Del57}$ displayed enhanced drought tolerance (Mei et al., 2022). Besides, *TaSPL6-D* was acquired using expression GWAS. The gene is a suppressor of TaHKT1;5-D, overexpression of $TaSPL6\text{-}D^{Del}$ increased wheat salt sensitivity. The discovery of these genes has greatly improved the resilience of wheat.

2.2.3 | Wheat quality

The demand for high quality flour is rising among consumers and industry due to the changing standards of living. There is a particularly strong demand for soft wheat flour, often employed in cakes and biscuits. The amount and characteristics of the constituent gluten proteins and starch primarily determine the wheat flour's end use value (Sharma et al., 2020). The polymeric glutenins and the monomeric gliadins, which give wheat dough its distinct viscoelastic qualities (Biesiekierski, 2017). In breeding for bread or noodles, key goal is to enhance baking properties and pasta color, respectively. L. Gao, Meng, et al. (2021) discovered the gene *Ta-NAC019-BI* to be exceptional for flour processing quality, emphasizing *TaNAC019* as a strong candidate for breeding higher quality wheat (Y. Gao, An, et al., 2021). Thus, it will greatly improve end-use quality.

2.2.4 | CRISPR-based genome editing tool for genomics research

CRISPR-based genome editing is a powerful tool for functional genomics, specifically for gene validation. The technology utilizes artificial nuclease to make targeted modifications to the genome (Ahmar et al., 2023). CRISPR has been developed to modify the wheat genome in a precise and predictable way without the introduction of foreign DNA fragments and can target desired agronomic features with great efficiency. The primary genetic alterations produced through genome editing include chromosomal rearrangements, point mutations, base substitutions, or targeted insertions or deletions (INDELs). Another advantage of genome editing is its ability to target multiple sites simultaneously. For instance, in hexaploid wheat, multiple gene-editing constructs have successfully edited two, three, four, and even five genes at up to

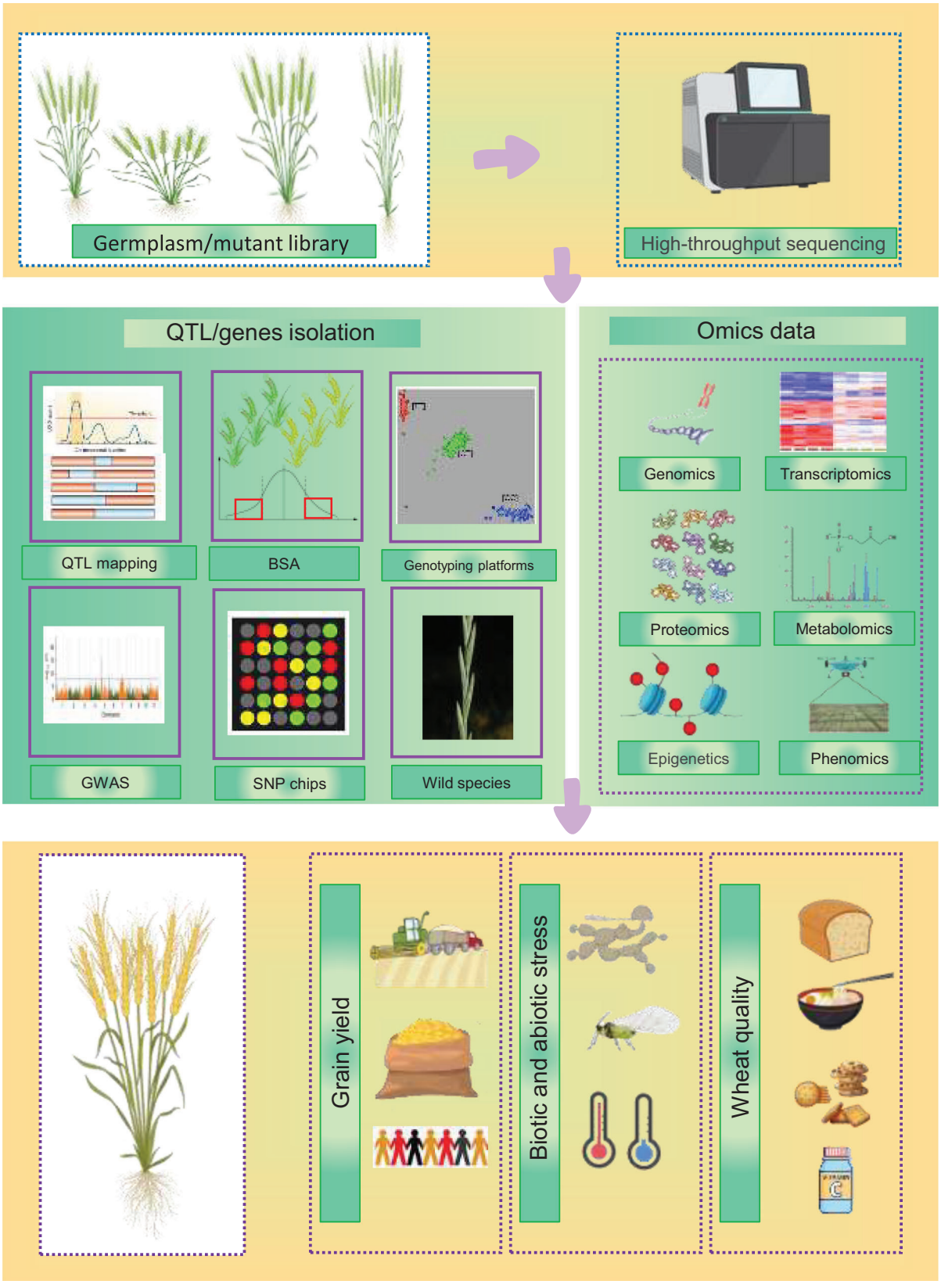

FIGURE 2 Schematic diagram of the wheat genome research program. This workflow illustrates the identification of quantitative trait loci (QTLs)/genes using genomic-based methods from a germplasm/mutant library and the production of multi-omics data through high-throughput sequencing, aiming to achieve stable high yields, superior grain quality, and robust resistance to stress.

15 genomic loci within a single generation. In the T1 generation, plants with inherited mutations at multiple genomic loci were successfully obtained, demonstrating the feasibility of using CRISPR for creating elite breeding materials with desirable alleles (J. Luo et al., 2021), as it accelerates the breeding process with unprecedented speed and cost-effectiveness (Ahmar et al., 2023; Awan et al., 2022; K. Chen et al., 2019; X. Zhou et al., 2023). Taken together, this capability has the potential beneficial for wheat improvement.

2.3 | Advances in epigenetics

Epigenetics encompasses the study of DNA methylation, histone modification, noncoding RNA regulation and chromatin three-dimensional structure reconstruction (Kohler & Springer, 2017). The two hybridization events that formed hexaploid wheat were accompanied by abundant epigenetic variation (X. Guo & Han, 2014; Y. Liu et al., 2021), but little is known about the magnitude and significance of the epigenetic modifications that occurred during the shift from diploid to tetraploid and hexaploid wheat. Genome-wide analysis of DNA methylation landscapes was performed to investigate the changes induced by the separation and merger of polyploid wheat genomes, revealing dynamic and reversible alterations in chromatin and DNA methylation that were associated with gene expression and transposon activity (Yuan et al., 2020). A study of the methylation status of Tausch's goatgrass during its interaction with powdery mildew revealed abundant differentially methylated regions with CHH (H = C, T, or A) hypomethylation near transposable elements. Silencing of a DOMAINS REARRANGED METHYLASE 2 (DRM2) homolog enhanced plant resistance to powdery mildew, through the upregulation of a pathogenesis-related *β-1,3-glucanse* gene. Thus, the study laid a foundation for the analysis of the interactions between epigenomics and plant immunity (Geng et al., 2019).

Histone modifications play a crucial role in most biological processes involving DNA manipulation and expression (T. Zhao et al., 2019). These modifications function as a type of "histone code," dominating the actions of genes and chromatin. Histone modifications appear to be important for plant development and responses to environmental stimuli. Histone H3K27 di-methylation (H3K27me2) and H3K27 tri-methylation (H3K27me3) plays a role in the regulation of gene expression and chromatin structure. Mapping the H3K27me2 and H3K27me3 genes in wheat revealed that H3K27me3 remained relatively stable across different ploidy levels. However, the ChIP-seq (chromatin immunoprecipitation) peak of H3K27me2 increased with the rise in ploidy. The H3K27me2 peak was co-localized with numerous amplified transposons in the euchromatin, which might explain the histone modification increase in H3K27me2 during polyploid wheat evolution. This may further explain the silencing of euchromatin transposons to maintain genome stability during polyploid wheat evolution (Y. Liu et al., 2021). In winter wheat, the key vernalization gene *VERNALIZATION1* (*VRN1*) exhibited opposing patterns for two core histone modifications, H3K27me3 and histone H3 lysine 36 trimethylation (H3K36me3), which corresponded to the gene's activation after cold exposure. After cold exposure, the H3K36me3 histone modification level at *VRN1* remained high, possibly maintaining its active methylation state (X. Liu, Deng, et al., 2024).

Meanwhile, techniques like ChIP-seq, DNA afinity purification sequencing, micrococcalnuclease sequencing, ATAC-seq (assay for transposase-accessible chromatin using sequencing), and CUT&Tag (cleavage under targets and tagmentation) are increasingly used to detect transcription factor binding sites and chromatin accessibility both in vitro and in vivo (Concia et al., 2020; Y. Liu, Liu, et al., 2024). In the future, increasing epigenetic studies will reveal more about the lesser-known mysteries of life, providing deeper insights into the biological processes that govern development and environmental responses.

2.4 | Translational genetics

Molecular genetics involves the utilization of methods that detect variations in plant DNA. DNA differences can be single nucleotide polymorphisms (SNPs) or INDELs made visible via molecular markers. When markers are closely linked to a genomic region of interest, they can help to indirectly select for desirable traits, which is named marker-assisted selection. Through QTL mapping, GWAS, and other molecular genetic analyses enabling map-based cloning, the last two decades have witnessed the identification of essential QTL/genes associated with agronomic traits (Colasuonno et al., 2021; Dreisigacker et al., 2021; Juliana et al., 2019; Song et al., 2023).

Many molecular marker technologies are available and widely utilized in wheat, including sequence tagged site, simple sequence repeat, genotyping by sequencing, SNP arrays, kompetitive allele-specific PCR, cleaved amplified polymorphic sequence, semi-thermal asymmetric reverse PCR, and genotyping by target sequencing, these techniques enable the separation of QTL/genes with their different efficiencies and advantages (Song et al., 2023). Molecular detection strategies have undergone significant innovation, with the emergence of solid-based or liquid-based SNP genotyping platforms that demonstrate high genotyping accuracy and ease of application across laboratories. Various types of SNP microarrays, such as 15K, 35K, 55K, 90 and 660K, as well as Wheat-Pan800K, 120K-4HWA, and TaNG have been developed for

wheat (Burridge et al., 2024; Sun et al., 2020). These arrays have been widely used for QTL mapping (F. Huang et al., 2023), phylogenetic analysis (L. Gao, Meng, et al., 2021), and haplotype detection (S. Yu et al., 2020). The 660K SNP array for wheat has been thoroughly employed to locate the genetic loci linked to quality characteristics, agronomic traits, and disease resistance in wheat (Ma et al., 2023; X. Yang et al., 2019).

Increasingly, whole genome sequencing (WGS) is being utilized to discover genetic variants in mapping populations (Schneeberger, 2014). For example, WGS has been employed to discover genomic variations in potential genes to Fe and Zn uptake among different genotypes, resulting in 254 genomic variants being isolated that have a deleterious impact on protein function (Kumar et al., 2022). Furthermore, WGS of 827 Watkins landraces and 208 modern cultivars, along with comprehensive field evaluations conducted over a decade, were followed by linkage disequilibrium-based haplotype and association genetics analyses. These analyses linked the Watkins genomes to high-resolution QTL and identified significant marker–trait associations. Numerous unique Watkins haplotypes were uncovered that could impart superior traits to modern wheat (Cheng et al., 2024).

Exome capture technology at accessible cost to cover adequate coverage in most gene coding regions can facilitate the finding of the causative genes (He et al., 2019). A total of 287 wheat accessions have been exome sequenced, 6.7% of the wheat genome has been identified within the selection sweeps occurring between landraces and cultivars, including the genes known to increase yield (A. Li, Hao, et al., 2022). GWAS was conducted to reveal marker-trait associations with heat tolerance traits and to evaluate their impact under favorable conditions. Three genetic loci derived from exotic sources were identified by assessing 149 spring wheat lines, which together can enhance yield and lower canopy temperature (Molero et al., 2023).

Bulk-segregant analysis (BSA) is an easy-to-use and affordable method for mapping QTL and genes (Zou et al., 2016). It involves creating two groups by crossing individuals with extremely opposite phenotypes, selecting individuals from the tails of the phenotypic distribution for pool sequencing. Allele frequencies are then estimated for the two groups, and differences will be observed between them if there are causal loci in the genome (Nguyen et al., 2019). To identify QTL/genes, different types of populations have been employed, including biparental populations (F2 or recombinant inbred lines), natural populations, multi-parent populations, and mutant libraries. Specific forms of BSA include QTL-seq, MutMap, and GradedPool-seq. As an example, the *early leaf senescence* (*els*) gene was cloned on chromosomal arm 2BS located in a 1.5 cM genomic region using BSA and RNA sequencing (RNA-seq) techniques (Nguyen et al., 2019).

GWAS uses high-throughput genotyping technologies to detect common genetic variants related to complex traits. By leveraging genetic diversity and principles of population genetics, GWAS can identify numerous natural allelic variants that influence complex agronomic traits (Yano et al., 2016). Comparatively, GWAS is regarded as a robust and cost-effective method for identifying QTL/genes as GWAS panels can be phenotyped for may trait at a time. GWAS has identified two underlying genes, *TaDEP1*, which encodes a G-protein, and *TaARF12*, which encodes an auxin response factor, both of which pleiotropically govern plant height and grain weight (Kong et al., 2023; A. Li, Hao, et al., 2022).

3 | FUTURE PERSPECTIVES

Based on the current advances in sequencing wheat and building diverse genomics resources, future research will likely include the following areas: pan-genomics, the mechanism of wheat domestication, funnel the outputs of functional genomics for deployment in wheat breeding, multi-omics studies facilitate genetic dissection, and the era of big data: creation, integration and utilization, and AI breeding (Figure 3).

3.1 | Pan-genomics

Genetic variation arises from various changes in the genome, such as SNPs, INDELs, and structural variants. Pan-genome analysis offers a framework for assessing the genetic diversity of a species by examining its complete collection of genomes (Igolkina et al., 2024; Rasheed et al., 2025; Tao et al., 2019). In recent years, third-generation sequencing has been widely applied to crops, utilizing the long-read sequencing technology on the PacBio platform for more accurate and efficient genome analysis. This advancement has shifted the study of species from relying on a single reference genome to incorporating multiple reference genomes, marking the dawn of the pan-genomic era in crop research (J. Shi et al., 2023). Using the pan-genome as a reference enables the identification of novel loci associated with important traits and enhances genomic analysis by uncovering additional genetic diversity and valuable genes with high precision.

Undoubtedly, pan-genome research could encourage the utilization of population DNA sequences to replace or supplement single linear genomes, making genetic analysis more efficient (Bayer et al., 2020). However, the main limitations of plant pangenomes stem from high computational costs, difficulties in managing complex genomes and repetitive sequences, and the lack of mature tools for advanced analysis. These challenges hinder the accurate representation of genetic diversity and the effective application of pangenome

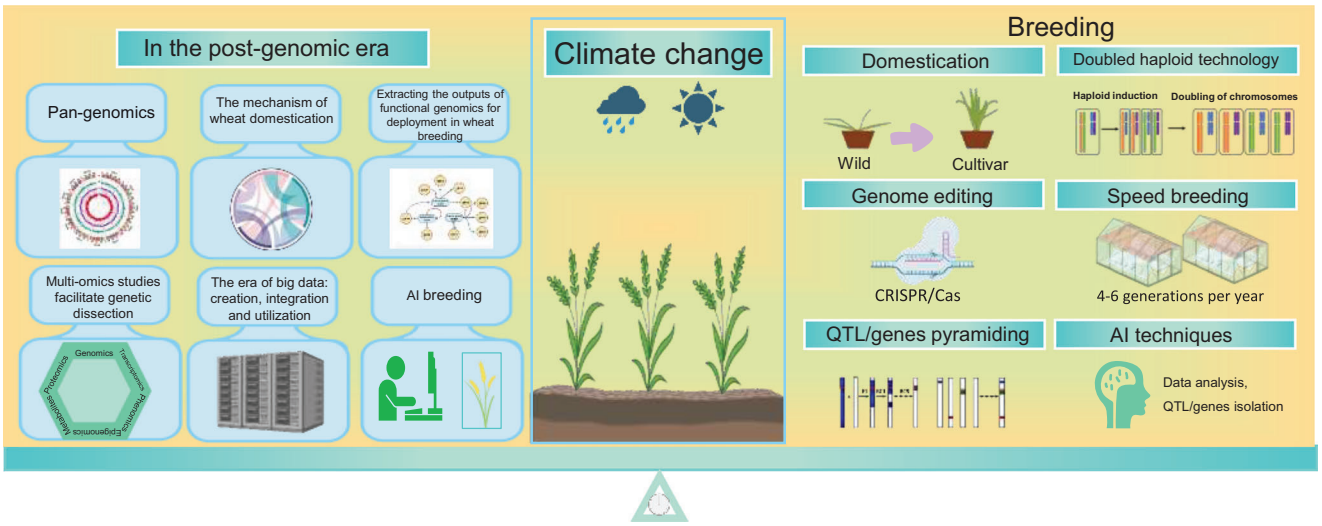

FIGURE 3 Major research areas in the post-genomic era of wheat. This diagram highlights pan-genomics, the mechanism of wheat domestication, extracting the outputs of functional genomics for deployment in wheat breeding, multi-omics studies facilitate genetic dissection, the era of big data: creation, integration and utilization, and artificial intelligence (AI) breeding, along with modern breeding techniques, will significantly contribute to advancing wheat breeding.

data in breeding programs. To fully utilize and benefit from this valuable resource, future research should shed light on the following: (i) grouping all the available genome sequences, one can create nonredundant pan-genome sequences; (ii) providing deep annotation for identified variable and core sequences/genes; and (iii) aligning all genomes to a high-quality backbone genome to identify variations and construct a graph pangenome.

3.2 | The mechanism of wheat domestication

Wheat is a polyploid species consisting of diploids, tetraploids, and hexaploids, making it an ideal model organism for studying the evolutionary dynamics of allopolyploid speciation, adaptation, and plant domestication (Han et al., 2025; Venske et al., 2019; Z. Wang et al., 2023). Domestication has led to genetic modifications in key traits such as brittle rachis, persistent glume, and non-free threshability, with several significant genes identified. Until now, only a small portion of chromosomal regions, or syndrome factors, are involved in wheat domestication. Following the completion of genome assemblies for diploid wheat species (*T. urartu* and *A. tauschii*), more domestication-associated genes are expected to be discovered, providing deeper insights into wheat's domestication process. To address this challenge, breeders must leverage wheat biodiversity and wild wheat species to preserve a diverse gene pool.

Key areas for future domestication research are (i) unraveling the connection between genomic and epigenomic diversity in the regulatory roles of noncoding genomes, (ii) identifying further functional and regulatory genes that were lost from the cultivars during the domestication process, and (iii) enhancing genetic diversity through the reintroduction of absent genes from wild relatives.

3.3 | Extracting the outputs of functional genomics for deployment in wheat breeding

QTL/genes discovery is accelerated due to the advent of genomics, yet there is a gap of efficient application of these discoveries in breeding programs (Purugganan & Jackson, 2021). For example, finding functional genes has become relatively straightforward, but integrating several favorable alleles together in combinations into a single variety for improved agronomic traits performance remains difficult and limited, especially for complex inherited traits.

Applying functional genomics to wheat breeding, unsolvable issues still hinder the translational progress. For instance, how can larger numbers of alleles be effectively utilized in breeding? How can the trade-offs among desired traits be balanced? To address these challenges and advance wheat breeding goals, it will be essential to prioritize the development of robust models and algorithms, as well as to creatively integrating different types of data (genomic, phenotypic, epigenomic, etc.), taking into account nonlinear interactions, including genotype-by-environment effects in genomic selection and genomic prediction approaches.

Historically, wheat improvement has largely been a mechanical process, centered on quantitative genetic breeding parameters and/or phenotypic observations. With a few notable exceptions, the molecular basis of agronomically significant traits or phenotypes have yet not been well under-

stood. Molecular geneticists have advanced in revealing the genetic foundation of specific traits, including flowering time, root branch, photosynthesis, and stress reaction. The challenge now lies in consistently applying this knowledge to practical wheat improvement. Advances in genomic technologies and computational methods are expanding the ability to investigate critical wheat traits, which could lead to more effective breeding practices.

3.4 | Multi-omics studies facilitate genetic dissection

The rapid accumulation of multi-omics data has ushered in the era of interactome big data for wheat genome research, enabling integrated analyses of wheats' genetic complexity. Apart from genomics, additional omics methodologies such as transcriptomics, proteomics, metabolomics, epigenomics, and phenomics (often combined with high-throughput sequencing strategies, ChIP-seq, CUT&Tag, and ATAC-seq etc.) now allow for precise measurement of thousands of corresponding elements simultaneously. Traditionally, each data type such as DNA, RNA, protein, or metabolite profiles, has been analyzed individually (Rhaman et al., 2024). DNA is the genetic material that carries instructions for an organism's development and function. RNA translates these instructions into proteins, which are essential for protein synthesis. Proteins perform various functions in the cell, such as catalyzing reactions and regulating biological processes. Cross-talk between multiple groups has not yet been correlated in research. The incorporation of multi-omics datasets holds great potential for discovering QTL/genes, elucidating regulatory networks and for predictive breeding. In the wheat variety Fielder, RNA-seq, ATAC-seq, and CUT&Tag techniques were employed to analyze transcriptional and chromatin changes during the early regeneration stages from the scutellum of immature embryos. It was discovered that 446 important transcription factors dominated the process of promoting wheat regeneration (X. Liu et al., 2023). Furthermore, epigenomic landscapes of the leaf, axillary bud, and shoot apex were created during wheat vernalization through combining RNA-seq, ATAC-seq, and ChIP-seq, revealing unique responses in various tissues. Making use of a range of complimentary functional data, including transcription factor binding, gene expression, chromatin accessibility, sequence motif, and regulation that has been conserved over time, wheat integrative gene regulatory network (wGRN) platform (http://wheat.cau.edu.cn/wGRN/) was built for exploring regulatory networks and discovering trait-associated genes (Y. Chen et al., 2023).

Spatiotemporal transcriptomics (ST) analysis, as a method for multi-omics, has been developing rapidly, with an increasing number of articles highlighting remarkable progress in revealing plant cell development and differentiation, biosynthetic pathways, responses to biotic and abiotic stresses, and analyzing cell type differentiation across species (Yin et al., 2023; X. Yu et al., 2023). By sequencing the single-cell transcriptome of plants, researchers gain insights into gene expression at various growth stages and under different environmental conditions. This precise genomic information helps identify key genes associated with plant traits and reveals the mechanisms underlying plant responses to adversity (e.g., drought, salinity, disease, etc.). In combination with single-cell transcriptome sequencing (single-cell RNA sequencing [scRNA-seq]), it enables the examination of cellular heterogeneity, classification of cell types, and establishment of cell lineages (Mo & Jiao, 2022; Shahan et al., 2022). Nonetheless, scRNA-seq demands cell dissociation from tissues, leading to a loss of spatial context. Conversely, ST allows for the analysis of single-cell heterogeneity and identification of cell types while preserving spatial information. The emergence of ST has led to discoveries in various fields. Using spatial location data from stereo-seq, researchers have differentiated different epidermal cells, together with palisade and sponge mesophyll cells. Additionally, these findings provide a wealth of markers for different types of leaf cells (Xia et al., 2022). ST application to wheat research is lacking and future efforts will need to address several issues: how to distinguish different tissue structures, how to simplify sample preparation, how to enhance capture efficiency with optimized statistical analysis, and how to handle the large amounts of data generated. In addition, the integration of multi-omics studies with plant single-cell transcriptome sequencing, in conjunction with other sequencing methods, will enable comprehensive and in-depth investigations of plants from various perspectives. Integrating multi-omics provides a comprehensive perspective on wheat research, but the associated costs can be a significant barrier for many researchers. To address this, cost-effective data integration methods utilizing existing tools and resources should be recommended. Promoting collaboration among researchers and institutions can also enhance access to shared resources and expertise, making multi-omics integration more feasible. Additionally, leveraging open-source software and publicly available datasets can help lower costs while still enabling robust analyses.

Multi-omics data are essential for better understanding wheat biology and isolating more efficient targets for wheat improvement. Future directions should focus on (i) choosing an appropriate data integration approach based on the biological question and the types of omics data available and (ii) conducting statistical and computational analyses to identify genes, proteins, metabolites, or other molecular features that are differentially expressed between conditions.

TABLE 2 Representative databases and tools for wheat research.

Database	Description	Website
GrainGenes	A database for Triticeae and *Avena*	http://wheat.pw.usda.gov
IWGSC	International Wheat Genome Sequencing Consortium	http://www.wheatgenome.org/
KOMUGI	Wheat Genetic Resources Database	https://shigen.nig.ac.jp/wheat/komugi/about/about.jsp
MASwheat	Marker-assisted selection in wheat	https://maswheat.ucdavis.edu/
TGT	Triticeae-GeneTribe	http://wheat.cau.edu.cn/TGT/
wGRN	A platform using wheat integrative regulatory networks to guide functional gene discovery	http://wheat.cau.edu.cn/wGRN/
WGVD	Wheat Genome Variation Database and selective signatures	https://db.cngb.org/WGVD/
WheatCNVb	Database of read depth based fingerprint in wheat	http://wheat.cau.edu.cn/WheatCNVb/
WheatComp Database	Genetic relationship information database for wheat germplasms	http://wheat.cau.edu.cn/WheatCompDB
WheatIS	International Wheat Information System	http://www.wheatis.org/
WheatOmics 1.0	A platform combining multiple omics data to accelerate functional genomics studies	http://wheatomics.sdau.edu.cn/
Wheat Proteome:	The Harvey Millar Group	https://wheatproteome.org/
Wheat SnpHub Portal	Genomic variation datasets of wheat and its progenitors	http://wheat.cau.edu.cn/Wheat_SnpHub_Portal/

3.5 | The era of big data: Creation, integration and utilization

As the era of big data progresses, numerous high-quality wheat single- and multi-omics databases have been established worldwide (Table 2), covering genomics, transcriptomics, proteomics, metabolomics, and phenomics data. This has transformed wheat biology into an information-intensive field. However, a major challenge remains in efficiently creating, integrating, and utilizing this vast amount of data. The datasets include complex multidimensional data, such as multilocation, multiyear, and multi-trait information, reflecting crop growth, responses to various stresses, and other environmental factors. For example, phenomics data (measured dynamically across crop cycles) encompass a wide range of phenotypic traits, including growth parameters, yield, and physiological responses. Such rich datasets offer valuable insights into the interactions between genetics, environment, and management practices, and are crucial for understanding the adaptive capacity of organisms under changing conditions.

For data integration, traditional data processing methods are no longer able to cope with the demands of modern big data. From local to international, there is also a pressing urgency to develop new platforms and algorithms to manage this complex data. The following measures can be taken: (i) establish efficient big data platforms for management, (ii) develop innovative data processing machine learning algorithms, (iii) build specialize tools and algorithms to enable cross-domain data integration and to mine useful information from it, (iv) optimize existed computational methods to make them more efficient and adaptable to large-scale data, and (v) produce visualization tools that can cope with high-dimensional data and large-scale data.

3.6 | AI breeding

AI is transforming several scientific fields and is well-known for its capabilities in large data analysis and pattern identification, including crop breeding (Farooq et al., 2024; C. Zhang et al., 2023). AI in crop breeding is increasingly at the forefront of modern agriculture, playing a key role in addressing climate change and improving production efficiency. Traditional breeding methods are often time-consuming, costly, and reliant on extensive trials and screening, whereas AI-driven breeding technologies accelerate and optimize the breeding process through machine learning. AI can analyze large volumes of genomic data, phenotypic information, and environmental factors, helping breeders predict relationships between plant traits and genes (Harfouche et al., 2019; Xu et al., 2022). However, AI breeding holds significant promise for advancing agricultural practices, yet its effectiveness remains uncertain due to several critical factors. One major concern is the dependence of machine learning models on the quality and representativeness of training data. If the data are biased or lack diversity, the models may yield misleading predictions, potentially resulting in ineffective breeding decisions. In addition, the biological complexity of plants and the variable environmental interactions complicate the accurate modeling of breeding outcomes, emphasizing the need for comprehensive datasets that capture genetic variability and real-world conditions. Furthermore, many traditional

breeders may lack the technical expertise in data science necessary to adopt these AI-driven technologies, which can hinder their integration into existing workflows. By addressing these challenges and enhancing understanding of AI's capabilities and limitations, the agricultural community can make informed decisions, ultimately improving productivity and sustainability in breeding programs. This will make breeding more digital and intelligent, ushering in a new era of AI breeding.

The combination of big data and AI is seen as the promise of a second green revolution. However, several concerns need to be addressed: (i) How can AI-assisted breeding be applied from theoretical study and evaluation to the practical breeding process? (ii) How can we predict which trait, thus streamlining the selection process? (iii) How can models be developed to predict the performance of different breeding strategies across various environmental conditions, helping breeders make informed decisions prior to conducting actual field trials? (iv) How can we effectively achieve data collection, storage, and utilization, thereby enhancing breeding information systems? In short, AI-driven breeding technologies offer new opportunities for modern agriculture, not only shortening the breeding cycle, but also dramatically improving crop productivity and environmental adaptability.

4 | CONCLUSION

While several aspects of wheat genomics have been summarized in previous reviews (Gupta et al., 2008; Haas et al., 2019; Tiwari et al., 2024). This review provides a chronological and comprehensive summary of the progress made in wheat genome over the past few decades and it offers a wealth of insightful and up-to-date perspectives on significant scientific issues based on the most recent research findings.

Conducting wheat genome research at an unprecedented pace allows wheat genomic resources and new technologies to accomplish critical goals. Over the past decades, the primary objectives of wheat genomics have included genome sequencing, functional genomics, epigenomics, and molecular genetics. With rapid technological advancements, the Gordian knot in wheat research can be untangled, revealing new insights into the genome diversity of wheat, gene networks, enable big data analytics, allowing environmental adaptation through predictive breeding.

In addition, more cutting-edge technologies, such as genome editing and AI techniques, will be integrated to completely transform wheat breeding methods. To address the challenges of population growth and climate change, we ultimately anticipate that the rapid advancement of wheat genome will accelerate and transform crop breeding.

AUTHOR CONTRIBUTIONS

Shaoshuai Liu: Conceptualization; funding acquisition; writing—original draft. **Shuaifeng Geng**: Conceptualization; funding acquisition; writing—original draft. **Susanne Dreisigacker**: Supervision; writing—review and editing.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ORCID

Shaoshuai Liu https://orcid.org/0009-0002-2851-7995
Susanne Dreisigacker https://orcid.org/0000-0002-3546-5989

REFERENCES

Ahmar, S., Hensel, G., & Gruszka, D. (2023). CRISPR/Cas9-mediated genome editing techniques and new breeding strategies in cereals—Current status, improvements, and perspectives. *Biotechnology Advances*, *69*, 108248. https://doi.org/10.1016/j.biotechadv.2023.108248

Ahmed, H. I., Heuberger, M., Schoen, A., Koo, D. H., Quiroz-Chavez, J., Adhikari, L., Raupp, J., Cauet, S., Rodde, N., Cravero, C., Callot, C., Lazo, G. R., Kathiresan, N., Sharma, P. K., Moot, I., Yadav, I. S., Singh, L., Saripalli, G., Rawat, N., … Krattinger, S. G. (2023). Einkorn genomics sheds light on history of the oldest domesticated wheat. *Nature*, *620*(7975), 830–838. https://doi.org/10.1038/s41586-023-06389-7

Akpinar, B. A., Leroy, P., Watson-Haigh, N., Baumann, U., Barbe, V., & Budak, H. (2022). The complete genome sequence of elite bread wheat cultivar, "Sonmez". *F1000Research*, *11*, 614. https://doi.org/10.12688/f1000research.121637.1

Arora, S., Steuernagel, B., Gaurav, K., Chandramohan, S., Long, Y., Matny, O., Johnson, R., Enk, J., Periyannan, S., Singh, N., Asyraf Md Hatta, M., Athiyannan, N., Cheema, J., Yu, G., Kangara, N., Ghosh, S., Szabo, L. J., Poland, J., Bariana, H., … Wulff, B. B. H. (2019). Resistance gene cloning from a wild crop relative by sequence capture and association genetics. *Nature Biotechnology*, *37*(2), 139–143. https://doi.org/10.1038/s41587-018-0007-9

Athiyannan, N., Abrouk, M., Boshoff, W. H. P., Cauet, S., Rodde, N., Kudrna, D., Mohammed, N., Bettgenhaeuser, J., Botha, K. S., Derman, S. S., Wing, R. A., Prins, R., & Krattinger, S. G. (2022). Long-read genome sequencing of bread wheat facilitates disease resistance gene cloning. *Nature Genetics*, *54*(3), 227–231. https://doi.org/10.1038/s41588-022-01022-1

Aury, J.-M., Engelen, S., Istace, B., Monat, C., Lasserre-Zuber, P., Belser, C., Cruaud, C., Rimbert, H., Leroy, P., Arribat, S., Dufau, I., Bellec, A., Grimbichler, D., Papon, N., Paux, E., Ranoux, M., Alberti, A., Wincker, P., & Choulet, F. (2022). Long-read and chromosome-scale assembly of the hexaploid wheat genome achieves high resolution for research and breeding. *GigaScience*, *11*, giac034. https://doi.org/10.1093/gigascience/giac034

Avni, R., Lux, T., Minz-Dub, A., Millet, E., Sela, H., Distelfeld, A., Deek, J., Yu, G., Steuernagel, B., Pozniak, C., Ens, J., Gundlach, H., Mayer, K. F. X., Himmelbach, A., Stein, N., Mascher, M., Spannagl, M., Wulff, B. B. H., & Sharon, A. (2022). Genome sequences of three *Aegilops* species of the section Sitopsis reveal phylogenetic

relationships and provide resources for wheat improvement. *The Plant Journal*, *110*(1), 179–192. https://doi.org/10.1111/tpj.15664

Avni, R., Nave, M., Barad, O., Baruch, K., Twardziok, S. O., Gundlach, H., Hale, I., Mascher, M., Spannagl, M., Wiebe, K., Jordan, K. W., Golan, G., Deek, J., Ben-Zvi, B., Ben-Zvi, G., Himmelbach, A., MacLachlan, R. P., Sharpe, A. G., Fritz, A., … Distelfeld, A. (2017). Wild emmer genome architecture and diversity elucidate wheat evolution and domestication. *Science*, *357*(6346), 93–97. https://doi.org/10.1126/science.aan0032

Awan, M. J. A., Pervaiz, K., Rasheed, A., Amin, I., Saeed, N. A., Dhugga, K. S., & Mansoor, S. (2022). Genome edited wheat—Current advances for the second green revolution. *Biotechnology Advances*, *60*, 108006. https://doi.org/10.1016/j.biotechadv.2022.108006

Bayer, P. E., Golicz, A. A., Scheben, A., Batley, J., & Edwards, D. (2020). Plant pan-genomes are the new reference. *Nature Plants*, *6*(8), 914–920. https://doi.org/10.1038/s41477-020-0733-0

Bibi, F., & Rahman, A. (2023). An overview of climate change impacts on agriculture and their mitigation strategies. *Agriculture*, *13*(8), 1508. https://doi.org/10.3390/agriculture13081508

Biesiekierski, J. R. (2017). What is gluten?. *Journal of Gastroenterology and Hepatology*, *32*(S1), 78–81. https://doi.org/10.1111/jgh.13703

Brinton, J., & Uauy, C. (2019). A reductionist approach to dissecting grain weight and yield in wheat. *Journal of Integrative Plant Biology*, *61*(3), 337–358. https://doi.org/10.1111/jipb.12741

Burridge, A. J., Winfield, M., Przewieslik-Allen, A., Edwards, K. J., Siddique, I., Barral-Arca, R., Griffiths, S., Cheng, S., Huang, Z., Feng, C., Dreisigacker, S., Bentley, A. R., Brown-Guedira, G., & Barker, G. L. (2024). Development of a next generation SNP genotyping array for wheat. *Plant Biotechnology Journal*, *22*(8), 2235–2247. https://doi.org/10.1111/pbi.14341

Cavalet-Giorsa, E., Gonzalez-Munoz, A., Athiyannan, N., Holden, S., Salhi, A., Gardener, C., Quiroz-Chavez, J., Rustamova, S. M., Elkot, A. F., Patpour, M., Rasheed, A., Mao, L., Lagudah, E. S., Periyannan, S. K., Sharon, A., Himmelbach, A., Reif, J. C., Knauft, M., Mascher, M., … Krattinger, S. G. (2024). Origin and evolution of the bread wheat D genome. *Nature*, *633*(8031), 848–855. https://doi.org/10.1038/s41586-024-07808-z

Chen, K., Wang, Y., Zhang, R., Zhang, H., & Gao, C. (2019). CRISPR/Cas genome editing and precision plant breeding in agriculture. *Annual Review of Plant Biology*, *70*, 667–697. https://doi.org/10.1146/annurev-arplant-050718-100049

Chen, Y., Guo, Y., Guan, P., Wang, Y., Wang, X., Wang, Z., Qin, Z., Ma, S., Xin, M., Hu, Z., Yao, Y., Ni, Z., Sun, Q., Guo, W., & Peng, H. (2023). A wheat integrative regulatory network from large-scale complementary functional datasets enables trait-associated gene discovery for crop improvement. *Molecular Plant*, *16*(2), 393–414. https://doi.org/10.1016/j.molp.2022.12.019

Cheng, S., Feng, C., Wingen, L. U., Cheng, H., Riche, A. B., Jiang, M., Leverington-Waite, M., Huang, Z., Collier, S., Orford, S., Wang, X., Awal, R., Barker, G., O'Hara, T., Lister, C., Siluveru, A., Quiroz-Chavez, J., Ramirez-Gonzalez, R. H., Bryant, R., … Griffiths, S. (2024). Harnessing landrace diversity empowers wheat breeding. *Nature*, *632*(8026), 823–831. https://doi.org/10.1038/s41586-024-07682-9

Choulet, F., Alberti, A., Theil, S., Glover, N., Barbe, V., Daron, J., Pingault, L., Sourdille, P., Couloux, A., Paux, E., Leroy, P., Mangenot, S., Guilhot, N., Le Gouis, J., Balfourier, F., Alaux, M., Jamilloux, V., Poulain, J., Durand, C., … Feuillet, C. (2014). Structural and functional partitioning of bread wheat chromosome 3B. *Science*, *345*(6194), 1249721. https://doi.org/10.1126/science.1249721

Colasuonno, P., Marcotuli, I., Gadaleta, A., & Soriano, J. M. (2021). From genetic maps to QTL cloning: An overview for durum wheat. *Plants (Basel)*, *10*(2), 315. https://doi.org/10.3390/plants10020315

Concia, L., Veluchamy, A., Ramirez-Prado, J. S., Martin-Ramirez, A., Huang, Y., Perez, M., Domenichini, S., Rodriguez Granados, N. Y., Kim, S., Blein, T., Duncan, S., Pichot, C., Manza-Mianza, D., Juery, C., Paux, E., Moore, G., Hirt, H., Bergounioux, C., Crespi, M., … Benhamed, M. (2020). Wheat chromatin architecture is organized in genome territories and transcription factories. *Genome Biology*, *21*(1), 104. https://doi.org/10.1186/s13059-020-01998-1

Delorean, E., Gao, L., Lopez, J. F. C., Wulff, B. B. H., Ibba, M. I., & Poland, J. (2021). High molecular weight glutenin gene diversity in *Aegilops tauschii* demonstrates unique origin of superior wheat quality. *Communications Biology*, *4*(1), 1242. https://doi.org/10.1038/s42003-021-02563-7

Dreisigacker, S., Crossa, J., Pérez-Rodríguez, P., Montesinos-López, O. A., Rosyara, U., Juliana, P., Mondal, S., Crespo-Herrera, L., Govindan, V., Singh, R. P., & Braun, H. J. (2021). Implementation of genomic selection in the CIMMYT global wheat program, findings from the past 10 years. *Crop Breeding, Genetics and Genomics*, *3*(2), e210004. https://doi.org/10.20900/cbgg20210005

Farooq, M. A., Gao, S., Hassan, M. A., Huang, Z., Rasheed, A., Hearne, S., Prasanna, B., Li, X., & Li, H. (2024). Artificial intelligence in plant breeding. *Trends in Genetics*, *40*(10), 891–908. https://doi.org/10.1016/j.tig.2024.07.001

Gao, L., Meng, C., Yi, T., Xu, K., Cao, H., Zhang, S., Yang, X., & Zhao, Y. (2021). Genome-wide association study reveals the genetic basis of yield- and quality-related traits in wheat. *BMC Plant Biology*, *21*(1), 144. https://doi.org/10.1186/s12870-021-02925-7

Gao, Y., An, K., Guo, W., Chen, Y., Zhang, R., Zhang, X., Chang, S., Rossi, V., Jin, F., Cao, X., Xin, M., Peng, H., Hu, Z., Guo, W., Du, J., Ni, Z., Sun, Q., & Yao, Y. (2021). The endosperm-specific transcription factor TaNAC019 regulates glutenin and starch accumulation and its elite allele improves wheat grain quality. *The Plant Cell*, *33*(3), 603–622. https://doi.org/10.1093/plcell/koaa040

Gasparis, S., & Miłoszewski, M. M. (2023). Genetic basis of grain size and weight in rice, wheat, and barley. *International Journal of Molecular Sciences*, *24*(23), 16921. https://doi.org/10.3390/ijms242316921

Gaurav, K., Arora, S., Silva, P., Sánchez-Martín, J., Horsnell, R., Gao, L., Brar, G. S., Widrig, V., John Raupp, W., & Singh, N. (2022). Population genomic analysis of *Aegilops tauschii* identifies targets for bread wheat improvement. *Nature Biotechnology*, *40*(3), 422–431. https://doi.org/10.1038/s41587-021-01058-4

Geng, S., Kong, X., Song, G., Jia, M., Guan, J., Wang, F., Qin, Z., Wu, L., Lan, X., Li, A., & Mao, L. (2019). DNA methylation dynamics during the interaction of wheat progenitor *Aegilops tauschii* with the obligate biotrophic fungus *Blumeria graminis* f. sp. *tritici*. *New Phytologist*, *221*(2), 1023–1035. https://doi.org/10.1111/nph.15432

Guo, W., Xin, M., Wang, Z., Yao, Y., Hu, Z., Song, W., Yu, K., Chen, Y., Wang, X., Guan, P., Appels, R., Peng, H., Ni, Z., & Sun, Q. (2020). Origin and adaptation to high altitude of Tibetan semi-wild wheat. *Nature Communications*, *11*(1), 5085. https://doi.org/10.1038/s41467-020-18738-5

Guo, X., & Han, F. (2014). Asymmetric epigenetic modification and elimination of rDNA sequences by polyploidization in wheat.

The Plant Cell, *26*(11), 4311–4327. https://doi.org/10.1105/tpc.114.129841

Gupta, P. K., Mir, R. R., Mohan, A., & Kumar, J. (2008). Wheat genomics: Present status and future prospects. *International Journal of Plant Genomics*, *2008*, 896451. https://doi.org/10.1155/2008/896451

Gutaker, R. M., & Purugganan, M. D. (2024). Adaptation and the geographic spread of crop species. *Annual Review of Plant Biology*, *75*(1), 679–706. https://doi.org/10.1146/annurev-arplant-060223-030954

Haas, M., Schreiber, M., & Mascher, M. (2019). Domestication and crop evolution of wheat and barley: Genes, genomics, and future directions. *Journal of Integrative Plant Biology*, *61*(3), 204–225. https://doi.org/10.1111/jipb.12737

Han, G., Yan, H., Li, L., & An, D. (2025). Advancing wheat breeding using rye: A key contribution to wheat breeding history. *Trends in Biotechnology*, *43*(9), 2170–2183. https://doi.org/10.1016/j.tibtech.2025.03.008

Harfouche, A. L., Jacobson, D. A., Kainer, D., Romero, J. C., Harfouche, A. H., Scarascia Mugnozza, G., Moshelion, M., Tuskan, G. A., Keurentjes, J. J. B., & Altman, A. (2019). Accelerating climate resilient plant breeding by applying next-generation artificial intelligence. *Trends in Biotechnology*, *37*(11), 1217–1235. https://doi.org/10.1016/j.tibtech.2019.05.007

He, F., Pasam, R., Shi, F., Kant, S., Keeble-Gagnere, G., Kay, P., Forrest, K., Fritz, A., Hucl, P., Wiebe, K., Knox, R., Cuthbert, R., Pozniak, C., Akhunova, A., Morrell, P. L., Davies, J. P., Webb, S. R., Spangenberg, G., Hayes, B., … Akhunov, E. (2019). Exome sequencing highlights the role of wild-relative introgression in shaping the adaptive landscape of the wheat genome. *Nature Genetics*, *51*(5), 896–904. https://doi.org/10.1038/s41588-019-0382-2

Huang, F., Li, X.-S., Du, X.-Y., Li, S.-C., Li, N.-N., Lü, Y.-J., Zou, S.-K., Zhang, Q., Wang, L.-N., Ni, Z.-F., Han, Y.-L., & Xing, J.-W. (2023). SNP-based identification of QTLs for thousand-grain weight and related traits in wheat 8762/Keyi 5214 DH lines. *Journal of Integrative Agriculture*, *22*(10), 2949–2960. https://doi.org/10.1016/j.jia.2023.03.004

Huang, X., Huang, S., Han, B., & Li, J. (2022). The integrated genomics of crop domestication and breeding. *Cell*, *185*(15), 2828–2839. https://doi.org/10.1016/j.cell.2022.04.036

Igolkina, A. A., Vorbrugg, S., Rabanal, F. A., Liu, H.-J., Ashkenazy, H., Kornienko, A. E., Fitz, J., Collenberg, M., Kubica, C., Morales, A. M., Jaegle, B., Wrightsman, T., Voloshin, V., Llaca, V., Nizhynska, V., Reichardt, I., Lanz, C., Bemm, F., Flood, P. J., … Nordborg, M. (2024). Towards an unbiased characterization of genetic polymorphism. *bioRxiv*. https://doi.org/10.1101/2024.05.30.596703

IWGSC. (2014). A chromosome-based draft sequence of the hexaploid bread wheat (*Triticum aestivum*) genome. *Science*, *345*(6194), 1251788. https://doi.org/10.1126/science.1251788

IWGSC. (2018). Shifting the limits in wheat research and breeding using a fully annotated reference genome. *Science*, *361*(6403), eaar7191. https://doi.org/10.1126/science.aar7191

Jia, J., Zhao, G., Li, D., Wang, K., Kong, C., Deng, P., Yan, X., Zhang, X., Lu, Z., Xu, S., Jiao, Y., Chong, K., Liu, X., Cui, D., Li, G., Zhang, Y., Du, C., Wu, L., Li, T., … Gao, L. (2023). Genome resources for the elite bread wheat cultivar Aikang 58 and mining of elite homeologous haplotypes for accelerating wheat improvement. *Molecular Plant*, *16*(12), 1893–1910. https://doi.org/10.1016/j.molp.2023.10.015

Jia, J., Zhao, S., Kong, X., Li, Y., Zhao, G., He, W., Appels, R., Pfeifer, M., Tao, Y., Zhang, X., Jing, R., Zhang, C., Ma, Y., Gao, L., Gao, C., Spannagl, M., Mayer, K. F. X., Li, D., Pan, S., … International Wheat Genome Sequencing Consortium. (2013). *Aegilops tauschii* draft genome sequence reveals a gene repertoire for wheat adaptation. *Nature*, *496*(7443), 91–95. https://doi.org/10.1038/nature12028

Jiao, C., Xie, X., Hao, C., Chen, L., Xie, Y., Garg, V., Zhao, L., Wang, Z., Zhang, Y., Li, T., Fu, J., Chitikineni, A., Hou, J., Liu, H., Dwivedi, G., Liu, X., Jia, J., Mao, L., Wang, X., … Zhang, X. (2024). Pan-genome bridges wheat structural variations with habitat and breeding. *Nature*, *637*(8045), 384–393. https://doi.org/10.1038/s41586-024-08277-0

Juliana, P., Poland, J., Huerta-Espino, J., Shrestha, S., Crossa, J., Crespo-Herrera, L., Toledo, F. H., Govindan, V., Mondal, S., Kumar, U., Bhavani, S., Singh, P. K., Randhawa, M. S., He, X., Guzman, C., Dreisigacker, S., Rouse, M. N., Jin, Y., Pérez-Rodríguez, P., … Singh, R. P. (2019). Improving grain yield, stress resilience and quality of bread wheat using large-scale genomics. *Nature Genetics*, *51*(10), 1530–1539. https://doi.org/10.1038/s41588-019-0496-6

Kale, S. M., Schulthess, A. W., Padmarasu, S., Boeven, P. H. G., Schacht, J., Himmelbach, A., Steuernagel, B., Wulff, B. B. H., Reif, J. C., Stein, N., & Mascher, M. (2022). A catalogue of resistance gene homologs and a chromosome-scale reference sequence support resistance gene mapping in winter wheat. *Plant Biotechnology Journal*, *20*(9), 1730–1742. https://doi.org/10.1111/pbi.13843

Kohler, C., & Springer, N. (2017). Plant epigenomics-deciphering the mechanisms of epigenetic inheritance and plasticity in plants. *Genome Biology*, *18*(1), 132. https://doi.org/10.1186/s13059-017-1260-9

Kong, X., Wang, F., Wang, Z., Gao, X., Geng, S., Deng, Z., Zhang, S., Fu, M., Cui, D., Liu, S., Che, Y., Liao, R., Yin, L., Zhou, P., Wang, K., Ye, X., Liu, D., Fu, X., Mao, L., & Li, A. (2023). Grain yield improvement by genome editing of TaARF12 that decoupled peduncle and rachis development trajectories via differential regulation of gibberellin signalling in wheat. *Plant Biotechnology Journal*, *21*(10), 1990–2001. https://doi.org/10.1111/pbi.14107

Kumar, J., Mishra, A., Kumar, A., Kaur, G., Sharma, H., Kaur, S., Sharma, S., Devi, K., Garg, M., Pandey, A. K., Bishnoi, M., Pareek, A., & Roy, J. (2022). Whole genome re-sequencing of Indian wheat genotypes for identification of genomic variants for grain iron and zinc content. *Molecular Biology Reports*, *49*(7), 7123–7133. https://doi.org/10.1007/s11033-022-07593-w

Levy, A. A., & Feldman, M. (2022). Evolution and origin of bread wheat. *The Plant Cell*, *34*(7), 2549–2567. https://doi.org/10.1093/plcell/koac130

Li, A., Hao, C., Wang, Z., Geng, S., Jia, M., Wang, F., Han, X., Kong, X., Yin, L., Tao, S., Deng, Z., Liao, R., Sun, G., Wang, K., Ye, X., Jiao, C., Lu, H., Zhou, Y., Liu, D., … Mao, L. (2022). Wheat breeding history reveals synergistic selection of pleiotropic genomic sites for plant architecture and grain yield. *Molecular Plant*, *15*(3), 504–519. https://doi.org/10.1016/j.molp.2022.01.004

Li, G., Ren, Y., Yang, Y., Chen, S., Zheng, J., Zhang, X., Li, J., Chen, M., Sun, X., Lv, C., Li, X., Zhang, B., Sun, X., Li, Y., Zhao, M., Dong, C., Tang, J., Huang, Z., Peng, Y., … Yin, G. (2024). Genomic analysis of Zhou8425B, a key founder parent, reveals its genetic contributions to elite agronomic traits in wheat breeding. *Plant Communications*, *6*(3), 101222. https://doi.org/10.1016/j.xplc.2024.101222

Li, G., Wang, L., Yang, J., He, H., Jin, H., Li, X., Ren, T., Ren, Z., Li, F., Han, X., Zhao, X., Dong, L., Li, Y., Song, Z., Yan, Z., Zheng, N., Shi, C., Wang, Z., Yang, S., … Wang, D. (2021). A high-quality genome

assembly highlights rye genomic characteristics and agronomically important genes. *Nature Genetics*, *53*(4), 574–584. https://doi.org/10.1038/s41588-021-00808-z

Li, L. F., Zhang, Z. B., Wang, Z. H., Li, N., Sha, Y., Wang, X. F., Ding, N., Li, Y., Zhao, J., Wu, Y., Gong, L., Mafessoni, F., Levy, A. A., & Liu, B. (2022). Genome sequences of five Sitopsis species of *Aegilops* and the origin of polyploid wheat B subgenome. *Molecular Plant*, *15*(3), 488–503. https://doi.org/10.1016/j.molp.2021.12.019

Ling, H. Q., Ma, B., Shi, X., Liu, H., Dong, L., Sun, H., Cao, Y., Gao, Q., Zheng, S., Li, Y., Yu, Y., Du, H., Qi, M., Li, Y., Lu, H., Yu, H., Cui, Y., Wang, N., Chen, C., … Liang, C. (2018). Genome sequence of the progenitor of wheat A subgenome *Triticum urartu*. *Nature*, *557*(7705), 424–428. https://doi.org/10.1038/s41586-018-0108-0

Liu, S., Li, K., Dai, X., Qin, G., Lu, D., Gao, Z., Li, X., Song, B., Bian, J., Ren, D., Liu, Y., Chen, X., Xu, Y., Liu, W., Yang, C., Liu, X., Chen, S., Li, J., Li, B., … Deng, X. W. (2025). A telomere-to-telomere genome assembly coupled with multi-omic data provides insights into the evolution of hexaploid bread wheat. *Nature Genetics*, *57*(4), 1008–1020. https://doi.org/10.1038/s41588-025-02137-x

Liu, X., Bie, X. M., Lin, X., Li, M., Wang, H., Zhang, X., Yang, Y., Zhang, C., Zhang, X. S., & Xiao, J. (2023). Uncovering the transcriptional regulatory network involved in boosting wheat regeneration and transformation. *Nature Plants*, *9*(6), 908–925. https://doi.org/10.1038/s41477-023-01406-z

Liu, X., Deng, M., Shi, B., Zhu, K., Chen, J., Xu, S., Bie, X., Zhang, X., Lin, X., & Xiao, J. (2024). Distinct roles of H3K27me3 and H3K36me3 in vernalization response, maintenance, and resetting in winter wheat. *Science China Life Sciences*, *67*(10), 2251–2266. https://doi.org/10.1007/s11427-024-2664-0

Liu, Y., Liu, P., Gao, L., Li, Y., Ren, X., Jia, J., Wang, L., Zheng, X., Tong, Y., Pei, H., & Lu, Z. (2024). Epigenomic identification of vernalization cis-regulatory elements in winter wheat. *Genome Biology*, *25*(1), 200. https://doi.org/10.1186/s13059-024-03342-3

Liu, Y., Yuan, J., Jia, G., Ye, W., Jeffrey Chen, Z., & Song, Q. (2021). Histone H3K27 dimethylation landscapes contribute to genome stability and genetic recombination during wheat polyploidization. *The Plant Journal*, *105*(3), 678–690. https://doi.org/10.1111/tpj.15063

Liu, Z., Yang, F., Deng, C., Wan, H., Tang, H., Feng, J., Wang, Q., Yang, N., Li, J., & Yang, W. (2024). Chromosome-level assembly of the synthetic hexaploid wheat-derived cultivar Chuanmai 104. *Scientific Data*, *11*(1), 670. https://doi.org/10.1038/s41597-024-03527-2

Luo, J., Li, S., Xu, J., Yan, L., Ma, Y., & Xia, L. (2021). Pyramiding favorable alleles in an elite wheat variety in one generation by CRISPR-Cas9-mediated multiplex gene editing. *Molecular Plant*, *14*(6), 847–850. https://doi.org/10.1016/j.molp.2021.03.024

Luo, M. C., Gu, Y. Q., Puiu, D., Wang, H., Twardziok, S. O., Deal, K. R., Huo, N., Zhu, T., Wang, L., Wang, Y., McGuire, P. E., Liu, S., Long, H., Ramasamy, R. K., Rodriguez, J. C., Van, S. L., Yuan, L., Wang, Z., Xia, Z., … Dvorak, J. (2017). Genome sequence of the progenitor of the wheat D genome *Aegilops tauschii*. *Nature*, *551*(7681), 498–502. https://doi.org/10.1038/nature24486

Ma, F., Xu, Y., Wang, R., Tong, Y., Zhang, A., Liu, D., & 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

Maccaferri, M., Harris, N. S., Twardziok, S. O., Pasam, R. K., Gundlach, H., Spannagl, M., Ormanbekova, D., Lux, T., Prade, V. M., Milner, S. G., Himmelbach, A., Mascher, M., Bagnaresi, P., Faccioli, P., Cozzi, P., Lauria, M., Lazzari, B., Stella, A., Manconi, A., … Cattivelli, L. (2019). Durum wheat genome highlights past domestication signatures and future improvement targets. *Nature Genetics*, *51*(5), 885–895. https://doi.org/10.1038/s41588-019-0381-3

Mao, L., Ling, H.-Q., & Wan, J. (2018). Wheat functional genomics research in China: A decade of development. *The Crop Journal*, *6*(1), 1–6. https://doi.org/10.1016/j.cj.2018.01.001

Mei, F., Chen, B., Du, L., Li, S., Zhu, D., Chen, N., Zhang, Y., Li, F., Wang, Z., Cheng, X., Ding, L., Kang, Z., & Mao, H. (2022). A gain-of-function allele of a DREB transcription factor gene ameliorates drought tolerance in wheat. *The Plant Cell*, *34*(11), 4472–4494. https://doi.org/10.1093/plcell/koac248

Mo, Y., & Jiao, Y. (2022). Advances and applications of single-cell omics technologies in plant research. *The Plant Journal*, *110*(6), 1551–1563. https://doi.org/10.1111/tpj.15772

Molero, G., Coombes, B., Joynson, R., Pinto, F., Pinera-Chavez, F. J., Rivera-Amado, C., Hall, A., & Reynolds, M. P. (2023). Exotic alleles contribute to heat tolerance in wheat under field conditions. *Communications Biology*, *6*(1), 21. https://doi.org/10.1038/s42003-022-04325-5

Nguyen, K. L., Grondin, A., Courtois, B., & Gantet, P. (2019). Next-generation sequencing accelerates crop gene discovery. *Trends in Plant Science*, *24*(3), 263–274. https://doi.org/10.1016/j.tplants.2018.11.008

Paraiso, F., Lin, H., Li, C., Woods, D. P., Lan, T., Tumelty, C., Debernardi, J. M., Joe, A., & Dubcovsky, J. (2024). LEAFY and WAPO1 jointly regulate spikelet number per spike and floret development in wheat. *Development*, *151*(15), dev202803. https://doi.org/10.1242/dev.202803

Purugganan, M. D., & Jackson, S. A. (2021). Advancing crop genomics from lab to field. *Nature Genetics*, *53*(5), 595–601. https://doi.org/10.1038/s41588-021-00866-3

Rasheed, A., Liu, J., Appels, R., & He, Z. (2025). Mobilizing Triticeae diversity from gene banks to farmer's field. *Molecular Plant*, *18*(4), 566–569. https://doi.org/10.1016/j.molp.2025.03.006

Rhaman, M. S., Ali, M., Ye, W., & Li, B. (2024). Opportunities and challenges in advancing plant research with single-cell omics. *Genomics, Proteomics & Bioinformatics*, *22*(2), qzae026. https://doi.org/10.1093/gpbjnl/qzae026

Sakuma, S., & Schnurbusch, T. (2020). Of floral fortune: Tinkering with the grain yield potential of cereal crops. *New Phytologist*, *225*(5), 1873–1882. https://doi.org/10.1111/nph.16189

Sato, K., Abe, F., Mascher, M., Haberer, G., Gundlach, H., Spannagl, M., Shirasawa, K., & Isobe, S. (2021). Chromosome-scale genome assembly of the transformation-amenable common wheat cultivar 'Fielder'. *DNA Research*, *28*(3), dsab008. https://doi.org/10.1093/dnares/dsab008

Schneeberger, K. (2014). Using next-generation sequencing to isolate mutant genes from forward genetic screens. *Nature Reviews Genetics*, *15*(10), 662–676. https://doi.org/10.1038/nrg3745

Senapati, N., Semenov, M. A., Halford, N. G., Hawkesford, M. J., Asseng, S., Cooper, M., Ewert, F., van Ittersum, M. K., Martre, P., Olesen, J. E., Reynolds, M., Rotter, R. P., & Webber, H. (2022). Global wheat production could benefit from closing the genetic yield gap. *Nature Food*, *3*(7), 532–541. https://doi.org/10.1038/s43016-022-00540-9

Seong, K., Kumar, R., Lunde, C., & Krasileva, K. (2023). *Chromosome-level genome assembly of Triticum turgidum var 'Kronos'*. Zenodo. https://doi.org/10.5281/zenodo.10215402

Shahan, R., Hsu, C. W., Nolan, T. M., Cole, B. J., Taylor, I. W., Greenstreet, L., Zhang, S., Afanassiev, A., Vlot, A. H. C., Schiebinger, G., Benfey, P. N., & Ohler, U. (2022). A single-cell Arabidopsis root atlas reveals developmental trajectories in wild-type and cell identity mutants. *Developmental Cell*, *57*(4), 543–560.e549. https://doi.org/10.1016/j.devcel.2022.01.008

Sharma, A., Garg, S., Sheikh, I., Vyas, P., & Dhaliwal, H. S. (2020). Effect of wheat grain protein composition on end-use quality. *Journal of Food Science and Technology*, *57*(8), 2771–2785. https://doi.org/10.1007/s13197-019-04222-6

Shi, J., Tian, Z., Lai, J., & Huang, X. (2023). Plant pan-genomics and its applications. *Molecular Plant*, *16*(1), 168–186. https://doi.org/10.1016/j.molp.2022.12.009

Shi, X., Cui, F., Han, X., He, Y., Zhao, L., Zhang, N., Zhang, H., Zhu, H., Liu, Z., Ma, B., Zheng, S., Zhang, W., Liu, J., Fan, X., Si, Y., Tian, S., Niu, J., Wu, H., Liu, X., … Ling, H. Q. (2022). Comparative genomic and transcriptomic analyses uncover the molecular basis of high nitrogen-use efficiency in the wheat cultivar Kenong 9204. *Molecular Plant*, *15*(9), 1440–1456. https://doi.org/10.1016/j.molp.2022.07.008

Shimizu, K. K., Copetti, D., Okada, M., Wicker, T., Tameshige, T., Hatakeyama, M., Shimizu-Inatsugi, R., Aquino, C., Nishimura, K., Kobayashi, F., Murata, K., Kuo, T., Delorean, E., Poland, J., Haberer, G., Spannagl, M., Mayer, K. F. X., Gutierrez-Gonzalez, J., Muehlbauer, G. J., … Handa, H. (2020). De novo genome assembly of the Japanese wheat cultivar Norin 61 highlights functional variation in flowering time and *Fusarium*-resistant genes in east Asian genotypes. *Plant and Cell Physiology*, *62*(1), 8–27. https://doi.org/10.1093/pcp/pcaa152

Song, L., Wang, R., Yang, X., Zhang, A., & Liu, D. (2023). Molecular markers and their applications in marker-assisted selection (MAS) in bread wheat (*Triticum aestivum* L.). *Agriculture*, *13*(3), 642. https://doi.org/10.3390/agriculture13030642

Steuernagel, B., Periyannan, S. K., Hernandez-Pinzon, I., Witek, K., Rouse, M. N., Yu, G., Hatta, A., Ayliffe, M., Bariana, H., Jones, J. D., Lagudah, E. S., & Wulff, B. B. (2016). Rapid cloning of disease-resistance genes in plants using mutagenesis and sequence capture. *Nature Biotechnology*, *34*(6), 652–655. https://doi.org/10.1038/nbt.3543

Sun, C., Dong, Z., Zhao, L., Ren, Y., Zhang, N., & Chen, F. (2020). The wheat 660K SNP array demonstrates great potential for marker-assisted selection in polyploid wheat. *Plant Biotechnology Journal*, *18*(6), 1354–1360. https://doi.org/10.1111/pbi.13361

Tao, Y., Zhao, X., Mace, E., Henry, R., & Jordan, D. (2019). Exploring and exploiting pan-genomics for crop improvement. *Molecular Plant*, *12*(2), 156–169. https://doi.org/10.1016/j.molp.2018.12.016

Tiwari, V. K., Saripalli, G., Sharma, P. K., & Poland, J. (2024). Wheat genomics: Genomes, pangenomes, and beyond. *Trends in Genetics*, *40*(11), 982–992. https://doi.org/10.1016/j.tig.2024.07.004

Ugarte, C., Calderini, D. F., & Slafer, G. A. (2007). Grain weight and grain number responsiveness to pre-anthesis temperature in wheat, barley and triticale. *Field Crops Research*, *100*(2–3), 240–248. https://doi.org/10.1016/j.fcr.2006.07.010

Venske, E., dos Santos, R. S., Busanello, C., Gustafson, P., & Costa de Oliveira, A. (2019). Bread wheat: A role model for plant domestication and breeding. *Hereditas*, *156*(1), 16. https://doi.org/10.1186/s41065-019-0093-9

Walkowiak, S., Gao, L., Monat, C., Haberer, G., Kassa, M. T., Brinton, J., Ramirez-Gonzalez, R. H., Kolodziej, M. C., Delorean, E., Thambugala, D., Klymiuk, V., Byrns, B., Gundlach, H., Bandi, V., Siri, J. N., Nilsen, K., Aquino, C., Himmelbach, A., Copetti, D., … Pozniak, C. J. (2020). Multiple wheat genomes reveal global variation in modern breeding. *Nature*, *588*(7837), 277–283. https://doi.org/10.1038/s41586-020-2961-x

Wan, C., Dang, P., Gao, L., Wang, J., Tao, J., Qin, X., Feng, B., & Gao, J. (2022). How does the environment affect wheat yield and protein content response to drought? A meta-analysis. *Frontiers in Plant Science*, *13*, 896985. https://doi.org/10.3389/fpls.2022.896985

Wang, C., & Han, B. (2022). Twenty years of rice genomics research: From sequencing and functional genomics to quantitative genomics. *Molecular Plant*, *15*(4), 593–619. https://doi.org/10.1016/j.molp.2022.03.009

Wang, H., Sun, S., Ge, W., Zhao, L., Hou, B., Wang, K., Lyu, Z., Chen, L., Xu, S., Guo, J., Li, M., Su, P., Li, X., Wang, G., Bo, C., Fang, X., Zhuang, W., Cheng, X., Wu, J., … Kong, L. (2020). Horizontal gene transfer of *Fhb7* from fungus underlies *Fusarium* head blight resistance in wheat. *Science*, *368*(6493), eaba5435. https://doi.org/10.1126/science.aba5435

Wang, L., Zhu, T., Rodriguez, J. C., Deal, K. R., Dubcovsky, J., McGuire, P. E., Lux, T., Spannagl, M., Mayer, K. F. X., Baldrich, P., Meyers, B. C., Huo, N., Gu, Y. Q., Zhou, H., Devos, K. M., Bennetzen, J. L., Unver, T., Budak, H., Gulick, P. J., … Dvorak, J. (2021). *Aegilops tauschii* genome assembly Aet v5.0 features greater sequence contiguity and improved annotation. *G3 Genes|Genomes|Genetics*, *11*(12), jkab325. https://doi.org/10.1093/g3journal/jkab325

Wang, W., Simmonds, J., Pan, Q., Davidson, D., He, F., Battal, A., Akhunova, A., Trick, H. N., Uauy, C., & Akhunov, E. (2018). Gene editing and mutagenesis reveal inter-cultivar differences and additivity in the contribution of *TaGW2* homoeologues to grain size and weight in wheat. *Theoretical and Applied Genetics*, *131*(11), 2463–2475. https://doi.org/10.1007/s00122-018-3166-7

Wang, X., Li, H., Shen, T., Wang, X., Yi, S., Meng, T., Sun, J., Wang, X., Qu, X., Chen, S., & Guo, L. (2024). A near-complete genome sequence of einkorn wheat provides insight into the evolution of wheat A subgenomes. *Plant Communications*, *5*(5), 100768. https://doi.org/10.1016/j.xplc.2023.100768

Wang, Z., Miao, L., Chen, Y., Peng, H., Ni, Z., Sun, Q., & Guo, W. (2023). Deciphering the evolution and complexity of wheat germplasm from a genomic perspective. *Journal of Genetics and Genomics*, *50*(11), 846–860. https://doi.org/10.1016/j.jgg.2023.08.002

Wang, Z., Miao, L., Tan, K., Guo, W., Xin, B., Appels, R., Jia, J., Lai, J., Lu, F., Ni, Z., Fu, X., Sun, Q., & Chen, J. (2025). Near-complete assembly and comprehensive annotation of the wheat Chinese spring genome. *Molecular Plant*, *18*(5), 892–907. https://doi.org/10.1016/j.molp.2025.02.002

Wittern, L. M., Barrero, J. M., Bovill, W. D., Verbyla, K. L., Hughes, T., Swain, S. M., Steed, G., Webb, A. A. R., Gardner, K., Greenland, A., Jacobs, J., Frohberg, C., Schmidt, R.-C., Cavanagh, C., Rohde, A., Davey, M. W., & Hannah, M. A. (2022). Overexpression of the *WAPO-A1* gene increases the number of spikelets per spike in bread wheat. *Scientific Reports*, *12*(1), 14229. https://doi.org/10.1038/s41598-022-18614-w

Xia, K., Sun, H.-X., Li, J., Li, J., Zhao, Y., Chen, L., Qin, C., Chen, R., Chen, Z., & Liu, G. (2022). The single-cell stereo-seq reveals region-specific cell subtypes and transcriptome profiling in Arabidopsis leaves. *Developmental Cell*, *57*(10), 1299–1310.E4. https://doi.org/10.1016/j.devcel.2022.04.011

Xu, Y., Zhang, X., Li, H., Zheng, H., Zhang, J., Olsen, M. S., Varshney, R. K., Prasanna, B. M., & Qian, Q. (2022). Smart breeding driven by big data, artificial intelligence, and integrated genomic-enviromic prediction. *Molecular Plant*, *15*(11), 1664–1695. https://doi.org/10.1016/j.molp.2022.09.001

Yang, N., & Yan, J. (2021). New genomic approaches for enhancing maize genetic improvement. *Current Opinion in Plant Biology*, *60*, 101977. https://doi.org/10.1016/j.pbi.2020.11.002

Yang, X., Pan, Y., Singh, P. K., He, X., Ren, Y., Zhao, L., Zhang, N., Cheng, S., & Chen, F. (2019). Investigation and genome-wide association study for *Fusarium* crown rot resistance in Chinese common wheat. *BMC Plant Biology*, *19*(1), 153. https://doi.org/10.1186/s12870-019-1758-2

Yang, Y., Cui, L., Lu, Z., Li, G., Yang, Z., Zhao, G., Kong, C., Li, D., Chen, Y., Xie, Z., Chen, Z., Zhang, L., Xia, C., Liu, X., Jia, J., & Kong, X. (2023). Genome sequencing of Sitopsis species provides insights into their contribution to the B subgenome of bread wheat. *Plant Communications*, *4*(4), 100567. https://doi.org/10.1016/j.xplc.2023.100567

Yano, K., Yamamoto, E., Aya, K., Takeuchi, H., Lo, P. C., Hu, L., Yamasaki, M., Yoshida, S., Kitano, H., Hirano, K., & Matsuoka, M. (2016). Genome-wide association study using whole-genome sequencing rapidly identifies new genes influencing agronomic traits in rice. *Nature Genetics*, *48*(8), 927–934. https://doi.org/10.1038/ng.3596

Yao, Y., Guo, W., Gou, J., Hu, Z., Liu, J., Ma, J., Zong, Y., Xin, M., Chen, W., Li, Q., Wang, Z., Zhang, R., Uauy, C., Baloch, F. S., Ni, Z., & Sun, Q. (2025). Wheat2035: Integrating pan-omics and advanced biotechnology for future wheat design. *Molecular Plant*, *18*(2), 272–297. https://doi.org/10.1016/j.molp.2025.01.005

Yin, R., Xia, K., & Xu, X. (2023). Spatial transcriptomics drives a new era in plant research. *The Plant Journal*, *116*(6), 1571–1581. https://doi.org/10.1111/tpj.16437

Yu, S., Wu, J., Wang, M., Shi, W., Xia, G., Jia, J., Kang, Z., & Han, D. (2020). Haplotype variations in QTL for salt tolerance in Chinese wheat accessions identified by marker-based and pedigree-based kinship analyses. *The Crop Journal*, *8*(6), 1011–1024. https://doi.org/10.1016/j.cj.2020.03.007

Yu, X., Liu, Z., & Sun, X. (2023). Single-cell and spatial multi-omics in the plant sciences: Technical advances, applications, and perspectives. *Plant Communications*, *4*(3), 100508. https://doi.org/10.1016/j.xplc.2022.100508

Yuan, J., Jiao, W., Liu, Y., Ye, W., Wang, X., Liu, B., Song, Q., & Chen, Z. J. (2020). Dynamic and reversible DNA methylation changes induced by genome separation and merger of polyploid wheat. *BMC Biology*, *18*(1), 171. https://doi.org/10.1186/s12915-020-00909-x

Zhang, C., Jiang, S., Tian, Y., Dong, X., Xiao, J., Lu, Y., Liang, T., Zhou, H., Xu, D., Zhang, H., Luo, M., & Xia, Z. (2023). Smart breeding driven by advances in sequencing technology. *Modern Agriculture*, *1*(1), 43–56. https://doi.org/10.1002/moda.8

Zhang, J., Zhang, H., Li, S., Li, J., Yan, L., & Xia, L. (2021). Increasing yield potential through manipulating of an ARE1 ortholog related to nitrogen use efficiency in wheat by CRISPR/Cas9. *Journal of Integrative Plant Biology*, *63*(9), 1649–1663. https://doi.org/10.1111/jipb.13151

Zhang, X., Jia, H., Li, T., Wu, J., Nagarajan, R., Lei, L., Powers, C., Kan, C. C., Hua, W., Liu, Z., Chen, C., Carver, B. F., & Yan, L. (2022). *TaCol-B5* modifies spike architecture and enhances grain yield in wheat. *Science*, *376*(6589), 180–183. https://doi.org/10.1126/science.abm0717

Zhang, Z., Hua, L., Gupta, A., Tricoli, D., Edwards, K. J., Yang, B., & Li, W. (2019). Development of an *Agrobacterium*-delivered CRISPR/Cas9 system for wheat genome editing. *Plant Biotechnology Journal*, *17*(8), 1623–1635. https://doi.org/10.1111/pbi.13088

Zhao, G., Zou, C., Li, K., Wang, K., Li, T., Gao, L., Zhang, X., Wang, H., Yang, Z., Liu, X., Jiang, W., Mao, L., Kong, X., Jiao, Y., & Jia, J. (2017). The *Aegilops tauschii* genome reveals multiple impacts of transposons. *Nature Plants*, *3*(12), 946–955. https://doi.org/10.1038/s41477-017-0067-8

Zhao, T., Zhan, Z., & Jiang, D. (2019). Histone modifications and their regulatory roles in plant development and environmental memory. *Journal of Genetics and Genomics*, *46*(10), 467–476. https://doi.org/10.1016/j.jgg.2019.09.005

Zhou, X., Zhao, Y., Ni, P., Ni, Z., Sun, Q., & Zong, Y. (2023). CRISPR-mediated acceleration of wheat improvement: Advances and perspectives. *Journal of Genetics and Genomics*, *50*(11), 815–834. https://doi.org/10.1016/j.jgg.2023.09.007

Zhou, Y., Bai, S., Li, H., Sun, G., Zhang, D., Ma, F., Zhao, X., Nie, F., Li, J., Chen, L., Lv, L., Zhu, L., Fan, R., Ge, Y., Shaheen, A., Guo, G., Zhang, Z., Ma, J., Liang, H., … Song, C.-P. (2021). Introgressing the *Aegilops tauschii* genome into wheat as a basis for cereal improvement. *Nature Plants*, *7*(6), 774–786. https://doi.org/10.1038/s41477-021-00934-w

Zhu, T., Wang, L., Rimbert, H., Rodriguez, J. C., Deal, K. R., De Oliveira, R., Choulet, F., Keeble-Gagnere, G., Tibbits, J., Rogers, J., Eversole, K., Appels, R., Gu, Y. Q., Mascher, M., Dvorak, J., & Luo, M. C. (2021). Optical maps refine the bread wheat *Triticum aestivum* cv. Chinese spring genome assembly. *The Plant Journal*, *107*(1), 303–314. https://doi.org/10.1111/tpj.15289

Zou, C., Wang, P., & Xu, Y. (2016). Bulked sample analysis in genetics, genomics and crop improvement. *Plant Biotechnology Journal*, *14*(10), 1941–1955. https://doi.org/10.1111/pbi.12559

How to cite this article: Liu, S., Geng, S., & Dreisigacker, S. (2026). Genomics in wheat improvement: Progress and perspectives. *The Plant Genome*, *19*, e70176. https://doi.org/10.1002/tpg2.70176