**The Open Agriculture Journal**
*DOI: 10.2174/0118743315475026091406194 5, 2026, 20, e187433154750*

**ISSN: 1874-3315**
***1***

**REVIEW ARTICLE** **OPEN ACCESS**

# Advances in Wheat (*Triticum aestivum* L.) Genetics, Genomics and Breeding: Current Status, Tools and Future Perspectives for Sustainable Food Security

Ashutosh Kumar[1], Sudhir Kumar[1,*], Mankesh Kumar[1] and Chandan Kishore[1]

[1]*Department of Genetics and Plant Breeding, Bihar Agricultural University, Sabour, Bhagalpur – 813210, Bihar, India*

**Abstract:**
Wheat (*Triticum aestivum* L.) is one of the most important cereal crops in the world. It supplies nearly 18–20% of global dietary calories and protein, sustaining the food security of over 2.5 billion people. Global food demand is projected to increase by 35–56% by 2050, placing additional pressure on wheat production and improvement programmes and making genetic improvement an urgent priority. This review synthesizes current advances in wheat genetics, genomics, and breeding. It discusses the origin and domestication of wheat, as well as the structure of the allohexaploid genome (AABBDD; $2n = 6x = 42$). Major genes and Quantitative Trait Loci (QTLs) governing yield, disease resistance, grain quality, and abiotic stress tolerance are critically reviewed. Key breeding approaches are evaluated, including doubled haploid technology, Marker-Assisted Selection (MAS), Genomic Selection (GS), speed breeding, and CRISPR/Cas9 genome editing. Stability analysis methods, particularly the Additive Main Effects and Multiplicative Interaction (AMMI) model and the Eberhart–Russell regression, are discussed in the context of multi-environment trial evaluation. The integration of Genome-Wide Association Studies (GWAS), pangenomics, multi-omics, and high-throughput phenotyping for precision wheat improvement is also covered. This review focuses primarily on India, with special attention to the North Eastern Plains Zone (NEPZ) and the eastern Indo-Gangetic Plains. In this region, terminal heat stress and monsoon variability pose major production challenges. Key challenges and strategic recommendations for developing climate-resilient, high-yielding, and nutritionally superior wheat varieties are outlined.

**Keywords:** *Triticum aestivum*, Genomics, Marker-assisted selection, Genomic selection, AMMI model, Eberhart–Russell, Stability analysis, CRISPR/Cas9, Genotype × environment interaction, Food security.



*Address correspondence to this author at the Department of Genetics and Plant Breeding, Bihar Agricultural University, Sabour, Bhagalpur – 813210, Bihar, India E-mail: sudhir.hzb@gmail.com

*Cite as:* Kumar A, Kumar S, Kumar M, Kishore C. Advances in Wheat (*Triticum aestivum* L.) Genetics, Genomics and Breeding: Current Status, Tools and Future Perspectives for Sustainable Food Security. Open Agric J, 2026; 20: e187433154750. http://dx.doi.org/10.2174/0118743315475026091406194

Received: April 21, 2026
Revised: July 10, 2026
Accepted: July 27, 2026
Published: September 16, 2026



## 1. INTRODUCTION

Wheat (*Triticum aestivum* L.) is one of the most important food crops globally and the most widely cultivated cereal by area. It is cultivated on approximately 220 million hectares and produces over 780 million tonnes of grain annually [1]. It provides nearly one-fifth of the total calories and protein consumed worldwide. It is particularly central to food and nutritional security across South Asia, Central Asia, North Africa, and Europe [2]. In India, wheat is the second most important staple crop, with production of approximately 110.6 million tonnes in 2022–23. For the purpose of varietal development and recommendation, India is divided into six agro-climatically distinct wheat-growing zones (Zone I to Zone VI), each characterized by unique soil, temperature, and rainfall conditions. Bihar, located in the eastern Indo-Gangetic Plains (EIGP), falls under Zone III, *i.e.*, the North Eastern Plains Zone (NEPZ), which covers eastern Uttar Pradesh, Bihar, Jharkhand, Odisha, West Bengal, Assam, and the plains of north-eastern states. This zone is recognized for

its unique cropping conditions including late sowing, terminal heat stress, and high humidity, making productivity enhancement a major national priority.

Global food demand is projected to increase by 35–56% by 2050 owing to rapid population growth, rising incomes, and shifting dietary patterns, placing additional pressure on wheat production and improvement programmes [3]. However, the annual rate of genetic gain in wheat yield has declined to approximately 0.9–1.1% per year in major producing countries, falling short of the 1.7% annual increase required [4, 5]. Some recent Indian estimates place the required rate even higher, at 2.4% per year [6]. Simultaneously, climate change is intensifying the frequency and severity of abiotic stresses such as terminal heat, drought, and erratic rainfall, which disproportionately impact wheat productivity in the EIGP region [7, 8]. The emergence of highly virulent pathogen races, including Ug99 stem rust [9] and new yellow rust biotypes, further threatens yield stability.

The completion of the reference genome sequence for bread wheat by the International Wheat Genome Sequencing Consortium [10] and subsequent pangenome assemblies [11] have transformed the genomics landscape for wheat research. These resources, integrated with advanced genotyping platforms, high-throughput phenotyping, and multi-omics analytical methods, are being leveraged to accelerate the discovery of genes and QTLs governing complex agronomic traits. Modern breeding technologies, including genomic selection, speed breeding, and CRISPR-based genome editing, are shortening the breeding cycle and enabling more precise manipulation of the wheat genome [12, 13].

Stability analysis is an indispensable component of multi-environment evaluation of wheat genotypes. Given the vast diversity of agro-climatic environments across India and the rest of the world, identifying genotypes that yield consistently across locations is a key breeding objective. Statistical models such as the Eberhart–Russell [14] regression model and AMMI [15] model provide powerful frameworks for partitioning Genotype × Environment Interaction (GEI) and selecting broadly adapted or specifically adapted genotypes. The present review integrates multiple dimensions of wheat improvement research and identifies priority areas for future research and investment.

## 2. ORIGIN, DOMESTICATION AND EVOLUTIONARY HISTORY

Wheat is one of the first crops domesticated by humanity, with origins tracing back approximately 10,000–12,000 years to the Fertile Crescent of the Near East [16]. The domestication of wheat from wild progenitors involved the selection of key traits including non-brittle rachis (preventing grain shattering), free-threshing grains, an erect growth habit, and a modified photoperiod response. These traits are collectively termed the ‘domestication syndrome’ [17]. Bread wheat (T. aestivum, 2n = 6x = 42; AABBDD) arose through two sequential polyploidization events. The first involved hybridization between Triticum urartu (A genome) and a species related to Aegilops speltoides (B genome). This produced tetraploid emmer wheat (T. dicoccoides, AABB; 2n = 4x = 28) approximately one million years ago. Subsequently, ~8,000–9,000 years ago, cultivated emmer hybridized with Aegilops tauschii (D genome donor) to give rise to hexaploid bread wheat [18]. The complete evolutionary pathway is presented in Fig. (**1**). Key domestication genes include the Q gene governing the free-threshing habit, Br (brittle rachis loci), and the vernalization and photoperiod response genes (Vrn and Ppd). Modern cultivars retain only a fraction of the genetic diversity present in wild progenitors and landraces due to repeated bottlenecks during domestication and subsequent breeding [19, 20]. This underscores the importance of exploiting wild relatives and landraces as sources of novel alleles for contemporary wheat improvement.

## 3. GENOME STRUCTURE, ORGANIZATION AND GENETIC DIVERSITY

### 3.1. Genome Structure and Complexity

The bread wheat genome is one of the largest and most complex among cultivated plants. It has an estimated size of approximately 16 Gb, distributed across 21 chromosome pairs and organized into three homeologous subgenomes (A, B, D) [10]. More than 85% of the genome consists of repetitive sequences, primarily transposable elements; this complicates genome assembly, gene annotation, and functional analysis. The IWGSC reference genome assembly (cultivar Chinese Spring) annotated approximately 107,891 high-confidence protein-coding genes, providing an unprecedented resource for wheat genomics and breeding research [10]. Multiple chromosome-level assemblies of diverse accessions have since been generated, forming the foundation for pangenome analysis.

### 3.2. Pangenomics and Haplotype Diversity

The wheat pangenome is assembled from the genomes of multiple diverse accessions. It captures the full range of gene content within the species, including core genes (present in all accessions) and dispensable genes (present in only some accessions). A 10-genome pangenome assembly identified approximately 140,500 protein-coding gene loci, of which approximately 22% were Presence-Absence Variants (PAVs) [11]. These PAVs are frequently associated with environmental adaptation, disease resistance, and variation in grain quality. Haplotype analysis of PAV regions has become a powerful approach for identifying novel alleles across global germplasm collections. The development of pangenome resources has substantially expanded the tractable genetic diversity for wheat improvement beyond what is accessible through single reference genome analysis. More recently, long-read sequencing technologies (PacBio HiFi and Oxford Nanopore) have enabled the assembly of chromosome-scale, near-complete genomes of diverse wheat accessions. This has substantially advanced the resolution

and completeness of haplotype-based pangenome analyses beyond the initial 10-genome reference [21]. In 2025, a telomere-to-telomere assembly of hexaploid bread wheat was completed, providing a near-complete, highly contiguous view of the wheat genome from end to end [22]. These high-quality assemblies are revealing structural variation, complex repeats, and novel gene families that were inaccessible through short-read sequencing, accelerating both gene discovery and deployment of pangenome-based breeding strategies. Recent syntheses have situated wheat-specific advances within the broader trajectory of crop pangenomics, underscoring its growing role in trait dissection, biodiversity conservation, and breeding decision-making across species [23, 24]. Illustrating this momentum, a 17-genome pangenome of Chinese wheat cultivars has resolved structural variants linked to breeding history, vernalization habit, and local adaptation, providing direct empirical support for haplotype-informed selection strategies [25].

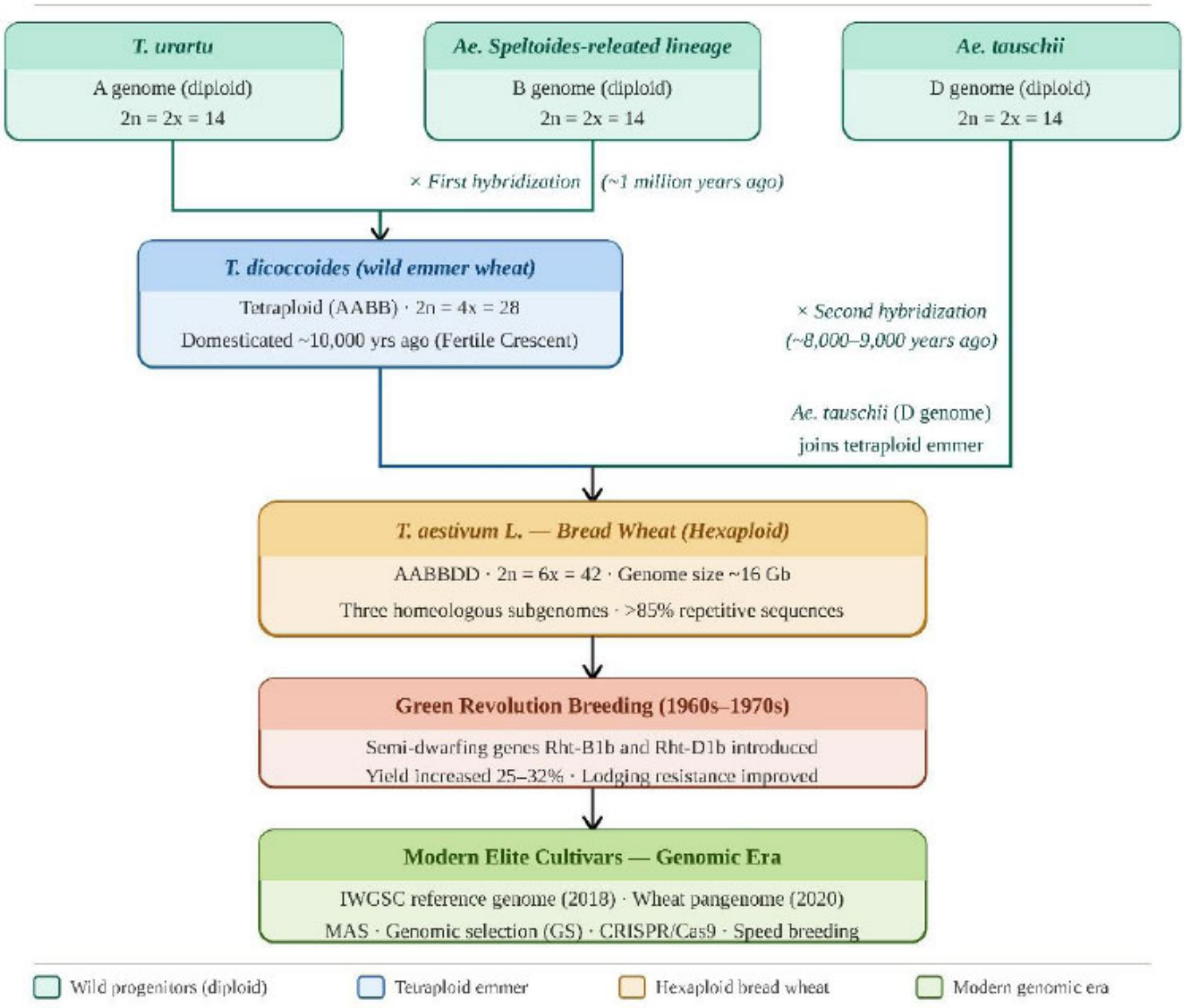


**Fig. (1).** Evolutionary pathway of wheat from wild diploid progenitors to modern bread wheat (Triticum aestivum L.; AABBDD; 2n = 6x = 42) through two sequential allopolyploidisation events, showing key milestones of the Green Revolution and the genomic era (Image adapted from subsequent studies [17, 18]).

**Abbreviations:** CRISPR = clustered regularly interspaced short palindromic repeats; IWGSC = International Wheat Genome Sequencing Consortium; MAS = marker-assisted selection; Rht = Reduced height.

### 3.3. Genetic Diversity and Germplasm Resources

Despite the complexity of its genome, modern elite wheat germplasm has a relatively narrow genetic base. SNP array and whole-genome resequencing studies have demonstrated that elite cultivars share approximately 90–95% of genomic content, reflecting the repeated use of a small number of elite parents in breeding programmes [20]. A comprehensive diversity analysis of over 80,000 wheat accessions using the DArTseq platform recently revealed distinct selection footprints in modern germplasm and highlighted under-utilized genetic material as a valuable resource for pre-breeding [26]. This genetic bottleneck severely limits the availability of novel alleles for future improvement. Major germplasm repositories including CIMMYT (Mexico), ICARDA (Lebanon/Morocco), NBPGR (New Delhi), and USDA-GRIN collectively conserve over 800,000 wheat accessions. Wild relatives of wheat, particularly Aegilops species, Agropyron, and Thinopyrum, are recognized reservoirs of novel alleles for disease resistance, drought tolerance, heat tolerance, and nutritional quality [27, 28]. For disease resistance specifically, wild relatives from both primary and secondary gene pools have been shown to continue providing valuable and unique resistance alleles not present in cultivated hexaploid wheat [28]. This finding underscores their strategic importance for durable resistance breeding. Synthetic hexaploid wheat lines, produced by hybridizing tetraploid wheat with Ae. tauschii, have been a major strategy for introducing D-genome diversity into elite germplasm [29].

## 4. MAJOR GENES AND QTLs FOR ECONOMICALLY IMPORTANT TRAITS

A summary of major genes and QTLs governing key agronomic traits in wheat is presented in Table **1**.

### 4.1. Yield and Yield Components

Grain yield in wheat is a complex quantitative trait governed by numerous genes and QTLs distributed across the three subgenomes. The semi-dwarfing genes Rht-B1b and Rht-D1b were the cornerstone of the Green Revolution. By reducing plant height and lodging susceptibility and improving harvest index, they underpinned the substantial wheat yield gains of the Green Revolution in Asia and Europe during the 1960s and 1970s [30]. The gene TaGW2 (Grain Width and Weight 2) negatively regulates grain width and weight; reduced TaGW2 expression is associated with wider, heavier grains [31], and a loss-of-function splice acceptor site mutation in TaGW2-A1 increased thousand-grain weight by 6.6%, grain width by 2.8%, and grain length by 2.1% in tetraploid and hexaploid backgrounds [31]. Major QTLs for yield components have been mapped on chromosomes 4A, 4B, 4D, 6B, and 7D.

### 4.2. Disease Resistance Genes

More than 80 Leaf rust resistance (Lr) genes, over 90 Yellow rust resistance (Yr) genes, and more than 60 Stem rust resistance (Sr) genes have been catalogued in wheat, with continuous additions as wild relative germplasm is screened [9, 33]. Durable Adult Plant Resistance (APR) genes for leaf rust include Lr34, Lr46, Lr67, and Lr68. These loci generally confer partial, durable adult-plant resistance and are valuable components of resistance gene pyramids; their frequency and effectiveness should be assessed within the target breeding population and pathogen context [9, 32]. The gene Lr37 (from the T2NS.2AS translocation from Aegilops ventricosa) confers race-specific leaf rust resistance, but it has been overcome by some virulent Puccinia triticina races and should be deployed in combination with APR genes [9].

For yellow rust (Puccinia striiformis f. sp. tritici; Pst), key resistance genes in Indian breeding include the race-specific Yr10, Yr15, and Yr17, and the durable APR genes Yr18 (=Lr34/Sr57) and Yr46 (=Lr67/Sr55/Pm46) [9, 35]. In addition, the race-specific genes Yr5, Yr7 and YrSP, which map to chromosome arm 2BL and encode nucleotide-binding leucine-rich-repeat proteins carrying an integrated zinc-finger BED domain, confer all-stage resistance; Yr5 remains highly effective, with only two of more than 6,000 Pst isolates tested worldwide found virulent, whereas Yr7 and YrSP have been overcome in the field, so these genes should be deployed in gene pyramids and monitored through regional pathotype surveillance [37]. Notably, Yr17 (part of the Lr37/Sr38/Yr17 complex on the T2NS.2AS translocation from Ae. ventricosa) is no longer effective against new virulent Pst races. Sr38, carried on the same translocation, is similarly ineffective against Ug99 Pgt races. Deployment of these genes must therefore be supplemented by pyramiding with functional APR genes or additional race-specific genes [9].

The emergence of Ug99 stem rust race (TTKSK; the pathotype designation code) in East Africa and its subsequent virulent lineages have renewed interest in effective Sr genes. Race-specific resistance genes are individually effective against Ug99 derivatives but are most valuable when deployed in combinations to delay resistance breakdown. These genes include Sr22, Sr25, Sr26, Sr33, Sr35, Sr45, and Sr50 [9, 48]. Non-race-specific Adult Plant Resistance (APR) genes confer slow-rusting, partial resistance not readily overcome by individual virulent races. These genes include Sr2, Sr55 (=Lr67/Yr46/Pm46), Sr57 (=Lr34/Yr18/Pm38/Sb1/Ltn1), Sr58 (=Lr46/Yr29/Pm39), and Sr63. Their value in durable resistance programmes is well established [9, 35]. A landmark finding in durable rust management has been the identification of three pleiotropic APR genes: Sr55 (=Lr67/Yr46/Pm46), Sr57 (=Lr34/Yr18/Pm38/Sb1/Ltn1), and Sr58 (=Lr46/Yr29/Pm39) [33, 35]. Each of these three genes confers slow-rusting, partial, non-race-specific resistance simultaneously against stem rust, leaf rust, yellow rust, and powdery mildew, providing multi-pathogen protection from a single genetic locus. Collectively, such pleiotropic and adult-plant resistance genes are among the most valuable and durable components available to wheat breeding programmes, particularly when pyramided with race-specific resistance genes [9, 35]. The gene Sr57 (=Lr34/Yr18) is also located at the same locus as Sb1 (spot blotch resistance against Bipolaris sorokiniana) and Bdv1 (barley yellow dwarf virus

tolerance), exemplifying the exceptional pleiotropic value of this gene for wheat breeding in humid environments [9]. The Fhb1 locus (chromosome 3BS), originally identified in Chinese wheat cv. Sumai 3, is a major source of Type II resistance and the most effective QTL for Fusarium Head Blight (FHB) resistance, and has been widely used in FHB-resistance breeding programmes [38, 49]. Powdery mildew resistance genes Pm21 (race-specific, from Haynaldia villosa via 6VS/6AL translocation) and TALEN-mediated mutation of all three TaMLO homoeologs (conferring heritable broad-spectrum mlo-mediated resistance) represent contrasting genetic strategies for powdery mildew management [39, 40].

### 4.3. Grain Quality Genes

Wheat grain quality is largely determined by gluten proteins, particularly High-Molecular-Weight Glutenin Subunits (HMW-GS) encoded by Glu-A1, Glu-B1, and Glu-D1 loci. The HMW-GS allele combination 5+10 at Glu-D1 has been associated with favourable dough rheological properties and breadmaking-quality traits, relative to the 2 + 12 allele in comparative studies [50]. Waxy (Wx) genes controlling amylose content are important for noodle and food processing quality. The Gpc-B1 locus on chromosome 6B, encoding a NAC transcription factor, regulates grain protein, zinc, and iron concentrations and is an important target for biofortification breeding [42, 51].

**Table 1. Major genes and QTLs governing economically important traits in wheat (*Triticum aestivum* L.).**

| Trait Category | Gene / QTL | Chromosome | Effect / Function | Key Reference |
|---|---|---|---|---|
| Yield/Dwarfism | *Rht-B1b, Rht-D1b* | 4B, 4D | Semi-dwarfism; improved harvest index; lodging resistance | [30] |
| Yield/Grain Weight | *TaGW2-A1* | 6AS | Natural expression variation and a characterized G2373A splice-acceptor loss-of-function allele are associated with increased grain weight and grain dimensions | [31] |
| Leaf Rust (APR) | *Lr34, Lr46, Lr67, Lr68* | 7D, 1B, 4D, 7B | Durable adult plant resistance; partial, broad-spectrum; Lr34=Sr57/Yr18 (pleiotropic) | [9, 32] |
| Leaf Rust (Race-specific) | *Lr37 (T2NS.2AS)* | 2A | Race-specific; from Ae. ventricosa; overcome by some virulent races; use with APR | [9, 33, 34] |
| Yellow Rust (APR) | *Yr18 (=Lr34/Sr57), Yr46 (=Lr67/Sr55)* | 7D, 4D | Durable APR; pleiotropic multi-pathogen resistance; slow-rusting | [9, 35] |
| Yellow Rust (Race-specific) | *Yr5, Yr7, YrSP* | 2BL, 2BL, 2BL | Race-specific (all-stage); Yr5, Yr7 and YrSP encode BED-domain NLRs; Yr5 remains broadly effective against prevailing Pst races, while Yr7 and YrSP have been overcome; Yr17 (T2NS translocation) has been overcome by new races. Yr15 virulence was detected in the United Kingdom in 2025, reported as the first large-scale breakdown of this gene recorded globally [36] | [9, 34, 36, 37] |
| Stem Rust (Race-specific) | *Sr22, Sr25, Sr26, Sr33, Sr35, Sr45, Sr50* | 7A, 7D, 6A, 1D, 3A, 1D, 1D | Effective against Ug99; most valuable in combinations to delay breakdown | [9, 34] |
| Stem Rust (APR) | *Sr2, Sr55(=Lr67), Sr57(=Lr34), Sr58(=Lr46)* | 3BS, 4D, 7D, 1B | Non-race-specific APR; slow-rusting; multi-pathogen pleiotropic genes | [9, 35] |
| FHB Resistance | *Fhb1* | 3BS | Type II FHB resistance; Sumai 3-derived | [38] |
| Powdery Mildew | *Pm21, TaMLO* | 6VS/6AL, 4A/4B/4D | Pm21: race-specific; TaMLO: susceptibility-gene family; TALEN-mediated mutation of all three homoeologs conferred heritable broad-spectrum powdery mildew resistance | [39, 40] |
| Breadmaking Quality | *Glu-D1 (5+10 subunit)* | 1D | Gluten protein composition associated with dough and breadmaking quality | [41] |
| Grain Protein/Micronutrients | *Gpc-B1 (NAC-TF)* | 6B | Increases grain protein, Zn and Fe; biofortification target | [42] |
| Heat Stress Tolerance | *QTLs: 2B, 7B, 7D* | Multiple | CTD, Grain Weight (TGW), and grain-filling duration under heat; reported QTLs require multi-environment validation in NEPZ germplasm | [43] |
| Drought Tolerance | *TaDREB1, TaWRKY, TaMYB* | Multiple | DREB/CBF pathway; osmotic adjustment; root architecture in wheat | [44, 45] |
| Salinity Tolerance | *Nax1 (2AL); Nax2/TmHKT1;5-A (5A)* | 2AL, 5A | Nax1: sodium exclusion in durum wheat [46]; Nax2/TmHKT1;5-A: xylem Na+ retrieval and reduced leaf Na+ accumulation [47] | [46, 47] |
| Photoperiod Response | *Ppd-D1, Ppd-B1* | 2D, 2B | Photoperiod insensitivity; adaptation to diverse environments | [17] |
| Vernalization | *Vrn-A1, Vrn-B1, Vrn-D1* | 5A, 5B, 5D | Spring *vs.* winter growth habit; flowering time | [17] |

**Abbreviations:** APR = Adult Plant Resistance (non-race-specific, slow-rusting, durable); Race-specific = all-stage resistance, effective only against matching pathogen races; Pleiotropic genes confer resistance to multiple diseases simultaneously: Sr57 (=Lr34/Yr18/Pm38/Sb1/Ltn1), Sr55 (=Lr67/Yr46/Pm46), Sr58 (=Lr46/Yr29/Pm39). QTL = Quantitative Trait Locus; BYDV = Barley Yellow Dwarf Virus; Pst = Puccinia striiformis f. sp. tritici (yellow rust); Pgt = Puccinia graminis f. sp. tritici (stem rust); Pt = Puccinia triticina (leaf rust); BED-NLR = nucleotide-binding leucine-rich-repeat protein with an N-terminal zinc-finger BED domain.

### 4.4. Abiotic Stress Tolerance

Terminal heat stress is one of the most serious threats to wheat production in the EIGP. Key QTLs for heat tolerance have been mapped on chromosomes 2B, 7B, and 7D, associated with canopy temperature depression, grain weight, and grain-filling rate under heat stress [43]. TaDREB/CBF and TaWRKY transcription factors have been implicated in abiotic-stress signalling in wheat and related experimental systems [44, 45]. The TaELF3 gene modulates photoperiod response and heat escape. The Nax1 locus was mapped to chromosome arm 2AL in durum wheat and accounted for approximately 38% of the phenotypic variation in leaf-blade Na+ concentration [46]. At the Nax2 locus, TmHKT1;5-A contributes to reduced Na+ transport to leaves through xylem Na+ retrieval [47].

## 5. WHEAT BREEDING STRATEGIES: CLASSICAL AND MODERN APPROACHES

A comparative overview of major wheat breeding strategies is presented in Table **2**. The integrated modern wheat breeding pipeline is illustrated in Fig. (**2**).

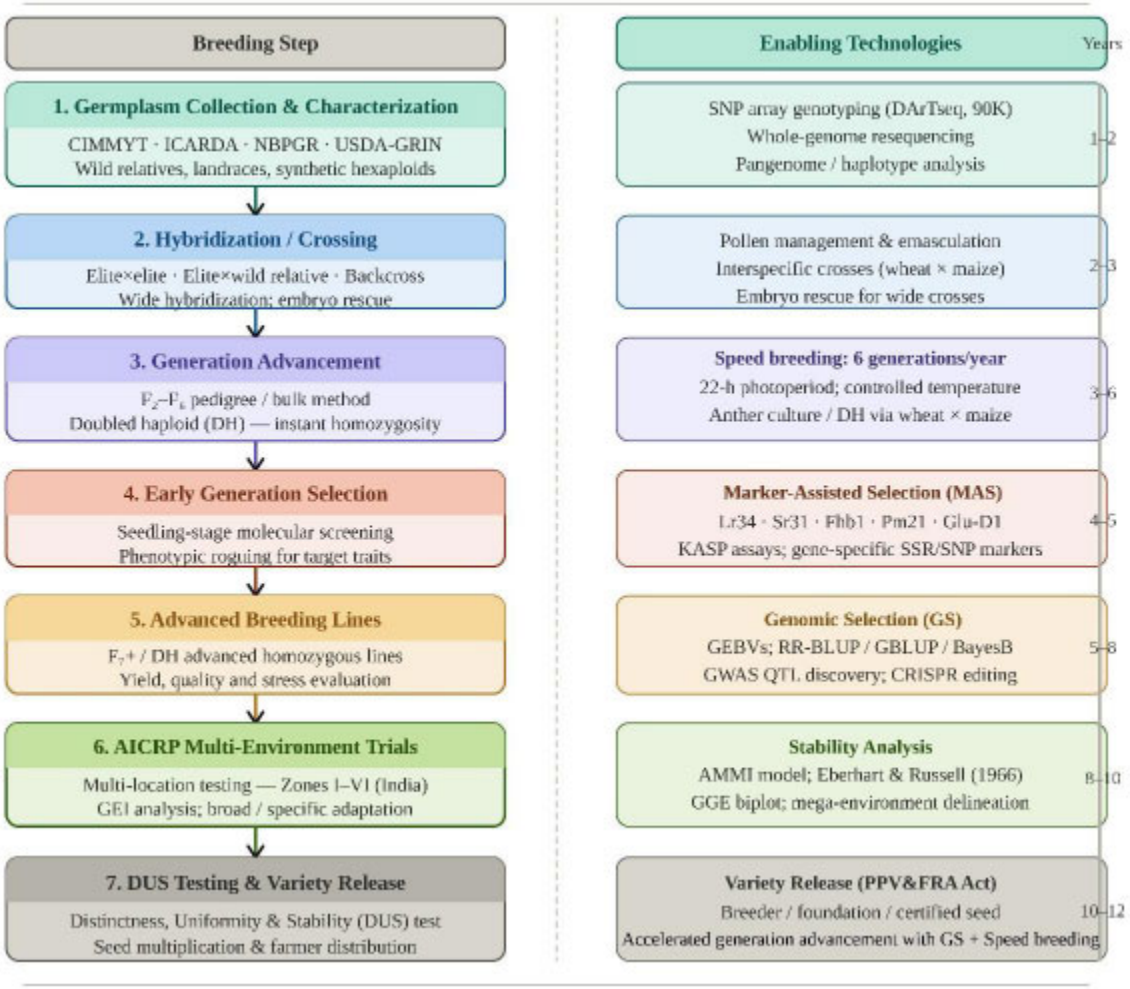


**Fig. (2).** Integrated wheat breeding pipeline from germplasm collection to variety release, with enabling biotechnological tools and approximate cumulative timeline. (Image adapted from previous studies [12, 13]).

**Abbreviations:** AICRP = All India Coordinated Research Project; AMMI = Additive Main effects and Multiplicative Interaction; CIMMYT = International Maize and Wheat Improvement Center; CRISPR = clustered regularly interspaced short palindromic repeats; GEBVs = genomic estimated breeding values; GEI = genotype × environment interaction; GBLUP = genomic best linear unbiased prediction; GGE = genotype main effect plus genotype-by-environment interaction; GWAS = genome-wide association study; ICARDA = International Center for Agricultural Research in the Dry Areas; KASP = kompetitive allele-specific PCR; NBPGR = National Bureau of Plant Genetic Resources; PPV&FRA = Protection of Plant Varieties and Farmers' Rights Authority; QTL = quantitative trait locus; RR-BLUP = ridge-regression best linear unbiased prediction; SNP = single nucleotide polymorphism; SSR = simple sequence repeat; USDA-GRIN = United States Department of Agriculture Germplasm Resources Information Network.

**Table 2. Comparative overview of major wheat breeding strategies, advantages, limitations and illustrative applications.**

| Method | Key Advantages | Limitations | Time to Variety | Example Applications |
|---|---|---|---|---|
| Conventional Hybridization | No special technology; proven track record | Slow; phenotypic selection confounded by GEI | ~12 years | Pedigree, bulk, backcross methods; AICRP wheat trials [52, 53] |
| Doubled Haploid (DH) | Instant homozygosity; saves 6–8 inbreeding generations | Genotype-dependent tissue culture; albinism | ~6–7 years | Mapping populations; elite line fixation in CIMMYT [54] |
| Marker-Assisted Selection (MAS) | Early-generation seedling selection; precise major gene transfer | Effective mainly for major-gene loci; linkage drag | ~8–10 years | *Lr34, Sr31, Fhb1, Pm21, Glu-D1 introgression programmes [55]* |
| Genomic Selection (GS) | Improves polygenic traits; shortens cycle; higher gain per year | Requires large training set and genotyping costs | ~4–6 years | CIMMYT international nurseries; yield and quality GS [56, 57] |
| Speed Breeding | 6 generations per year; compatible with MAS and GS | Controlled environment; high infrastructure cost | Accelerates generation advancement (up to ~6 generations/year in suitable spring wheat); end-to-end cultivar release still depends on crossing design, field evaluation, seed multiplication, and national release requirements | CIMMYT, Univ. Queensland, Rothamsted Research [12, 58] |
| CRISPR/Cas9 Editing | Precise multiplex editing across homeologs; novel variation | Regulatory hurdles; transformation efficiency limits broad adoption | Variable | *TaMLO (mildew), TaGW2 (grain weight), TaDEP1 (yield) [40, 59, 60]* |

### 5.1. Conventional Breeding

Conventional wheat breeding based on hybridization and selection continues to underpin national wheat improvement programmes in India and worldwide. The pedigree method, bulk population method, backcross method, and recurrent selection are the most widely used approaches. In India, the Indian Agricultural Research Institute (IARI), the ICAR-Indian Institute of Wheat and Barley Research (ICAR-IIWBR) Karnal, and Punjab Agricultural University (PAU) Ludhiana have made significant contributions. Despite its proven efficacy, conventional breeding is time-intensive, typically requiring 10–12 years from a cross to variety release, and relies on phenotypic selection that may be confounded by Genotype × Environment Interaction (GEI).

### 5.2. Doubled Haploid Technology

Doubled Haploid (DH) technology produces completely homozygous lines in a single generation through anther culture or wheat × maize wide hybridization, bypassing the 6–8 generations required for inbreeding in conventional programmes. DH lines have been widely used in wheat for developing mapping populations and accelerating elite line development [54]. Limitations include genotype-dependent tissue-culture responses and albinism in some anther-derived plants, which constrain broad adoption across diverse genetic backgrounds.

### 5.3. Marker-assisted Selection

Marker-Assisted Selection (MAS) enables breeders to select desirable alleles at the seedling stage, reducing the influence of environmental variation and accelerating the breeding cycle. The evolution from RFLPs and SSRs to high-density SNP arrays has substantially expanded the capacity of MAS. It has been particularly effective for introgression of major gene loci such as Lr34, Sr31, Pm21 (powdery mildew resistance), Fhb1 (FHB resistance), and Glu-D1 (breadmaking quality) into elite backgrounds [55]. Institutions including IARI New Delhi have applied MAS in developing rust-resistant and FHB-resistant varieties for the Indian subcontinent.

### 5.4. Genomic Selection

Genomic Selection (GS) is a genome-wide prediction approach that uses dense marker data to estimate Genomic Estimated Breeding Values (GEBVs) for all candidates in a population. This approach enables selection of complex quantitative traits without prior identification of specific QTLs [56]. Statistical models including RR-BLUP, GBLUP, BayesB (a Bayesian variable-selection genomic model), and machine learning methods have been applied to wheat GS [13, 61]. Genomic selection can shorten breeding cycles and increase genetic gain per unit time when robust, routinely updated training populations and high-quality phenotypes are available; the magnitude of benefit is programme-, trait-, and environment-specific and should be empirically evaluated within each breeding pipeline [62]. CIMMYT semi-arid

wheat trials have reported realised genetic gains of approximately 1.4–1.8% per year, with the highest relative rate recorded in low-yielding environments [63]. These gains reflect the performance of the combined breeding system and should not be attributed solely to genomic selection.

### 5.5. Speed Breeding

Speed breeding accelerates plant generation advancement by extending the photoperiod to 22 hours and manipulating temperature in controlled growth facilities. Under speed-breeding conditions, spring wheat can complete up to six generations per year, compared with 1–2 field generations [12]. Speed breeding, when integrated with genomic selection and marker-assisted selection, substantially compresses the breeding cycle and is now adopted in major programmes at CIMMYT, the University of Queensland, and Rothamsted Research [58]. Combining speed breeding with genomic selection can increase genetic gain per unit time by shortening generation intervals and improving selection efficiency [13, 64, 65]. Wider adoption still faces practical barriers. These include the cost of controlled-environment facilities, limited technical training, and the need for reliable electricity and cooling infrastructure, which are especially relevant for SAUs in the NEPZ [64].

### 5.6. Genome Editing and CRISPR/Cas9

CRISPR/Cas9 enables targeted modification of specific genomic sequences, including simultaneous editing of all three homeologous gene copies in hexaploid wheat. Multiplex mutation of TaMLO homoeologs conferring heritable powdery mildew resistance was first demonstrated using TALENs; the same study also demonstrated CRISPR/Cas9 editing of TaMLO-A1 [40]. Subsequent reports include editing of TaGW2 for increased grain weight, TaGASR7 for grain weight improvement using DNA-free RNP delivery, and TaDEP1 for enhanced spike architecture [59, 66]. The development of GRF4–GIF1 chimeric gene approaches has significantly improved wheat transformation efficiency, broadening the applicability of CRISPR across diverse elite genotypes [67]. Base editing and prime editing platforms are being adapted for wheat to allow precise single-nucleotide changes without double-strand breaks. Complementary approaches using transgenic overexpression of wheat transcription factors (*e.g.*, TaCR4-A) have also significantly improved grain size and weight [68]. Comprehensive reviews of CRISPR/Cas applications in crop improvement underscore the transformative potential of precision genome editing for wheat breeding [60].

### 5.7. Critical Appraisal: A SWOT Analysis of Wheat Breeding Strategies for Indian Breeding Programmes

A critical review must move beyond description to evaluate breeding strategies against the practical constraints and opportunities of the target breeding system. Table **3** [12, 40, 55, 57] presents a structured SWOT (Strengths, Weaknesses, Opportunities, Threats) analysis of four key modern breeding strategies. These are Marker-Assisted Selection (MAS), Genomic Selection (GS), Speed Breeding, and CRISPR/Cas9 Genome Editing. These strategies are evaluated specifically in the context of Indian Council of Agricultural Research (ICAR) national institutes and State Agricultural Universities (SAUs) operating within the Indian wheat breeding infrastructure, with special consideration of the NEPZ (North Eastern Plains Zone).

**Table 3. SWOT analysis of major modern wheat breeding strategies evaluated in the context of Indian (ICAR/SAU) breeding programmes, with specific relevance to the NEPZ.**

| Strategy | Strengths | Weaknesses | Opportunities | Threats |
|---|---|---|---|---|
| **Marker-Assisted Selection (MAS)** | Precise introgression of major genes (Lr34, Fhb1, Pm21); early-generation seedling selection; established KASP/SSR marker systems at IARI, ICAR-IIWBR, PAU; reduces GEI effect on selection. | Limited effectiveness for polygenic traits (yield, heat tolerance); linkage drag; requires prior QTL knowledge; Requires access to reliable marker platforms, validated assays, and technical capacity. | Declining KASP cost; integration with speed breeding for rapid gene pyramiding; ICAR BIG programme expanding MAS to SAUs; AICRP nurseries providing pre-selected advanced lines for SAU evaluation. | Rapid pathogen evolution overcoming pyramided resistance genes; over-reliance on narrow gene combinations; loss of effectiveness of Sr31 to Ug99 stem rust as precedent. |
| **Genomic Selection (GS)** | Superior for complex traits, including yield and heat tolerance; shortens cycle to 4–6 years; Can increase genetic gain per unit time when prediction accuracy, training-population relevance, and cycle time are optimized. | Requires large training population (>1,000 lines); requires sustained investment in genotyping, phenotyping, and data-analysis capacity; bioinformatics expertise needed; prediction accuracy declines across diverse environments; limited NEPZ-specific training data. | Declining genotyping costs (GBS platforms); NEPZ multi-environment data could support development of locally relevant training populations, subject to adequate phenotypic standardization and data governance; potential to build NEPZ-specific GS training populations. | GEI reduces prediction accuracy across zones; limited public funding for GS at most SAUs; technology gap between international centres and state universities; risk of genetic erosion under intense selection. |

| Strategy | Strengths | Weaknesses | Opportunities | Threats |
|---|---|---|---|---|
| **Speed Breeding** | Up to 6 generations/year; compatible with MAS and GS in same generation; accelerates backcross conversion; scalable; eliminates seasonal constraints on generation advancement. | High infrastructure cost (growth chambers, LED lighting, climate control); not accessible at most Indian SAUs; photoperiod manipulation unsuitable for vernalization-requiring types; requires stable power supply. | Government investment in controlled environment facilities; modular, low-cost speed breeding chambers; high-altitude summer nurseries (Shimla/Manali) as a partial alternative; CIMMYT-CSISA protocol adoption. | Erratic power supply in Bihar/EIGP region; high recurring energy cost; genotype-specific differential response; field adaptation cannot be fully captured in controlled environments. |
| **CRISPR/Cas9 Genome Editing** | Precise multiplex editing of all three homeologs; creates novel variation beyond natural allele pools; potential to generate edited products without stable foreign-DNA integration when appropriate transient or DNA-free delivery methods are used; rapid functional validation of candidate genes. | Regulatory requirements in India vary by genome-editing category. Plants developed through SDN-1 or SDN-2 and free of exogenous introduced DNA are exempt from Rules 7–11 of the Rules, 1989, subject to the applicable 2022 guidelines and standard operating procedures; products outside these exempt categories require assessment under the applicable regulatory framework; low transformation efficiency in elite Indian genotypes; delivery system challenges; off-target assessment and molecular characterisation required at a level appropriate to the edit, delivery method, and applicable regulatory framework; whole-genome sequencing may be valuable in selected cases. | India's 2022 framework, under which SDN-1 and SDN-2 genome-edited plants free of exogenous introduced DNA are exempt from specified provisions of the 1989 Rules, subject to the applicable guidelines and SOPs; improving wheat transformation protocols (GRF4-GIF1); potential to stack heat tolerance with rust resistance; public-private partnerships for gene editing platforms. | Uncertain regulatory requirements and assessment pathways for SDN-3 edits; public perception barriers; IP restrictions on CRISPR patents; significant time lag from gene editing to field-ready variety. |

**Abbreviations:** GEI = genotype-environment interaction; SAU = State Agricultural University; KASP = Kompetitive Allele Specific PCR; GEBV = Genomic Estimated Breeding Value; GBS = Genotyping by Sequencing; NEPZ = North Eastern Plains Zone; SDN = Site-Directed Nuclease (SDN-1 = small insertions/deletions, no foreign DNA).

## 6. STABILITY ANALYSIS OF WHEAT GENOTYPES IN MULTI-ENVIRONMENT TRIALS

The conceptual framework for stability analysis is depicted in Fig. (**3**) [69].

### 6.1. Genotype × Environment Interaction (GEI)

Genotype × Environment Interaction (GEI) occurs when genotypes differ in their relative performance across environments, complicating the selection of broadly adapted varieties. GEI is ubiquitous in wheat multi-location trials due to the wide diversity of soil types, temperature regimes, rainfall patterns, and crop management across the target environments of India. Effective partitioning and interpretation of GEI is essential for identifying stable, broadly adapted genotypes and for defining mega-environments for targeted varietal deployment [70].

### 6.2. Eberhart and Russell Regression Model

Eberhart and Russell [14] proposed a linear regression model that partitions the phenotypic response of a genotype across environments into: (i) the genotype mean (μi); (ii) the regression coefficient (bi, measuring response to improving environments); and (iii) the deviation from regression ($S^2di$, measuring unpredictable stability). A broadly adapted, stable genotype is characterized by a mean yield above the trial mean, bi = 1 (average response to environmental change), and $S^2di \approx 0$ (consistent performance). Genotypes with bi > 1 are suited to high-input, favourable environments, while those with bi < 1 are adapted to low-input or stress environments. This model has been widely applied in AICRP wheat trials across India for variety evaluation [53].

### 6.3. AMMI Model

The AMMI (Additive Main effects and Multiplicative Interaction) model [15] combines ANOVA for additive main effects with Principal Component Analysis (PCA) for the multiplicative interaction component (GEI). The GEI sum of squares is decomposed into several Interaction Principal Component Axes (IPCAs), with each axis capturing a decreasing proportion of the GEI pattern. The AMMI Stability Value (ASV), calculated from the first two IPCA scores [71], provides a single numeric index for genotype stability: genotypes with low ASV are broadly stable, while a high ASV only reflects strong genotype × environment interaction; such genotypes can only be considered specifically adapted when the high ASV is paired with high mean performance in the target environment. The AMMI biplot, plotting IPCA1 against mean yield, allows simultaneous visualization of genotype mean performance and stability, facilitating identification of ideal genotypes [72].

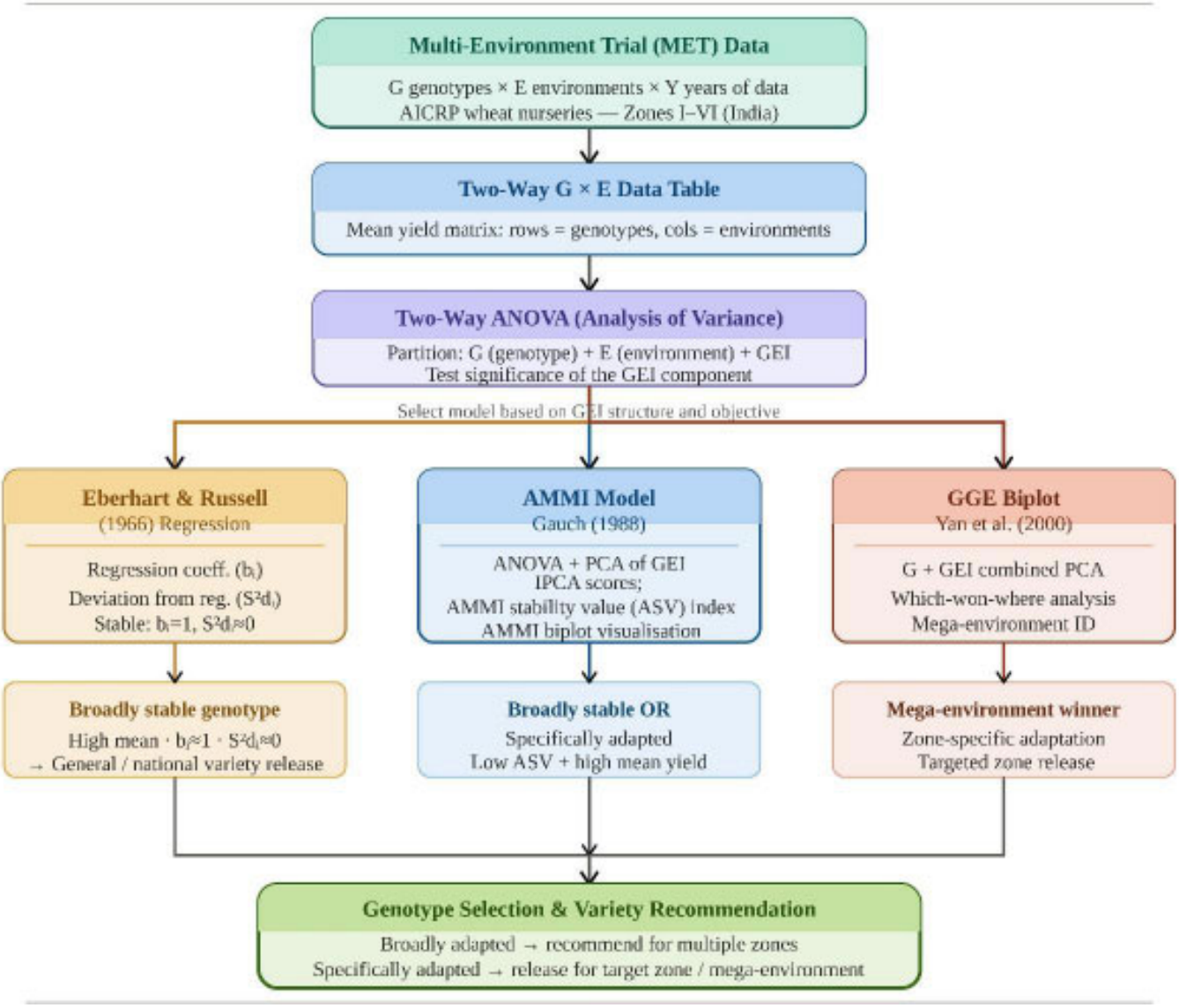


**Fig. (3).** Analytical framework for stability analysis of multi-environment wheat trial data, illustrating pathways from G × E data assembly and two-way ANOVA to three alternative stability models converging on genotype selection and variety recommendation [14, 15, 69].
**Abbreviations:** AICRP = All India Coordinated Research Project; AMMI = Additive Main effects and Multiplicative Interaction; GEI = genotype × environment interaction; GGE = genotype main effect plus genotype-by-environment interaction; IPCA = interaction principal component axis; PCA = principal component analysis.

### 6.4. GGE Biplot and Complementary Methods

The GGE biplot [69] combines Genotype (G) main effects with GEI into a single biplot, enabling 'which-won-where' pattern analysis, mega-environment delineation, and assessment of discriminating ability of test environments. Complementary stability statistics including Wricke's ecovalence, Shukla's stability variance, and Finlay–Wilkinson regression provide additional perspectives on GEI. A comparative summary of these stability analysis models is presented in Table **4**. The selection of the most appropriate model depends on the structure and magnitude of GEI, as well as the specific objectives of the breeding programme.

## 7. ADVANCED GENOMIC AND BIOTECHNOLOGICAL TOOLS

The multi-omics integration framework for wheat trait improvement is illustrated in Fig. (**4**) [73].

**Table 4. Comparative features of major stability analysis models used in multi-environment wheat trials.**

| Feature | Eberhart and Russell [14] | AMMI Model [15] | GGE Biplot [69] | Finlay-wilkinson Regression |
|---|---|---|---|---|
| Statistical basis | Linear regression of genotype on environmental index | ANOVA + PCA of GEI | PCA of G + GEI | Linear regression on environment mean |
| Stability parameter | Regression coeff. (bi) and deviation ($S^2di$) | AMMI Stability Value (ASV); IPCA scores | PC1 and PC2 scores; biplot | Regression coefficient (b) |
| Visual output | Scatter plot (bi *vs.* mean) | AMMI biplot (IPCA1 *vs.* IPCA2 or mean) | GGE biplot (PC1 *vs.* PC2) | Regression lines per genotype |
| GEI partitioning | Single regression captures linear GEI only | Multiple axes capture complex GEI patterns | G + GEI combined in single analysis | Linear component of GEI only |
| Mega-environment identification | Not directly applicable | Partially applicable via biplot clusters | Directly applicable (which-won-where) | Not applicable |
| Broadly stable genotype selection | bi = 1; $S^2di$ = 0; high mean yield | Low ASV; IPCA scores near origin; high mean | Close to the "ideal genotype" on the average-environment axis; high mean yield | b = 1; high mean yield |
| Key advantage | Simple; widely used; interpretable | Best GEI partitioning; flexible; graphical | Comprehensive visual analysis; mega-environment delineation | Simple; easy computation |
| Limitation | Assumes linear GEI only; less powerful for complex GEI | Computationally intensive; axis selection subjective | Intentionally combines G and GEI effects, so their individual contributions cannot be separated | Single regression may underfit complex GEI |
| Software | SPSS, SAS, R (agricolae) | R (agricolae, metan), GenStat | R (GGEbiplot), GenStat, Minitab | GenStat, SAS, R |

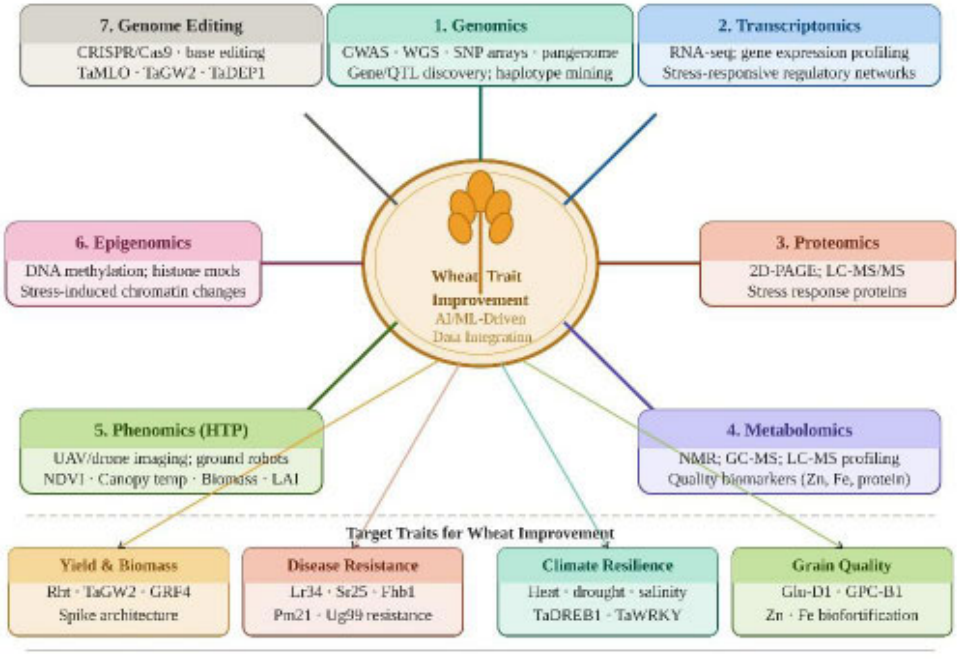


**Fig. (4).** Integration of multi-omics and genomic tools for wheat trait improvement. Genomics, transcriptomics, proteomics, metabolomics, phenomics, GWAS, epigenomics, bioinformatics, and genome editing collectively inform wheat trait improvement and contribute to the development of climate-resilient, high-yielding, disease-resistant, and quality-enhanced wheat varieties (Image adapted from a previous study [73]).

**Abbreviations:** GWAS = genome-wide association study; QTL = quantitative trait locus; SNP = single nucleotide polymorphism; CRISPR = clustered regularly interspaced short palindromic repeats; GS = genomic selection; MAS = marker-assisted selection; NGS = next-generation sequencing.

### 7.1. Genome-wide Association Studies (GWAS)

GWAS leverages natural variation across diverse association panels to identify marker-trait associations at high mapping resolution, without the need to first develop a dedicated QTL mapping population. High-density SNP arrays (90K iSelect, 660K Axiom) and Genotyping-by-Sequencing (GBS) have enabled GWAS in large and diverse panels. Notable GWAS findings in wheat include associations for FHB resistance [74] and grain zinc and iron concentrations relevant to biofortification [75, 76]. GWAS results complement biparental QTL mapping by operating across a broader spectrum of haplotypic diversity.

### 7.2. High-throughput Phenotyping

High-Throughput Phenotyping (HTP) platforms include Unmanned Aerial Vehicles (UAVs) equipped with multispectral, thermal, and RGB cameras, ground-based robots, and controlled-environment imaging systems. These platforms have substantially expanded the capacity for precise, non-destructive phenotyping of large breeding populations. Key measurable traits include canopy temperature, Normalized Difference Vegetation Index (NDVI), leaf area index, biomass estimation, heading date, plant height, and lodging score. Integration of HTP data with genomic prediction models has been shown to improve accuracy for complex traits such as grain yield and drought tolerance [77-79].

### 7.3. Multi-omics Integration

Integration of genomics, transcriptomics, proteomics, metabolomics, and epigenomics (multi-omics) provides a holistic systems-level approach to deciphering the molecular mechanisms underlying complex agronomic traits in wheat. Transcriptomic analyses have identified key gene regulatory networks governing grain filling, response to terminal heat stress, and pathogen defence. Metabolomic profiling enables the identification of biomarkers for grain quality and stress tolerance. Epigenomic studies have revealed the role of DNA methylation and histone modifications in regulating gene expression under environmental stress. Artificial Intelligence (AI) and Machine Learning (ML) methods are increasingly applied to integrate multi-omics layers with phenotypic data to prioritize candidate genes and optimize selection decisions [73, 79]. In particular, multivariate deep learning architectures are being applied to integrate whole-genome marker data, hyperspectral imagery, and environmental covariates for genomic prediction of complex traits in wheat. These architectures include Convolutional Neural Networks (CNNs) and Long Short-Term Memory (LSTM) networks. These approaches have improved prediction accuracy in some wheat datasets, particularly when genomic, phenomic, and environmental covariates are integrated; however, performance relative to GBLUP and other conventional models is data- and validation-design-dependent, and independent evaluation is required before routine deployment [73, 79]. These deep learning frameworks represent a frontier of methodological development with potential relevance to the NEPZ wheat breeding context, though their application will require validation against NEPZ-specific training data. In this setting, multi-environment genomic prediction accuracy for terminal heat stress adaptation traits could be substantially improved by harnessing the non-linear relationships between marker profiles and environmental responses. This trajectory is corroborated by recent benchmarking studies in wheat genomic prediction and phenomic–genomic integration [80-82].

## 8. CHALLENGES AND FUTURE PERSPECTIVES

### 8.1. Key Challenges

Despite remarkable advances, several formidable challenges limit the pace of wheat genetic improvement. The narrow genetic base of elite germplasm, a product of progressive selection and genetic drift during domestication and breeding, restricts the availability of novel alleles for yield enhancement and stress adaptation. Climate change is steadily shifting temperature and rainfall regimes in major wheat-growing regions, making existing varieties increasingly less suited to emerging conditions [7, 83]. Rapidly evolving pathogen races, including new Ug99 lineages and virulent yellow rust strains, can overcome deployed resistance genes [9, 48, 84]. As described in Section 4.2, the emergence of Pst races virulent to widely deployed race-specific genes such as Yr17 [84] underscores the need for continued regional surveillance and resistance-gene monitoring. The continued emergence of virulent Pst biotypes, including those overcoming previously effective race-specific resistance genes, underscores the urgency of pyramiding multiple APR genes (Yr18, Yr46) and race-specific genes in new varieties. An additional emerging transboundary threat is wheat blast (Magnaporthe oryzae pathotype Triticum), which caused severe epidemics in eight southwestern districts of Bangladesh in 2016 with yield losses reaching up to 100% in affected fields under conducive conditions; the Bangladesh outbreak raised concern that wheat blast could spread to major wheat-producing areas in neighbouring South Asian countries; active surveillance and resistance-breeding preparedness are therefore warranted in the region [85]. The complex regulatory environment for gene-edited crops in India delays the translation of CRISPR-based innovations into field-ready varieties. Furthermore, the high cost of genotyping and phenotyping infrastructure remains a barrier to the adoption of genomic breeding in resource-limited national programme settings.

#### *8.1.1. NEPZ-specific Challenges and Documented Breeding Outcomes*

The North Eastern Plains Zone (NEPZ/Zone III), encompassing Bihar, eastern Uttar Pradesh, Jharkhand, West Bengal, Assam, and Odisha, presents a unique combination of production constraints: late sowing (post-rice harvest), terminal heat stress during grain filling (March–April), high humidity, and spot blotch pressure. These constraints demand zone-specific breeding solutions

rather than simple extrapolation from national programmes. The All India Coordinated Research Project on Wheat and Barley (AICRP-W&B) centre at Sabour, Bihar (then part of Bihar Agricultural College under Rajendra Agricultural University, and now Bihar Agricultural University (BAU), Sabour), was strengthened in 1988. Since then, the breeding programme has been directed towards developing varieties for both rainfed and irrigated conditions across the NEPZ. The mandate of the centre includes breeding high-yielding, disease-resistant wheat varieties for different agro-climatic zones of Bihar; developing early-maturing, terminal heat-tolerant varieties suitable for late sowing; and identifying suitable genotypes for terminal heat and leaf blight tolerance. Terminal heat stress is a major constraint for wheat production in the NEPZ, particularly under late-sown conditions. QTL mapping studies have identified heat tolerance QTLs on chromosomes 2B, 7B, and 7D, associated with Canopy Temperature Depression (CTD), grain weight, and grain-filling duration under heat stress [43]. These reported QTLs provide candidate regions for further validation in NEPZ-adapted germplasm across representative target environments before marker-assisted deployment [43, 86, 87]. These findings highlight the potential for genomics-assisted breeding to address terminal heat stress in the EIGP region.

### 8.2. Strategic Recommendations

Broadening the genetic base through systematic utilization of landraces, wild relatives, and pre-bred lines in crossing programmes should be prioritized. The primary gene pool provides the most accessible route for introgression of D-genome diversity [27, 29]. This includes Ae. tauschii and synthetic hexaploids in particular. The secondary gene pool (including Triticum timopheevii, Aegilops kotschyi, Ae. variabilis, and Ae. umbellulata), however, harbours unique disease resistance genes, heat tolerance alleles, and drought adaptation traits unavailable in the primary gene pool [28]. The tertiary gene pool includes Thinopyrum elongatum, Th. intermedium, Leymus racemosus, and Agropyron cristatum. It offers genetic material for extreme heat and drought adaptation, FHB resistance, and novel agronomic traits not present in cultivated wheat or its closer relatives. This pool should be systematically explored through structured pre-breeding programmes [27, 28]. Introgression from secondary and tertiary pool species requires chromosome engineering, but multiple successful transfer events have been documented, including the 7Ag.7DL translocation from Th. ponticum carrying the Lr19 leaf rust resistance gene. Developing heat- and drought-tolerant varieties through introgression of adaptive alleles combined with genomic selection represents a high-priority avenue for EIGP-specific breeding. Investment in controlled environment speed breeding facilities, high-throughput genotyping platforms, and drone-based phenotyping infrastructure at SAUs is essential. Continued implementation and clarification of science-based regulatory frameworks for gene-edited crops, building on India's 2022 SDN-1/SDN-2 exemption and drawing on approaches adopted in the USA and Brazil, could facilitate the development and translation of CRISPR-derived wheat varieties in India. Public-private partnerships modelled on those established in the hybrid seed sector should be encouraged to catalyse investment in advanced wheat breeding technologies.

### 8.3. Future Directions

The future of wheat breeding lies in seamlessly integrating advanced genomic tools, precision phenotyping, and accelerated generation advancement into efficient and cost-effective breeding pipelines. AI and ML methods applied to multi-environment trial data analysis, genomic prediction, and crossing scheme optimization hold significant promise for increasing genetic gain per year [79]. Developing hybrid wheat systems that exploit Cytoplasmic Male Sterility (CMS) and chemical hybridizing agents could further enhance yield potential by capturing heterosis. De novo domestication of wild wheat relatives using CRISPR technology offers a long-term avenue for developing new crop variants combining superior stress tolerance with high yield potential [88]. Systematically harnessing pangenome-level diversity through haplotype-based breeding will be a defining feature of the next generation of wheat improvement programmes.

## CONCLUSION

Wheat remains an indispensable crop for global and Indian food security. Its genetic improvement is more urgent than ever, given a rapidly growing population, accelerating climate change, and evolving biotic stresses. This review has synthesized current knowledge across the spectrum of wheat genetics, genomics, and breeding. The completion of the bread wheat reference genome, development of pangenome resources, and the application of genomic selection, speed breeding, GWAS, and CRISPR-based editing have collectively transformed the wheat improvement landscape. Stability analysis frameworks, including the AMMI model and Eberhart–Russell regression, provide essential statistical tools for identifying broadly adapted and specifically adapted genotypes for multi-environment deployment. This capability is particularly critical for the diverse agro-climatic zones of Bihar and the broader EIGP. The integration of multi-omics data, high-throughput phenotyping, and AI-driven analytical methods within a coherent and well-funded national breeding programme will be essential for achieving the yield gains required to sustainably feed India and the world in the coming decades. Institutions such as IARI and ICAR-IIWBR will play a central role in supporting this effort.

## AUTHORS' CONTRIBUTIONS

The authors confirm their contributions to the paper as follows: A.K: Conceptualization, literature review, writing - original draft preparation, revision and editing. M.K: Literature search, data compilation, writing - review and editing. C.K: Literature synthesis, figure preparation, writing - review. S.K: Supervision, validation, and writing -

final review and editing. All authors reviewed the results and approved the final version of the manuscript.

## LIST OF ABBREVIATIONS

| | | |
|---|---|---|
| CBF | = | C-repeat Binding Factor |
| CIMMYT | = | International Maize and Wheat Improvement Center |
| CSISA | = | Cereal Systems Initiative for South Asia |
| DArTseq | = | Diversity Arrays Technology Sequencing |
| DNA | = | Deoxyribonucleic Acid |
| DREB | = | Dehydration-Responsive Element-Binding |
| GIF1 | = | GRF-Interacting Factor 1 |
| ICARDA | = | International Center for Agricultural Research in the Dry Areas |
| IIWBR | = | Indian Institute of Wheat and Barley Research |
| LED | = | Light-Emitting Diode |
| NAC | = | NAM, ATAF, and CUC transcription factor family |
| PCR | = | Polymerase Chain Reaction |
| RFLPs | = | Restriction Fragment Length Polymorphisms |
| RGB | = | Red-Green-Blue (imaging) |
| RNP | = | Ribonucleoprotein |
| SAS | = | Statistical Analysis System |
| SPSS | = | Statistical Package for the Social Sciences |

## CONSENT FOR PUBLICATION

Not applicable.

## FUNDING

None.

## CONFLICT OF INTEREST

The authors declare no conflict of interest, financial or otherwise.

## ACKNOWLEDGEMENTS

The authors sincerely acknowledge the Department of Genetics and Plant Breeding, Bihar Agricultural University (BAU), Sabour, Bhagalpur, Bihar, for providing the necessary facilities and academic support for this work. This manuscript bears BAU Communication Number 2705/260710. The authors are also grateful to the scientific community and publishers whose valuable works have been cited and reviewed in this manuscript.

## REFERENCES

[1] FAO. FAOSTAT Statistical Database. 2023. Available from: https://www.fao.org/faostat

[2] Shiferaw B, Smale M, Braun HJ, Duveiller E, Reynolds M, Muricho G. Crops that feed the world 10. Past successes and future challenges to the role played by wheat in global food security. Food Secur 2013; 5(3): 291-317. http://dx.doi.org/10.1007/s12571-013-0263-y

[3] van Dijk M, Morley T, Rau ML, Saghai Y. A meta-analysis of projected global food demand and population at risk of hunger for the period 2010–2050. Nat Food 2021; 2(7): 494-501. http://dx.doi.org/10.1038/s43016-021-00322-9 PMID: 37117684

[4] Ray DK, Mueller ND, West PC, Foley JA. Yield trends are insufficient to double global crop production by 2050. PLoS One 2013; 8(6): e66428. http://dx.doi.org/10.1371/journal.pone.0066428 PMID: 23840465

[5] Fischer RA, Byerlee D, Edmeades GO. Crop Yields and Global Food Security: Will Yield Increase Continue to Feed the World? ACIAR Monograph No 158. Canberra: Australian Centre for International Agricultural Research 2014.

[6] Khan H, Mamrutha HM, Mishra CN, *et al*. Harnessing high yield potential in wheat (Triticum aestivum L.) under climate change scenario. Plants 2023; 12(6): 1271. http://dx.doi.org/10.3390/plants12061271 PMID: 36986959

[7] Lobell DB, Schlenker W, Costa-Roberts J. Climate trends and global crop production since 1980. Science 2011; 333(6042): 616-20. http://dx.doi.org/10.1126/science.1204531 PMID: 21551030

[8] Jägermeyr J, Müller C, Ruane AC, *et al*. Climate impacts on global agriculture emerge earlier in new generation of climate and crop models. Nat Food 2021; 2(11): 873-85. http://dx.doi.org/10.1038/s43016-021-00400-y PMID: 37117503

[9] Singh RP, Hodson DP, Jin Y, *et al*. Emergence and spread of new races of wheat stem rust fungus: continued threat to food security and prospects of genetic control. Phytopathology 2015; 105(7): 872-84. http://dx.doi.org/10.1094/PHYTO-01-15-0030-FI PMID: 26120730

[10] Appels R, Eversole K, Stein N, *et al*. Shifting the limits in wheat research and breeding using a fully annotated reference genome. Science 2018; 361(6403): eaar7191. http://dx.doi.org/10.1126/science.aar7191 PMID: 30115783

[11] Walkowiak S, Gao L, Monat C, *et al*. Multiple wheat genomes reveal global variation in modern breeding. Nature 2020; 588(7837): 277-83. http://dx.doi.org/10.1038/s41586-020-2961-x PMID: 33239791

[12] Watson A, Ghosh S, Williams MJ, *et al*. Speed breeding is a powerful tool to accelerate crop research and breeding. Nat Plants 2018; 4(1): 23-9. http://dx.doi.org/10.1038/s41477-017-0083-8 PMID: 29292376

[13] Crossa J, Pérez-Rodríguez P, Cuevas J, *et al*. Genomic selection in plant breeding: methods, models, and perspectives. Trends Plant Sci 2017; 22(11): 961-75. http://dx.doi.org/10.1016/j.tplants.2017.08.011 PMID: 28965742

[14] Eberhart SA, Russell WA. Stability parameters for comparing varieties. Crop Sci 1966; 6(1): 36-40. http://dx.doi.org/10.2135/cropsci1966.0011183X000600010011x

[15] Gauch HG. Model selection and validation for yield trials with interaction. Biometrics 1988; 44(3): 705-15. http://dx.doi.org/10.2307/2531585

[16] Feldman M, Kislev ME. Domestication of emmer wheat and evolution of free-threshing tetraploid wheat. Isr J Plant Sci 2007; 55(3): 207-21. http://dx.doi.org/10.1560/IJPS.55.3-4.207

[17] Dubcovsky J, Dvorak J. Genome plasticity a key factor in the success of polyploid wheat under domestication. Science 2007; 316(5833): 1862-6. http://dx.doi.org/10.1126/science.1143986 PMID: 17600208

[18] Peng JH, Sun D, Nevo E. Domestication evolution, genetics and genomics in wheat. Mol Breed 2011; 28(3): 281-301. http://dx.doi.org/10.1007/s11032-011-9608-4

[19] Salamini F, Özkan H, Brandolini A, Schäfer-Pregl R, Martin W. Genetics and geography of wild cereal domestication in the near east. Nat Rev Genet 2002; 3(6): 429-41. http://dx.doi.org/10.1038/nrg817 PMID: 12042770

[20] Balfourier F, Bouchet S, Robert S, *et al*. Worldwide phylogeography and history of wheat genetic diversity. Sci Adv

2019; 5(5): eaav0536.
http://dx.doi.org/10.1126/sciadv.aav0536 PMID: 31149630

[21] Aury JM, Engelen S, Istace B, *et al*. Long-read and chromosome-scale assembly of the hexaploid wheat genome achieves high resolution for research and breeding. Gigascience 2022; 11: giac034.
http://dx.doi.org/10.1093/gigascience/giac034 PMID: 35482491

[22] Liu S, Li K, Dai X, *et al*. A telomere-to-telomere genome assembly coupled with multi-omic data provides insights into the evolution of hexaploid bread wheat. Nat Genet 2025; 57(4): 1008-20.
http://dx.doi.org/10.1038/s41588-025-02137-x PMID: 40195562

[23] Tiwari VK, Saripalli G, Sharma PK, Poland J. Wheat genomics: genomes, pangenomes, and beyond. Trends Genet 2024; 40(11): 982-92.
http://dx.doi.org/10.1016/j.tig.2024.07.004 PMID: 39191555

[24] Schreiber M, Jayakodi M, Stein N, Mascher M. Plant pangenomes for crop improvement, biodiversity and evolution. Nat Rev Genet 2024; 25(8): 563-77.
http://dx.doi.org/10.1038/s41576-024-00691-4 PMID: 38378816

[25] Jiao C, Xie X, Hao C, *et al*. Pan-genome bridges wheat structural variations with habitat and breeding. Nature 2025; 637(8045): 384-93.
http://dx.doi.org/10.1038/s41586-024-08277-0 PMID: 39604736

[26] Sansaloni C, Franco J, Santos B, *et al*. Diversity analysis of 80,000 wheat accessions reveals consequences and opportunities of selection footprints. Nat Commun 2020; 11(1): 4572.
http://dx.doi.org/10.1038/s41467-020-18404-w PMID: 32917907

[27] Ogbonnaya FC, Abdalla O, Mujeeb-Kazi A, Kazi AG, Xu SS, Gosman N, *et al*. Synthetic hexaploids: harnessing species of the primary gene pool for wheat improvement. Plant Breed Rev 2013; 37: 35-122.
http://dx.doi.org/10.1002/9781118497869.ch2

[28] Mohler V, Paczos-Grzęda E, Sowa S. Loving the Alien: The Contribution of the Wild in Securing the Breeding of Cultivated Hexaploid Wheat and Oats. Agriculture 2023; 13(11): 2060.
http://dx.doi.org/10.3390/agriculture13112060

[29] Ali M, Danting S, Wang J, *et al*. Genetic diversity and selection signatures in synthetic-derived wheats and modern spring wheat. Front Plant Sci 2022; 13: 877496.
http://dx.doi.org/10.3389/fpls.2022.877496 PMID: 35903232

[30] Hedden P. The genes of the Green Revolution. Trends Genet 2003; 19(1): 5-9.
http://dx.doi.org/10.1016/S0168-9525(02)00009-4 PMID: 12493241

[31] Simmonds J, Scott P, Brinton J, *et al*. A splice acceptor site mutation in TaGW2-A1 increases thousand grain weight in tetraploid and hexaploid wheat through wider and longer grains. Theor Appl Genet 2016; 129(6): 1099-112.
http://dx.doi.org/10.1007/s00122-016-2686-2 PMID: 26883045

[32] Huerta-Espino J, Singh RP, Germán S, *et al*. Global status of wheat leaf rust caused by Puccinia triticina. Euphytica 2011; 179(1): 143-60.
http://dx.doi.org/10.1007/s10681-011-0361-x

[33] Hafeez AN, Arora S, Ghosh S, Gilbert D, Bowden RL, Wulff BBH. Creation and judicious application of a wheat resistance gene atlas. Mol Plant 2021; 14(7): 1053-70.
http://dx.doi.org/10.1016/j.molp.2021.05.014 PMID: 33991673

[34] McIntosh RA, Dubcovsky J, Rogers WJ, Morris C, Appels R, Xia XC. Catalogue of gene symbols for wheat: 2013–2014 supplement. Annu Wheat Newsl 2014; 60: •••.https://wheat.pw.usda.gov/GG3/sites/default/files/WGC-2014.pdf

[35] Herrera-Foessel SA, Singh RP, Lillemo M, *et al*. Lr67/Yr46 confers adult plant resistance to stem rust and powdery mildew in wheat. Theor Appl Genet 2014; 127(4): 781-9.
http://dx.doi.org/10.1007/s00122-013-2256-9 PMID: 24408377

[36] Davis HR, Chia T, Rhodes H, *et al*. First large-scale breakdown of Yr15 resistance to wheat yellow rust (Puccinia striiformis f. sp. tritici) recorded globally. New Dis Rep 2025; 52(2): e70067.
http://dx.doi.org/10.1002/ndr2.70067

[37] Marchal C, Zhang J, Zhang P, *et al*. BED-domain-containing immune receptors confer diverse resistance spectra to yellow rust. Nat Plants 2018; 4(9): 662-8.
http://dx.doi.org/10.1038/s41477-018-0236-4 PMID: 30150615

[38] Liu S, Hall MD, Griffey CA, McKendry AL. Meta-analysis of QTL associated with Fusarium head blight resistance in wheat. Crop Sci 2009; 49(6): 1955-68.
http://dx.doi.org/10.2135/cropsci2009.03.0115

[39] Chen PD, Qi LL, Zhou B, Zhang SZ, Liu DJ. Development and molecular cytogenetic analysis of wheat-Haynaldia villosa 6VS/6AL translocation lines specifying resistance to powdery mildew. Theor Appl Genet 1995; 91(91): 1125-8.
http://dx.doi.org/10.1007/BF00223930 PMID: 24170007

[40] Wang Y, Cheng X, Shan Q, *et al*. Simultaneous editing of three homoeoalleles in hexaploid bread wheat confers heritable resistance to powdery mildew. Nat Biotechnol 2014; 32(9): 947-51.
http://dx.doi.org/10.1038/nbt.2969 PMID: 25038773

[41] Shewry PR, Hey SJ. The contribution of wheat to human diet and health. Food Energy Secur 2015; 4(3): 178-202.
http://dx.doi.org/10.1002/fes3.64 PMID: 27610232

[42] Uauy C, Distelfeld A, Fahima T, Blechl A, Dubcovsky J. A NAC Gene regulating senescence improves grain protein, zinc, and iron content in wheat. Science 2006; 314(5803): 1298-301.
http://dx.doi.org/10.1126/science.1133649 PMID: 17124321

[43] Paliwal R, Röder MS, Kumar U, Srivastava JP, Joshi AK. QTL mapping of terminal heat tolerance in hexaploid wheat (T. aestivum L.). Theor Appl Genet 2012; 125(3): 561-75.
http://dx.doi.org/10.1007/s00122-012-1853-3 PMID: 22476874

[44] Morran S, Eini O, Pyvovarenko T, *et al*. Improvement of stress tolerance of wheat and barley by modulation of expression of DREB/CBF factors. Plant Biotechnol J 2011; 9(2): 230-49.
http://dx.doi.org/10.1111/j.1467-7652.2010.00547.x PMID: 20642740

[45] Wang C, Deng P, Chen L, *et al*. A wheat WRKY transcription factor TaWRKY10 confers tolerance to multiple abiotic stresses in transgenic tobacco. PLoS One 2013; 8(6): e65120.
http://dx.doi.org/10.1371/journal.pone.0065120 PMID: 23762295

[46] Lindsay MP, Lagudah ES, Hare RA, Munns R. A locus for sodium exclusion (Nax1), a trait for salt tolerance, mapped in durum wheat. Funct Plant Biol 2004; 31(11): 1105-14.
http://dx.doi.org/10.1071/FP04111 PMID: 32688978

[47] Munns R, James RA, Xu B, *et al*. Wheat grain yield on saline soils is improved by an ancestral Na+ transporter gene. Nat Biotechnol 2012; 30(4): 360-4.
http://dx.doi.org/10.1038/nbt.2120 PMID: 22407351

[48] Prasad P, Thakur R, Bhardwaj SC, *et al*. Virulence and genetic analysis of *Puccinia graminis tritici* in the Indian sub-continent from 2016 to 2022 and evaluation of wheat varieties for stem rust resistance. Front Plant Sci 2023; 14: 1196808.
http://dx.doi.org/10.3389/fpls.2023.1196808 PMID: 37521927

[49] Wu L, He X, He Y, *et al*. Genetic sources and loci for Fusarium head blight resistance in bread wheat. Front Genet 2022; 13: 988264.
http://dx.doi.org/10.3389/fgene.2022.988264 PMID: 36246592

[50] Farahani H, Moghaddam ME, Mohammadi A, Nezhad KZ, Naghipour F. Effect of high molecular weight glutenin subunits on wheat quality properties, across a wide range of climates and environments in Iran. Physiol Mol Biol Plants 2023; 29(6): 889-902.
http://dx.doi.org/10.1007/s12298-023-01324-6 PMID: 37520809

[51] Gupta OP, Singh A, Pandey V, *et al*. Critical assessment of wheat biofortification for iron and zinc: a comprehensive review of conceptualization, trends, approaches, bioavailability, health impact, and policy framework. Front Nutr 2024; 10: 1310020.
http://dx.doi.org/10.3389/fnut.2023.1310020 PMID: 38239835

[52] Rajaram S, van Ginkel M, Fischer RA. CIMMYT's wheat breeding mega-environments (ME). Proceedings of the 8th International Wheat Genetics Symposium. 1993 Jul 20–25; Beijing, China. Beijing: China: Agricultural Scientech Press 1994; pp. 1101-6.

[53] Khare V, Shukla RS, Pandey S, Singh SK, Singh C. Exploring the genotype-environment interaction of bread wheat in ambient and high-temperature planting conditions: a rigorous investigation. Sci Rep 2024; 14(1): 2402. http://dx.doi.org/10.1038/s41598-024-53052-w PMID: 38287162

[54] Forster BP, Heberle-Bors E, Kasha KJ, Touraev A. The resurgence of haploids in higher plants. Trends Plant Sci 2007; 12(8): 368-75. http://dx.doi.org/10.1016/j.tplants.2007.06.007 PMID: 17629539

[55] Miedaner T, Korzun V. Marker-assisted selection for disease resistance in wheat and barley breeding. Phytopathology 2012; 102(6): 560-6. http://dx.doi.org/10.1094/PHYTO-05-11-0157 PMID: 22568813

[56] Meuwissen THE, Hayes BJ, Goddard ME. Prediction of total genetic value using genome-wide dense marker maps. Genetics 2001; 157(4): 1819-29. http://dx.doi.org/10.1093/genetics/157.4.1819 PMID: 11290733

[57] Rutkoski JE, Heffner EL, Sorrells ME. Genomic selection for durable stem rust resistance in wheat. Euphytica 2011; 179(1): 161-73. http://dx.doi.org/10.1007/s10681-010-0301-1

[58] Ghosh S, Watson A, Gonzalez-Navarro OE, *et al*. Speed breeding in growth chambers and glasshouses for crop breeding and model plant research. Nat Protoc 2018; 13(12): 2944-63. http://dx.doi.org/10.1038/s41596-018-0072-z PMID: 30446746

[59] Zhang Y, Liang Z, Zong Y, *et al*. Efficient and transgene-free genome editing in wheat through transient expression of CRISPR/Cas9 DNA or RNA. Nat Commun 2016; 7(1): 12617. http://dx.doi.org/10.1038/ncomms12617 PMID: 27558837

[60] Chen K, Wang Y, Zhang R, Zhang H, Gao C. CRISPR/Cas genome editing and precision plant breeding in agriculture. Annu Rev Plant Biol 2019; 70(1): 667-97. http://dx.doi.org/10.1146/annurev-arplant-050718-100049 PMID: 30835493

[61] Alemu A, Åstrand J, Montesinos-López OA, *et al*. Genomic selection in plant breeding: Key factors shaping two decades of progress. Mol Plant 2024; 17(4): 552-78. http://dx.doi.org/10.1016/j.molp.2024.03.007 PMID: 38475993

[62] Dreisigacker S, Pérez-Rodríguez P, Crespo-Herrera L, Bentley AR, Crossa J. Results from rapid-cycle recurrent genomic selection in spring bread wheat. G3 (Bethesda) 2023; 13(4): jkad025. http://dx.doi.org/10.1093/g3journal/jkad025 PMID: 36702618

[63] Crespo-Herrera LA, Crossa J, Huerta-Espino J, *et al*. Genetic gains for grain yield in CIMMYT's semi-arid wheat yield trials grown in suboptimal environments. Crop Sci 2018; 58(5): 1890-8. http://dx.doi.org/10.2135/cropsci2018.01.0017 PMID: 33343013

[64] Ćeran M, Miladinović D, Đorđević V, *et al*. Genomics-assisted speed breeding for crop improvement: present and future. Front Sustain Food Syst 2024; 8: 1383302. http://dx.doi.org/10.3389/fsufs.2024.1383302

[65] Voss-Fels KP, Cooper M, Hayes BJ. Accelerating crop genetic gains with genomic selection. Theor Appl Genet 2019; 132(3): 669-86. http://dx.doi.org/10.1007/s00122-018-3270-8 PMID: 30569365

[66] Liang Z, Chen K, Li T, *et al*. Efficient DNA-free genome editing of bread wheat using CRISPR/Cas9 ribonucleoprotein complexes. Nat Commun 2017; 8(1): 14261. http://dx.doi.org/10.1038/ncomms14261 PMID: 28098143

[67] Debernardi JM, Tricoli DM, Ercoli MF, *et al*. A GRF–GIF chimeric protein improves the regeneration efficiency of transgenic plants. Nat Biotechnol 2020; 38(11): 1274-9. http://dx.doi.org/10.1038/s41587-020-0703-0 PMID: 33046875

[68] Qian Q, Hu W, Yu Y, *et al*. Overexpression of TaCR4-A positively regulates grain size in Triticum aestivum. BMC Plant Biol 2025; 25(1): 1273. http://dx.doi.org/10.1186/s12870-025-07345-5 PMID: 41034700

[69] Yan W, Hunt LA, Sheng Q, Szlavnics Z. Cultivar evaluation and mega-environment investigation based on the GGE biplot. Crop Sci 2000; 40(3): 597-605. http://dx.doi.org/10.2135/cropsci2000.403597x

[70] Yan W, Kang MS. GGE Biplot Analysis: A Graphical Tool for Breeders, Geneticists, and Agronomists. Boca Raton: CRC Press 2003.

[71] Purchase JL, Hatting H, van Deventer CS. Genotype × environment interaction of winter wheat ( *Triticum aestivum* L.) in South Africa: II. Stability analysis of yield performance. S Afr J Plant Soil 2000; 17(3): 101-7. http://dx.doi.org/10.1080/02571862.2000.10634878

[72] Gauch HG, Zobel RW. AMMI analysis of yield trials. In: Kang MS, Gauch HG, Eds. Genotype-by-Environment Interaction. Boca Raton: CRC Press 1996; pp. 85-122. http://dx.doi.org/10.1201/9781420049374.ch4

[73] Reynolds M, Atkin OK, Bennett M, *et al*. Addressing research bottlenecks to crop productivity. Trends Plant Sci 2021; 26(6): 607-30. http://dx.doi.org/10.1016/j.tplants.2021.03.011 PMID: 33893046

[74] Kollers S, Rodemann B, Ling J, *et al*. Whole genome association mapping of Fusarium head blight resistance in European winter wheat (Triticum aestivum L.). PLoS One 2013; 8(2): e57500. http://dx.doi.org/10.1371/journal.pone.0057500 PMID: 23451238

[75] Velu G, Singh RP, Crespo-Herrera L, *et al*. Genetic dissection of grain zinc concentration in spring wheat for mainstreaming biofortification in CIMMYT wheat breeding. Sci Rep 2018; 8(1): 13526. http://dx.doi.org/10.1038/s41598-018-31951-z PMID: 30201978

[76] Tong J, Zhao C, Sun M, *et al*. High-resolution genome-wide association studies reveal rich genetic architectures of grain zinc and iron in common wheat (Triticum aestivum L.). Front Plant Sci 2022; 13: 840614. http://dx.doi.org/10.3389/fpls.2022.840614 PMID: 35371186

[77] Araus JL, Cairns JE. Field high-throughput phenotyping: the new crop breeding frontier. Trends Plant Sci 2014; 19(1): 52-61. http://dx.doi.org/10.1016/j.tplants.2013.09.008 PMID: 24139902

[78] Bhandari M, Chang A, Jung J, *et al*. Unmanned aerial system-based high-throughput phenotyping for plant breeding. Plant Phenome J 2023; 6(1): e20058. http://dx.doi.org/10.1002/ppj2.20058

[79] Sandhu KS, Mihalyov PD, Lewien MJ, Pumphrey MO, Carter AH. Combining genomic and phenomic information for predicting grain protein content and grain yield in spring wheat. Front Plant Sci 2021; 12: 613300. http://dx.doi.org/10.3389/fpls.2021.613300 PMID: 33643347

[80] Montesinos-López A, Crespo-Herrera L, Dreisigacker S, *et al*. Deep learning methods improve genomic prediction of wheat breeding. Front Plant Sci 2024; 15: 1324090. http://dx.doi.org/10.3389/fpls.2024.1324090 PMID: 38504889

[81] Kaushal S, Gill HS, Billah MM, *et al*. Enhancing the potential of phenomic and genomic prediction in winter wheat breeding using high-throughput phenotyping and deep learning. Front Plant Sci 2024; 15: 1410249. http://dx.doi.org/10.3389/fpls.2024.1410249 PMID: 38872880

[82] Wang C, Zhang D, Ma Y, Zhao Y, Liu P, Li X. WheatGP, a genomic prediction method based on CNN and LSTM. Brief Bioinform 2025; 26(2): bbaf191. http://dx.doi.org/10.1093/bib/bbaf191 PMID: 40275535

[83] Rezaei EE, Webber H, Asseng S, *et al*. Climate change impacts on crop yields. Nat Rev Earth Environ 2023; 4(12): 831-46. http://dx.doi.org/10.1038/s43017-023-00491-0

[84] Singh H, Kaur J, Bala R, *et al*. Residual effect of defeated stripe rust resistance genes/QTLs in bread wheat against prevalent pathotypes of Puccinia striiformis f. sp. tritici. PLoS One 2022; 17(4): e0266482. http://dx.doi.org/10.1371/journal.pone.0266482 PMID: 35363829

[85] Islam MT, Croll D, Gladieux P, *et al*. Emergence of wheat blast in Bangladesh was caused by a South American lineage of Magnaporthe oryzae. BMC Biol 2016; 14(1): 84. http://dx.doi.org/10.1186/s12915-016-0309-7 PMID: 27716181

[86] Manjunath KK, Krishna H, Devate NB, *et al*. QTL mapping: insights into genomic regions governing component traits of yield under combined heat and drought stress in wheat. Front Genet 2024; 14: 1282240.

http://dx.doi.org/10.3389/fgene.2023.1282240 PMID: 38269367

[87] Kumar S, Kumar H, Gupta V, *et al*. Capturing agro-morphological variability for tolerance to terminal heat and combined heat–drought stress in landraces and elite cultivar collection of wheat. Front Plant Sci 2023; 14: 1136455. http://dx.doi.org/10.3389/fpls.2023.1136455 PMID: 37251757

[88] Fernie AR, Yan J. De novo domestication: An alternative route toward new crops for the future. Mol Plant 2019; 12(5): 615-31. http://dx.doi.org/10.1016/j.molp.2019.03.016 PMID: 30999078