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Wheat Quality and Biofortification: Genetic Basis, Breeding Progress, and Future Prospects

Jagdeep Singh Randhawa[1], Lenika Kashyap[2], Satinder Singh[2], Arshvir Kaur Boparai[2], Satinder Kaur[3] and Achla Sharma[2]

[1] *Department of Biochemistry, Punjab Agricultural University, Ludhiana-141001, Punjab, India*
[2] *Department of Plant Breeding & Genetics, Punjab Agricultural University, Ludhiana-141001, Punjab, India*
[3] *School of Agricultural Biotechnology, Punjab Agricultural University, Ludhiana-141001, Punjab, India*

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****Corresponding author:***
E-mail: deeprandhawa716@gmail.com

Abstract

Wheat (*Triticum aestivum* L.) is a major global staple crop, providing a significant share of dietary calories and protein. However, its low micronutrient density, particularly in iron (Fe) and zinc (Zn), contributes to widespread hidden hunger. This review synthesizes current knowledge on the biochemical, genetic, and molecular determinants of wheat grain quality, including protein composition, starch structure, lipids, dietary fiber, vitamins, and minerals, with emphasis on the interaction of genetic and environmental factors (G × E). Recent advances in breeding approaches, including QTL mapping, genome-wide association studies (GWAS), marker-assisted selection, and genome editing, have accelerated the development of nutritionally improved wheat varieties. Key challenges such as storage protein regulation, imbalanced amino acid composition, and reduced micronutrient bioavailability due to antinutritional factors like phytic acid are also highlighted. The review further explores physiological and molecular mechanisms underlying micronutrient uptake, transport, and grain loading, identifying critical targets for biofortification. It emphasizes the integration of genetic improvement with agronomic strategies and advanced phenotyping as a sustainable approach to enhance nutrient density. Overall, a multidisciplinary strategy combining genetics, physiology, and agronomy is essential to develop high-yielding, nutritionally superior wheat varieties for improved global food and nutritional security.

Keywords: Bioavailability, biofortification, micronutrients, minerals, quality, wheat

1. Introduction

Wheat (*Triticum aestivum* L.) is one of the most widely cultivated cereal crops worldwide and serves as a major source of energy, protein, and essential micronutrients for more than one-third of the global population. Beyond its quantitative contribution to food security, wheat plays a central role in human nutrition, making its grain quality a critical determinant of both processing performance and dietary value (Tanin *et al.*, 2024). Wheat grain quality is a complex and multifactorial trait governed by the interaction of genetic, environmental, and management factors. Although continuous genetic improvement has led to substantial gains in yield and adaptability, this progress has often been accompanied by a narrowing of genetic diversity, particularly for traits related to grain quality, nutritional composition, and health-promoting components (Hickey *et al.*, 2019). As a consequence, many modern high-yielding cultivars exhibit reduced grain protein concentration, lower micronutrient density, limited diversity of bioactive compounds, and suboptimal

starch and dietary fibre profiles. Micronutrients such as iron (Fe), zinc (Zn), selenium (Se), and magnesium (Mg) are essential for human health; however, their concentrations in wheat grain are frequently insufficient to meet dietary requirements (Islam *et al.*, 2024). This inadequacy contributes to micronutrient malnutrition, or "hidden hunger," which affects billions of people worldwide and is further exacerbated by climate change. Deficiencies of Fe and Zn, in particular, are associated with impaired immune function, reduced cognitive development, and increased disease burden (Amiri *et al.*, 2018). Despite increases in global food production, improvements in nutritional quality have lagged behind, underscoring the urgent need to enhance the nutrient density of staple crops (Shahid *et al.*, 2025).

Enhancing the nutritional quality of wheat is therefore essential, particularly for economically vulnerable populations that rely heavily on it as a dietary staple (Singla and Grover, 2017). Simultaneously, evolving dietary patterns, increased consumer awareness, and the rising prevalence of lifestyle-related disorders such as diabetes and cardiovascular diseases have intensified the demand for wheat varieties with improved functional and nutritional properties (Simmonds, 1989; Giraldo *et al.*, 2020). In this context, biofortification has emerged as a sustainable and cost-effective strategy to improve the micronutrient content of staple crops. It involves enhancing both nutrient concentration and bioavailability through genetic (breeding and biotechnology) as well as agronomic interventions (Dagnaw *et al.*, 2022). Among these approaches, genetic biofortification offers a long-term solution, particularly suited for resource-limited regions. However, improving micronutrient density in wheat remains challenging due to the need to balance yield, grain quality, and nutritional traits, all of which are influenced by complex genotype × environment interactions (Zhao *et al.*, 2009). The strategies employed to improve wheat quality and nutritional value have evolved considerably over the past several decades, progressing from conventional phenotype-based selection to increasingly precise molecular and genomic approaches. Early improvement programs relied primarily on hybridization, phenotypic selection, and the exploitation of genetic variation present in landraces and wild relatives. Subsequent advances in molecular genetics introduced quantitative trait locus (QTL) mapping, marker-assisted selection (MAS), and genome-wide association studies (GWAS), enabling the identification and targeted utilization of genomic regions associated with grain quality and micronutrient accumulation (Li *et al.*, 2025). More recently, genomic selection (GS), high-throughput phenotyping, multi-omics approaches, and precision genome-editing technologies such as CRISPR/Cas have further accelerated wheat improvement by facilitating the simultaneous selection and modification of multiple complex traits (Hao *et al.*, 2024). In particular, advances in genomics and breeding have enabled the identification of QTLs and candidate genes underlying iron (Fe) and zinc (Zn) accumulation, providing new opportunities to mitigate the long-standing trade-off between grain yield and micronutrient concentration (Guarin *et al.*, 2022). However, increasing the concentration of Fe and Zn alone does not necessarily translate into improved nutritional value, because the physiological availability of these minerals is strongly influenced by their chemical environment within the grain. Antinutritional compounds, particularly phytic acid, can bind Fe and Zn and reduce their absorption in the human gastrointestinal tract, whereas compounds such as ascorbic acid, sulfur-containing amino acids, and carotenoids can enhance mineral bioavailability (Hakeem *et al.*, 2025). Thus, the focus of wheat biofortification is gradually shifting from simply increasing mineral concentration toward a more comprehensive strategy that considers both nutrient accumulation and bioavailability. Integrating these complementary targets with advances in genomics, molecular breeding, and precision biotechnology could therefore provide a more effective route for developing wheat cultivars with enhanced nutritional quality and greater potential to alleviate micronutrient malnutrition (Velu *et al.*, 2014).

Despite significant progress in identifying genomic regions, candidate genes, and breeding approaches for micronutrient enhancement, the available information remains fragmented across genetic, physiological, and breeding studies. A comprehensive synthesis integrating advances in genomics, molecular breeding, biofortification strategies, and factors influencing micronutrient bioavailability is still lacking, limiting the effective utilization of these findings in wheat improvement programs. To address this gap, the present review systematically compiles and critically evaluates published literature from peer-reviewed journals, focusing on the

genetic basis of iron and zinc accumulation, genomic tools, breeding strategies, and determinants of micronutrient bioavailability. By integrating these diverse aspects, this review aims to provide a comprehensive understanding of current progress, identify existing knowledge gaps, and highlight future research directions for developing nutritionally enriched wheat cultivars.

2. Wheat grain quality: Concepts and determinants

Wheat grain is primarily composed of carbohydrates, proteins, and cell wall polysaccharides, which together account for about 90% of its dry weight, while minor components are lipids, phenolics, vitamins, and minerals (Shewry, 2024). Structurally, the grain consists of germ (2–3%), bran (13–17%), and endosperm (80–85%). The bran, forming the outer protective layers, is rich in B vitamins, minerals, and dietary fiber. It mainly contains cellulose and pentosans (arabinoxylans), which are complex polymers of xylose and arabinose associated with proteins. Bran also contains ~16% proteins and carbohydrates combined and 2–7% minerals (Cornell, 2012). The aleurone layer, the innermost part of the bran, consists of living cells rich in proteins and enzymes essential for germination. The endosperm, particularly the mealy endosperm, constitutes the bulk of the grain and contains ~13% protein and ~1.5% fat. It includes storage proteins (glutenins and gliadins) that form gluten, along with albumins and globulins. However, it has relatively low mineral and dietary fiber content. The relative distribution and interaction of these components ultimately define wheat grain quality, influencing milling performance, dough characteristics, and end-use applications. The distribution of these constituents within different grain tissues ultimately determines milling performance, flour composition, dough rheology, nutritional quality, and processing characteristics. Consequently, wheat grain quality arises from the combined influence of physical grain attributes together with the biochemical composition of proteins and starch.

Among the physical determinants, grain hardness stands out as a defining trait, shaping wheat classification, milling behavior, and product suitability. This property is largely controlled by the Hardness (Ha) locus on chromosome 5DS, where the *Pina-D1* and *Pinb-D1* genes encode puroindoline proteins that regulate the interaction between starch granules and the surrounding protein matrix. Functional alleles promote a softer kernel texture, whereas mutations disrupt this interaction, producing harder grains with distinct milling and functional characteristics (Issarny *et al.*, 2017; Saini *et al.*, 2022). However, traits such as kernel size, uniformity, and test weight collectively determine the efficiency with which wheat can be processed. Test weight, an indicator of grain bulk density and overall soundness, reflects both genetic background and environmental influences during grain development (Saini *et al.*, 2022). Uniform kernel size further enhances milling consistency, ensuring predictable flour yield and quality (Fu *et al.*, 2017). These physical characteristics ultimately converge during milling, where they dictate flour extraction efficiency and economic return. Typical flour recovery ranges between 70–80%, but this is highly dependent on grain integrity and composition. Beyond milling, the functional implications of these traits become even more pronounced, as wheat is transformed into a wide array of food products with distinct quality requirements (Shahid *et al.*, 2025). For bread-making, medium to hard wheat is generally preferred due to its superior water absorption and strong gluten network, which together support dough elasticity, gas retention, and final loaf volume. In contrast, products such as *chapati* require a more extensible dough with moderate protein strength, while steamed bread demands softer texture and lighter color. Noodle production introduces additional complexity, where both protein content and starch properties must be finely balanced: softer wheat with higher starch viscosity is suited for white salted noodles, whereas firmer gluten strength is essential for alkaline noodle types (Nagao, 1995; Peña, 2002; Hao *et al.*, 2024). Durum wheat represents a specialized case, primarily used for pasta and related products. Its inherently hard texture enables the production of coarse semolina with high purity and desirable particle size. Although these physical properties largely determine processing efficiency, the functional quality of wheat products is primarily dictated by the biochemical composition of the grain, particularly its proteins and starch (Subira *et al.*, 2014).

Proteins constitute the principal biochemical determinant of wheat processing quality because they govern dough formation, viscoelastic behavior, and end-product characteristics. Based on method developed by T.B. Osborne, wheat proteins are categorized according to

their extractability and solubility in various solvents. Based on this, wheat proteins are grouped into four fractions: albumins (water-soluble), globulins (salt-soluble), gliadins (alcohol-soluble), and glutenins (soluble in dilute acid or alkali). Each fraction contributes uniquely to flour functionality–gliadins impart viscosity and extensibility, while glutenins provide elasticity and strength–together defining the processing and end-use quality of wheat. Despite the emergence of advanced proteomic tools, this solubility-based system continues to underpin modern analytical approaches such as SDS-PAGE and HPLC (Neeraja *et al.*, 2017; Gupta *et al.*, 2024). Albumins and globulins constitute the metabolically active fraction of wheat proteins, generally characterized by lower and overlapping molecular weight ranges. These fractions are rich in enzymes and regulatory proteins involved in grain development, germination, and cellular metabolism. However, their separation is not always precise, as extraction conditions can lead to partial overlap or cross-contamination, highlighting the practical limitations of strict classification (Gupta *et al.*, 2021; Hao *et al.*, 2024). In contrast, gliadins and glutenins are the principal storage proteins of the wheat endosperm, collectively accounting for the majority of total grain protein. Gliadins are monomeric and confer dough extensibility, whereas glutenins form large polymeric structures through disulfide bonding, providing elasticity and strength. Upon hydration, their interaction gives rise to the viscoelastic gluten network that is central to wheat's unique bread-making properties. Although predominantly localized in the endosperm, trace amounts of these proteins may also be detected in outer grain layers depending on extraction and tissue separation methods (Shewry *et al.*, 2013). Alongside proteins, starch represents the second major biochemical determinant of wheat quality, accounting for approximately 60–75% of grain dry weight and serving as the primary energy reserve. Wheat starch occurs as granules of two types: large lenticular granules (25–40 µm) formed within the first 15 days after pollination, and small spherical granules (5–10 µm) that develop between 10 and 30 days and account for about 88% of total granules (Gupta *et al.*, 2024).

Starch consists of two glucose polymers: amylose, a mostly linear α-(1→4)-linked polymer with a degree of polymerization of 1,000–5,000, and amylopectin, a highly branched polymer with α-(1→4) chains and α-(1→6) linkages, with an average chain length of 20–25 units and much higher molecular weight (Guzman and Alvarez, 2016). In wheat, the amylose to amylopectin ratio remains relatively constant at about 20–30% and 70–80%, respectively. Recent advances in wheat genomics, molecular breeding, and genome editing have transformed starch from a passive storage component into an important breeding target for improving both processing quality and nutritional value. Its composition can be strategically modified through alterations in key biosynthetic pathways, thereby enabling the development of wheat with tailored functional and nutritional properties (Nirmani *et al.*, 2024).

Starch biosynthesis is orchestrated by a coordinated network of enzymes, including ADP-glucose pyrophosphorylase, starch synthases, and branching and debranching enzymes, which collectively regulate the architecture of amylose and amylopectin. Variations in the activity of these enzymes–arising from natural mutations or targeted interventions–have been shown to significantly alter starch structure. For example, disruption of starch synthase IIa (SSIIa) function across the wheat genomes leads to elevated amylose content, while suppression of starch-branching enzymes results in profound shifts in starch organization and functionality (Yamamori *et al.*, 2000; Regina *et al.*, 2006; Konik-Rose *et al.*, 2007). These structural modifications are of particular interest due to their direct impact on the formation of resistant starch (RS), a physiologically important fraction that escapes digestion in the small intestine and is fermented in the colon. High-amylose wheat lines, in particular, are closely associated with increased RS content, linking starch architecture with enhanced nutritional value (Jia *et al.*, 2025).

From a health perspective, resistant starch plays a multifaceted role by promoting the production of short-chain fatty acids, especially butyrate, which supports colonic health, improves glycemic regulation, and reduces the risk of metabolic disorders such as type II diabetes. This major significance leads to starch modification as a critical target in modern wheat improvement strategies. A comprehensive classification and functional overview of these resistant starch types is presented in Table 1.

Table 1. Classification of resistant starch

Type	Nature	Occurrence	Digestibility	References
RS1	Physically encapsulated starch granules within intact cell walls or protein matrices	Whole or coarsely milled wheat kernels	Rapidly digested after milling or homogenization	Wang *et al.*, 2026
RS2 (RS2A: raw amylopectin; RS2B: raw amylose)	Native granular starch with compact B-type crystallinity	Raw potatoes, banana, high-amylose maize	Rapidly digested after heating	Wang *et al.*, 2026
RS3	Retrograded starch formed when gelatinized starch cools	Cooked bread and potatoes; high-amylose corn and wheat-based products	Resistant to enzymatic degradation	Nguyen *et al.*, 2023; Wang *et al.*, 2025
RS4	Chemically modified starches (phosphate-crosslinked, esterified, etherified, acetylated)	Engineered modified starches	Resistant to digestive enzymes due to chemical modification	Jia *et al.*, 2025

Overall, wheat grain quality emerges from the coordinated interplay of grain structure, physical attributes, protein composition, starch architecture, and nutrient metabolism, underpinned by a complex genetic framework and modulated by the environment (Nirmani *et al.*, 2024). Understanding these interrelationships provides the basis for dissecting the genetic determinants of quality and for combining favorable alleles through modern breeding approaches. Advances in genomics, high-throughput phenotyping, and precision breeding are therefore creating new opportunities to simultaneously improve processing performance, nutritional value, and health-promoting properties in wheat.

3. Genetic basis of wheat quality: From storage protein families to starch composition

3.1. Glutenin and gliadin gene families

Wheat quality is primarily determined by storage proteins, especially glutenins and gliadins. Alleles such as *Glu-D1* (5+10) and *Glu-B1* (17+18) are linked to superior dough strength and elasticity (Payne, 1987). Although six genes encode High-Molecular-Weight Glutenin Subunits (HMW-GS), gene silencing limits expression to three to five subunits per genotype (Ma *et al.*, 2003). The *Ay* subunit and avenin-like proteins further enhance grain protein content and dough quality (Roy *et al.*, 2021; Chen *et al.*, 2020), and HMW-GS allele scoring remains valuable in breeding. Grain quality traits are polygenic, controlled by multiple QTLs. Major loci for grain protein content occur on chromosomes 2A, 2B, 2D, 3D, 4A, 6B, 7A, and 7D, with strong effects on 6B and 7A (Zhou *et al.*, 2025). Combined QTL and GWAS analyses have refined key regions on 3B, 7A, and 7B, along with stable SNPs on 6B (Gao *et al.*, 2018). Loci for glutenin macropolymer content on 2A, 3B, 4A, 7A, and 7B further emphasize the importance of 3B and 7B in protein quality regulation (Gao *et al.*, 2018). Given the complexity and polygenic nature of wheat quality traits, numerous genes and molecular markers have been identified that collectively regulate protein composition, grain hardness, and starch functionality (Gupta *et al.*, 2024; Che *et al.*, 2025). A summary of major genes associated with wheat end-use quality traits is presented in Table 2.

These genes highlight the interconnected genetic control of wheat quality traits, where protein composition, starch structure, and grain texture collectively determine end-use performance

3.2. Transcriptional and epigenetic regulation of wheat storage proteins

Wheat seed storage protein synthesis is a tightly regulated process that is initiated during the middle to late stages of grain filling and is predominantly controlled at the transcriptional level (Gao *et al.*, 2021). This regulation is mediated through conserved cis-acting elements present in the promoter regions of storage protein genes, including GCN4-like motifs, G-box, P-box, RY-box, and MYB binding sites, which collectively coordinate endosperm-specific gene expression (Ravel *et al.*, 2014). A complex network of transcription factors (TFs) interacts with these regulatory elements to modulate the expression of glutenin and gliadin genes. These TFs function both independently

Table 2. Major Genes Associated with Wheat End-Use Quality Traits

Trait	Gene	Key Alleles/ Subunits	Chromosome	Marker Type	References
Grain Protein Content (GPC)	*Gpc-B1*	Functional allele	6BS	SSR	Vishwakarma *et al.*, 2014; Fandade *et al.*, 2026
HMW-GS	*Glu-A1*	Ax1, Ax2*, AxNull	1AL	AS-PCR, KASP	Ma *et al.*, 2023; Wang *et al.*, 2024
	Glu-B1	Bx7, Bx7OE, Bx17	1BL	AS-PCR, KASP	Ma *et al.*, 2022
	Glu-D1	Dx5+Dy10, Dx2+Dy12	1DL	AS-PCR, KASP	Ma *et al.*, 2024; Zhao *et al.*, 2024
LMW-GS	*Glu-A3*	a, b, c	1AS	STS, KASP	Wang *et al.*, 2024
	Glu-B3	b, g, h	1BS	AS-PCR, KASP	Li *et al.*, 2025
	Glu-D3	a, b, c	1DS	STS	Chen *et al.*, 2023; Zhao *et al.*, 2024
Grain Hardness	*Pina-D1*	Pina-D1a, Pina-D1b	5DS	AS-PCR	Ding *et al.*, 2025
	Pinb-D1	Pinb-D1a–e	5DS	STS, CAPS	Wang *et al.*, 2022; Fan *et al.*, 2024
Starch (Waxy genes)	*Wx-A1*	Wx-A1a, Wx-A1b, Null	7AS	SSR, KASP	Guo *et al.*, 2023
	Wx-B1	Wx-B1a, Wx-B1b, Null	4AL	SSR, STS	Tian *et al.*, 2024
	Wx-D1	Wx-D1a, Wx-D1b	7DS	SSR, STS	Wang *et al.*, 2024
Grain Colour (Red/White)	*R-A1*	R-A1a (red), R-A1b (white)	3AL	SSR, KASP	Arif *et al.*, 2022
	R-B1	R-B1a (red), R-B1b (white)	3BL	SSR, KASP	Jiang *et al.*, 2022
	R-D1	R-D1a (red), R-D1b (white)	3DL	SSR, KASP	Ma *et al.*, 2023; Ding *et al.*, 2025

and synergistically, forming regulatory modules that fine-tune storage protein accumulation. For instance, TaSPA interacts with TaFUSCA3, while TaNAC019 coordinates with TaGAMyb to activate high-molecular-weight glutenin subunit (HMW-GS) gene expression (Peng *et al.*, 2022; Gao *et al.*, 2021). In contrast, epigenetic regulation also plays a crucial role, as promoter demethylation of the *TaDME* gene has been shown to suppress the expression of LMW-GS and gliadin genes (Wen *et al.*, 2013; Che *et al.*, 2025). Given the complexity of these interactions, a range of key transcription factors, their target genes, and associated cis-regulatory elements have been identified and are summarized in Table 3. Together, these regulatory components form an integrated network that governs both the quantity and composition of storage proteins. A deeper understanding of these fine-scale regulatory processes will be essential for precision breeding strategies aimed at tailoring wheat quality for specific end-use applications (Gao *et al.*, 2023).

3.3. Genes controlling starch composition

Starch composition represents a major determinant of wheat grain quality, influencing both processing performance and nutritional attributes. A growing body of evidence indicates that, unlike storage proteins which are primarily regulated at the transcriptional level, starch-related traits are governed by a complex network of structural genes and quantitative trait loci (QTLs) that control carbohydrate biosynthesis. Studies have consistently shown that the synthesis of amylose is largely regulated by the waxy (*Wx*) gene family, which plays a central role in determining starch functionality. However, emerging evidence suggests that starch composition is not controlled by *Wx* genes alone. Multiple QTLs distributed across chromosomes 1B, 3A, 3B, 4A, 5A,

Table 3. Regulatory transcription factors, target genes, and cis-elements controlling wheat grain storage proteins

Transcription Factor	Regulatory Role	Target Genes/ Promoters	Cis-Acting Element(s)	References
SPA (Storage Protein Activator)	Activator	Glutenin promoters	G-box; GLM	Merlino *et al.*, 2023
SHP (SPA Heterodimerizing Protein)	Repressor	Glutenin promoters	G-box; GLM	Merlino *et al.*, 2023
WPBF (Wheat Prolamin Box Binding Factor)	Activator	Gliadin promoters	P-box	Qu *et al.*, 2023
TaPBF-D	Activator	HMW-GS promoters	P-box	Qu *et al.*, 2023
TaGAMyb	Activator	HMW-GS promoters	C/TAACAAA	Chen *et al.*, 2024
TaFUSCA3	Activator	HMW-GS promoters	RY-box	Merlino *et al.*, 2023
TaNAC019	Activator	Glutenin promoters	[AT]NNNNNNNNTC[G]AC[AG]NTACTA	Liu *et al.*, 2025
TaNAC100	Repressor	HMW-GS promoters	CATGTG	Cao *et al* 2024; Liu *et al.*, 2025

6B, and 7A have been identified, indicating a highly quantitative and polygenic genetic architecture (Kumar *et al.*, 2019). Furthermore, loci located in close proximity to *Wx* genes on chromosomes 4A, 7A, and 7D suggest coordinated regulation of amylose and amylopectin biosynthesis (Jia *et al.*, 2025). Importantly, several studies highlight the presence of pleiotropic genomic regions that simultaneously influence both protein and starch traits, emphasizing the interconnected nature of wheat grain quality regulation. Chromosomes such as 3B, 4A, 6B, and 7A have repeatedly been identified as key regulatory hubs across independent studies. In particular, the chromosome 3B region has emerged as a major hotspot associated with multiple quality traits, underscoring its central role in integrating genetic control (Gao *et al.*, 2021). Collectively, these findings demonstrate that starch composition is not an isolated trait but is tightly linked with protein quality through shared genetic regions and regulatory pathways. This interconnected genetic architecture presents both opportunities and challenges for wheat improvement, as selection for one quality trait may inadvertently influence others.

3.4. The genetic vs. environmental interplay: balancing quality and stability

Genetic architecture of wheat grain quality provides the foundation for trait expression, however, its realization in the field is strongly influenced by environmental conditions. A substantial body of research indicates that wheat quality traits are governed by the dynamic interaction between genotype (G), environment (E), and their interaction (G × E), which ultimately determines both trait performance and stability across diverse production systems (Miner *et al.*, 2022). Genotype × environment (G × E) interactions play a pivotal role in determining wheat grain quality; however, their magnitude differs among individual quality traits. Recent multi-environment studies have demonstrated that traits such as grain protein content, grain hardness, test weight, and micronutrient concentrations (Fe and Zn) exhibit varying contributions of genotype, environment, and G × E interaction, highlighting that their expression is trait-dependent rather than uniform across environments (Harisha *et al.*, 2024). In contrast, intrinsic quality attributes, including storage protein composition (gliadin and glutenin fractions) and starch structural characteristics, are generally under stronger genetic control and tend to maintain relatively stable genotypic rankings across environments, although their quantitative expression can still be influenced by environmental conditions during grain development (Lullien-Pellerin, 2024; Shevkani *et al.*, 2024). Environmental factors such as temperature, water availability, and grain-filling duration can alter protein accumulation, starch biosynthesis, and grain composition,

thereby modulating the phenotypic expression of genetically controlled traits and ultimately influencing processing and end-use quality. These findings emphasize the importance of evaluating wheat quality traits across diverse environments to identify genotypes with superior performance as well as greater stability. Notably, starch-related properties, including paste viscosity, are reported to be more strongly influenced by genotypic factors–particularly amylose content–than by G × E interactions, further highlighting the robustness of starch composition as a genetically controlled trait (Raffo and Jensen, 2023). However, even in such cases, environmental fluctuations can subtly influence trait expression, especially under stress conditions. Collectively, these interactions define the delicate balance between productivity, processing quality, and nutritional value in wheat. Understanding this interplay is therefore essential for developing cultivars that not only possess superior genetic potential but also maintain consistent performance across variable environments (Fig. 1)

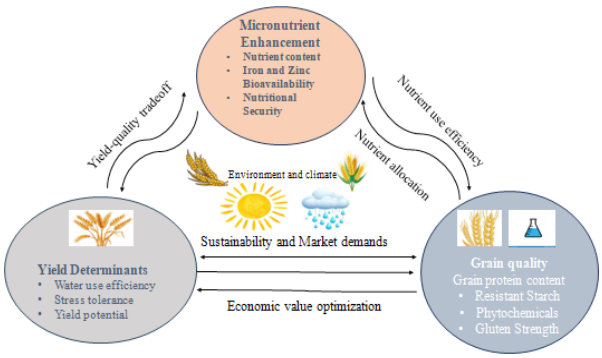

Fig. 1: Integrated model of interactions among wheat yield, grain quality, and nutritional traits under genetic and environmental influences.

4. Biofortification and Micronutrient Bioavailability: Sustainable Strategies Against Micronutrient Malnutrition

4.1. Biofortification in wheat: rationale and targets

Despite advances in improving wheat yield and processing quality, the nutritional dimension of wheat remains a major global concern. The genetic and environmental constraints discussed in the previous sections further complicate efforts to enhance micronutrient density in a stable and consistent manner. As a result, micronutrient malnutrition, commonly referred to as hidden hunger, continues to affect a significant proportion of the global population, particularly in developing regions (Tanin *et al.*, 2024; Hui *et al.*, 2025). Conventional approaches such as dietary supplementation and industrial food fortification have shown limited long-term success, especially among resource-poor populations. In contrast, biofortification–defined as the enhancement of micronutrient content in crops through genetic improvement–has emerged as a sustainable and cost-effective strategy (Monasterio *et al.*, 2007; Li *et al.*, 2025). This approach specifically targets populations that rely heavily on staple crops like wheat for daily nutrition. Biofortification in wheat involves the identification and utilization of genetic variability, selection of high-nutrient donor lines, and incorporation of desirable traits into elite cultivars while maintaining agronomic performance (Gupta *et al.*, 2021). However, its success depends not only on genetic improvement but also on trait stability across environments and farmer adoption, which ultimately determine its impact at the population level (Cakmak, 2008).

4.2. Major micronutrients and its deficiency

Among essential micronutrients, iron (Fe) and zinc (Zn) deficiencies represent some of the most pressing global health challenges, contributing to impaired growth, weakened immune function, and cognitive disorders (Prasad *et al.*, 2007). Iron deficiency is particularly severe among pregnant women and children, where it is associated with anemia, tissue hypoxia, and increased maternal mortality (Hao *et al.*, 2024). In wheat grains, micronutrient distribution is highly uneven. Zinc is predominantly localized in the embryo and aleurone layer (approximately 150 mg/kg), whereas the endosperm–the primary component of refined flour–contains significantly lower concentrations (around 15 mg/kg) (Ozturk *et al.*, 2006). Similarly, grain iron concentrations range from 28.8 to 56.5 mg/kg, indicating considerable scope for genetic enhancement. Selenium (Se), another essential micronutrient with antioxidant properties, is deficient in many agricultural soils worldwide. Wheat can contribute substantially to dietary Se intake, although its accumulation depends strongly on soil chemistry. Selenate is more readily available in alkaline soils, whereas in acidic or iron-rich conditions, selenium forms insoluble complexes that limit plant uptake. While agronomic approaches such as selenium fertilization are effective, genetic biofortification offers a more sustainable solution, supported by existing variability in wheat germplasm

(Gao *et al.*, 2023). The major genes and QTLs associated with iron and zinc accumulation are summarized in Table 4, highlighting the genetic potential for improving micronutrient density in wheat.

4.3. Micronutrient bioavailability

Micronutrient bioavailability determines the efficiency of nutrient absorption and utilization in humans and is influenced by factors such as age, health, genetics, and food matrix. Interactions among nutrients can enhance absorption; for instance, provitamin A, iron (Fe), and zinc (Zn) can positively influence each other's bioavailability (Neeraja *et al.*, 2017). Both dietary and host-related factors regulate absorption, with nutrient form and composition playing key roles. Ascorbic acid enhances Fe absorption, whereas polyphenols and phytic acid inhibit Fe and Zn availability by forming insoluble complexes (Wang *et al.*, 2025). Carotenoids such as lutein, zeaxanthin, and β-carotene improve Fe absorption; β-carotene enhances Fe solubility and uptake, and lutein supplementation (1.8 mg) has been shown to significantly increase Fe absorption (Sheera *et al.*, 2022). In cereals, Fe and Zn are largely stored with phytic acid in globoids in protein storage vacuole, within aleurone and embryo tissues, limiting their bioavailability (Sharma *et al.*, 2018). Dietary fiber components (cellulose, hemicellulose, lignin) can further reduce mineral absorption, whereas compounds like Beta-carotene increases Fe solubility, leading in enhancement of its bioavailability and inulin which enhances Fe and Zn bioavailability through fermentation (Shahryari *et al.*,2025). Heme iron is more bioavailable than non-heme iron due to more efficient absorption and lack of inhibitory interactions. Biofortification strategies therefore focus on improving mineral deposition, reducing inhibitors like phytic acid, and enhancing nutrient mobilization (Cakmak, 2008; Nasim *et al* 2025).

4.4. Physiological and molecular basis of micronutrient accumulation

4.4.1. Uptake mechanisms

Iron (Fe) and zinc (Zn) uptake in plants occurs via two primary strategies. Non-graminaceous species utilize a reduction-based mechanism (Strategy I), where Fe^{3+} is reduced to Fe^{2+} and transported by Iron Regulated Transport (IRT) and Natural Resistance-Associated Macrophage Protein (NRAMP) transporters (Wang *et al.*, 2025).

In contrast, graminaceous crops such as wheat adopt a chelation-based mechanism (Strategy II), involving the release of phytosiderophores (e.g., mugineic acid) that chelate Fe^{3+} and Zn^{2+}, with uptake mediated by YSL transporters (Chen *et al.*, 2017). Phytosiderophore biosynthesis is regulated by enzymes including NAS, NAAT, and DMAS. Despite Strategy II dominance, partial overlap with Strategy I components exists. Zinc uptake is mainly facilitated by ZIP transporters, which may also transport Fe under deficiency (Roy *et al.*, 2022). Selenium (Se) is absorbed as selenate (Se^{6+}) via sulfate transporters and as selenite (Se^{4+}) through phosphate transporters and

Table 4. Recent genes and QTLs associated with Fe and Zn biofortification in wheat

Trait	Chromosome/ QTL	Gene/Marker	Function	Key Finding	Reference
Zn	2A, 7B	TaZIP family	Zn transporter	Enhances Zn uptake and translocation	Nasim *et al.*, 2025
Fe	6B	Gpc-B1 (NAM-B1)	Nutrient remobilization	Increases Fe & Zn in grain via senescence	Chen *et al.*, 2017
Zn	3B, 7A	QTL regions	Zn accumulation	Stable QTLs across environments	Velu *et al.*, 2020
Fe/Zn	Multiple	TaNAS genes	Nicotianamine synthesis	Improves Fe/Zn mobility and loading	Chen *et al.*, 2017
Fe	1D	TaYSL transporters	Metal transport	Enhances Fe transport to grain	Xiao *et al.*, 2024
Zn	5A	TaHMA2	Heavy metal ATPase	Zn translocation to shoots/grains	Wang *et al.*, 2025

aquaporins, without a dedicated uptake system (Wang *et al.*, 2022; Xiao *et al.*, 2024).

4.4.2. Transport and translocation

Following uptake, Fe and Zn are transported radially to the xylem and translocated to aerial tissues. Chelators such as nicotianamine (NA) and deoxymugineic acid (DMA) facilitate long-distance transport through both xylem and phloem. Multiple transporter families, including ZIP, YSL, NRAMP, HMA, and MTP, regulate metal movement across cellular compartments (Balk *et al.*, 2019). In wheat, YSL transporters play a central role in Fe–DMA translocation, particularly under deficiency conditions, while HMA transporters are crucial for Zn loading into the xylem and its redistribution within the plant as shown in Fig 2. Vacuolar transporters such as VIT and MTP contribute to intracellular sequestration, thereby maintaining metal homeostasis (Wang *et al.*, 2022). Whereas, Selenium transport follows sulfur assimilation pathways, where selenate is reduced and incorporated into seleno-amino acids such as selenocysteine (SeCys) and selenomethionine (SeMet). These organic forms are translocated via amino acid transport systems (Liu *et al.*, 2021; Leonova *et al.*, 2024).

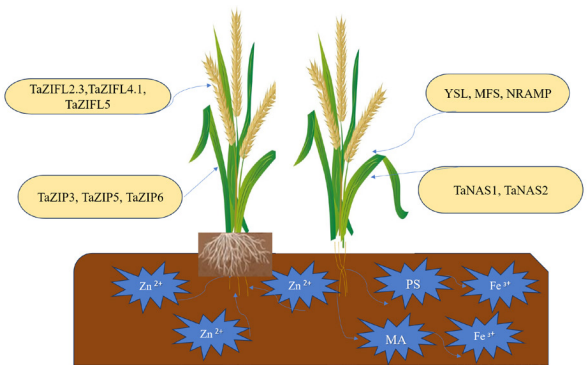

Fig. 2: Schematic representation of Fe and Zn uptake, transport, and accumulation in wheat (Nasim *et al.*, 2025)

4.4.3. Remobilization and grain loading

During grain filling, micronutrients are supplied either through continued root uptake or via remobilization from vegetative tissues, particularly leaves. Under nutrient-deficient conditions, remobilization becomes the dominant source. In wheat, phloem transport is the primary route for delivering Fe and Zn to developing grains due to the discontinuous nature of the xylem (Bhatta *et al.*, 2018). Chelators such as Nicotianamine and Deoxymugineic Acid, along with organic acids, facilitate efficient phloem loading and unloading. Regulatory genes such as Gpc-B1 (NAM-B1) enhance nutrient remobilization from senescing tissues to grains, thereby increasing grain Fe and Zn concentrations (Roy *et al.*, 2022). Selenium accumulation in grains largely depends on the transport of organic Se forms, particularly SeMet, from senescing leaves. Transporters such as amino acid permeases (AAPs) and nitrate transporters (e.g., NRT1.1B) contribute to Se loading into grains. Organic Se is predominantly localized in the embryo and outer grain layers (Nasim *et al.*, 2025).

4.5. Phytic acid: A critical constraint in micronutrient bioavailability

Although significant progress has been made in understanding the physiological mechanisms governing micronutrient uptake, transport, and grain loading, the nutritional effectiveness of these processes ultimately depends on the bioavailability of minerals in the edible portion of the grain. In this context, phytic acid (PA) emerges as a major limiting factor, linking grain composition with human nutrition. Phytic acid serves as the primary storage form of phosphorus in wheat seeds and plays an essential role in seed development and germination. Its accumulation is tightly regulated through transport and sequestration processes mediated by ATP-binding cassette (ABC) transporters such as *TaABCC13* and *TaMRP3*, which facilitate the deposition of PA into protein storage vacuoles (Aggarwal *et al.*, 2015; Silva *et al.*, 2021). However, despite its physiological importance, PA has a strong affinity for divalent cations such as iron (Fe) and zinc (Zn), forming insoluble complexes that significantly reduce their bioavailability in the human diet (Roy *et al.*, 2022; Rathan *et al.*, 2022). This dual role of PA–as both a vital component of seed physiology and a major anti-nutritional factor–creates a critical challenge in wheat biofortification. While reducing PA levels can enhance micronutrient absorption, but excessive reduction may negatively impact seed viability, germination, and early plant development (Nasim *et al.*, 2025). Therefore, effective biofortification strategies must strike a careful balance between enhancing mineral bioavailability and maintaining essential physiological functions. Current approaches focus on moderate reduction of PA, redistribution of minerals within the grain, and integration of genetic and agronomic interventions to optimize both nutritional quality and crop performance. Although

physiological mechanisms define how micronutrients are acquired and distributed within the plant, their effective improvement relies on the availability and exploitation of underlying genetic variation (Aggarwal *et al.*, 2015; Chondrou *et al.*, 2024).

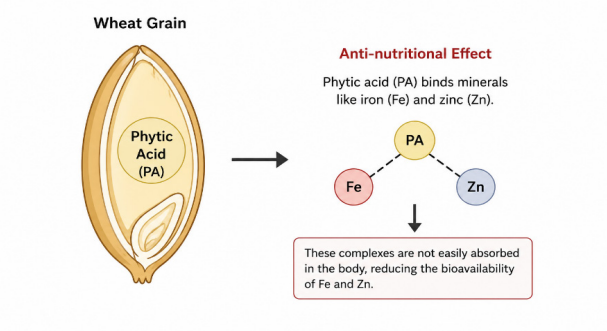

Fig. 4: Phytic acid (PA) in wheat grain and its anti-nutritional effect on mineral bioavailability

5. Genetic architecture of biofortification traits

5.1. Natural variation and germplasm resources

The physiological and biochemical constraints discussed in the previous sections–particularly the limited bioavailability of micronutrients and the trade-offs associated with phytic acid–underscore the need for robust genetic solutions to enhance nutritional quality in wheat. Central to these efforts is the exploitation of natural genetic variation present within diverse germplasm resources. Landraces are dynamic, heterogeneous populations shaped through long-term interaction with local environments and traditional farming practices. They harbor rich allelic diversity for key agronomic and physiological traits, including tolerance to drought, heat, salinity, and diseases, making them valuable resources for broadening the genetic base of wheat (Adhikari *et al.*, 2022). This enhances their importance in biofortification and the development of nutritionally improved cultivars. Wild relatives and synthetic wheats further complement landraces as vital genetic resources. Wild species provide unique alleles for stress and disease resistance, while synthetic wheats enable introgression of novel diversity into elite lines (Aggarwal *et al.*, 2015). The identification of genetic variation associated with quality and biofortification traits provides the foundation for breeding strategies aimed at translating this knowledge into improved wheat cultivars (Phogat *et al.*, 2021).

6. Breeding strategies for quality and biofortification

The pursuit of improved wheat quality and nutritional value has evolved considerably over the past several decades, reflecting advances in plant breeding, genetics, and biotechnology. Initial breeding efforts during the Green Revolution focused predominantly on increasing grain yield and broad adaptation through conventional hybridization and phenotypic selection. Although these programs substantially enhanced wheat productivity, improvements in nutritional quality and processing characteristics remained secondary objectives. The recognition of widespread micronutrient deficiencies and increasing demand for superior end-use quality subsequently shifted breeding priorities towards enhancing grain protein content, micronutrient concentration, gluten functionality, and processing performance. A major milestone in this transition was the identification of naturally occurring genes controlling important quality traits, such as Gpc-B1 (NAM-B1) from wild emmer wheat for enhanced grain protein, iron, and zinc accumulation (Uauy *et al.*, 2006), and the Puroindoline (*Pina-D1* and *Pinb-D1*) genes governing grain hardness and milling quality (Bhave and Morris, 2008). These discoveries established the genetic basis of wheat quality improvement and facilitated the development of molecular markers for breeding. Subsequently, advances in quantitative trait locus (QTL) mapping, marker-assisted selection (MAS), and genome-wide association studies (GWAS) enabled breeders to efficiently identify and introgress favorable alleles controlling complex quality traits (Velu *et al.*, 2018; Roy *et al.*, 2022). The rapid development of high-throughput genotyping, genomic selection (GS), multi-omics technologies, and genome-editing tools such as CRISPR/Cas systems has further transformed wheat breeding from phenotype-based selection to predictive and precision breeding (Sun *et al.*, 2024; Crossa *et al.*, 2025; Qian *et al.*, 2025). More recently, the integration of artificial intelligence, high-throughput phenotyping, and speed breeding has accelerated the identification and deployment of superior genotypes, enabling the simultaneous improvement of grain quality, nutritional value, yield, and climate resilience. Thus, modern wheat breeding has progressed from selecting superior phenotypes to designing cultivars through the integrated use of conventional, molecular, genomic, and digital

breeding technologies. The following sections discuss these breeding strategies and their contributions to wheat quality improvement and biofortification in greater detail.

6.1. Conventional approaches

Conventional breeding remains the cornerstone of wheat quality improvement and biofortification by exploiting the natural genetic variation present in landraces, elite cultivars, and wild relatives. Among these, landraces are particularly valuable because they are readily cross-compatible with modern wheat and possess favorable alleles for grain protein content, micronutrient accumulation, stress tolerance, and yield stability. A notable example is the transfer of the Gpc-B1 (NAM-B1) allele from wild emmer wheat (*Triticum turgidum* ssp. *dicoccoides*), which accelerates nutrient remobilization during grain filling and significantly enhances grain protein, iron, and zinc concentrations. This allele has been successfully incorporated into breeding programs worldwide and remains a key genetic resource for wheat biofortification (Uauy *et al.*, 2006; Tabbita *et al.*, 2021). The direct utilization of landraces is often limited by undesirable agronomic traits, including low yield potential, lodging, and disease susceptibility. To overcome these constraints, pre-breeding strategies involving hybridization, selection, and the development of intermediate breeding lines are employed to introgress desirable alleles while minimizing linkage drag (Sreekanth *et al.*, 2023). Recent advances in high-throughput phenotyping, genomic characterization, and the establishment of core and mini-core collections have further improved the efficient identification and utilization of superior donor lines (Yadav *et al.*, 2025). Conventional breeding has also achieved significant practical success through both national and international biofortification initiatives. For example, the HarvestPlus–CIMMYT breeding program has developed and released high-zinc wheat cultivars, including Zinc Shakti demonstrating that conventional breeding can simultaneously improve grain zinc concentration while maintaining competitive yield and adaptation. These achievements highlight the continued importance of conventional breeding as the foundation for developing nutritionally enhanced wheat, particularly when integrated with modern genomic and phenotyping tools (Shewry *et al.*, 2024; Yadav *et al.*, 2025).

6.2. Marker-assisted and genomic selection

While conventional approaches provide a foundation, modern molecular breeding techniques have significantly accelerated the improvement of wheat quality and biofortification traits. Marker-assisted selection (MAS) and genomic selection (GS) have revolutionized wheat breeding by enabling the efficient improvement of complex quality and biofortification traits through the use of molecular markers and genome-wide information. MAS is particularly effective for traits governed by major genes or stable QTLs, allowing the precise introgression of favorable alleles into elite cultivars while minimizing linkage drag. For instance, functional markers linked to the Gpc-B1 (NAM-B1) gene have been widely used to enhance grain protein, iron, and zinc concentrations, whereas markers associated with Pina-D1 and Pinb-D1 have facilitated the selection of desirable grain hardness, an important determinant of milling and end-use quality (Roy *et al.*, 2022; Sun *et al.*, 2024). Similarly, stable QTLs for grain zinc concentration identified on chromosomes 2B, 4B, and 7A have provided valuable targets for marker-assisted introgression into high-yielding wheat backgrounds (Velu *et al.*, 2018; Kumar *et al.*, 2024). Unlike MAS, which targets a limited number of loci, GS simultaneously exploits thousands of genome-wide markers to predict the breeding value of complex polygenic traits. This approach has substantially improved prediction accuracy for grain protein content, grain yield, dough quality, and micronutrient concentration, enabling early-generation selection and reducing the time required to develop improved cultivars. Recent studies integrating genomic selection with high-throughput phenotyping and environmental data have further enhanced prediction accuracy by effectively capturing genotype × environment interactions, thereby increasing selection efficiency for wheat quality traits under diverse production environments (Crossa *et al.*, 2024; Lado *et al.*, 2024). The complementary application of MAS and GS is increasingly being adopted in modern wheat breeding programs, where major-effect genes are introgressed through MAS while genome-wide marker information is exploited through GS to improve quantitatively inherited traits. This integrated strategy enables simultaneous enhancement of grain quality, micronutrient density, and agronomic performance, making it one of the most promising approaches for

accelerating wheat biofortification and developing climate-resilient, nutritionally superior cultivars.

7. Advances in biotechnology and genome editing

While conventional and molecular breeding strategies have significantly improved wheat quality and biofortification traits, their progress is often constrained by long breeding cycles and complex polyploid genetics. In this context, modern biotechnological tools provide precise and efficient approaches for targeted crop improvement. Transgenic and genome-editing technologies have emerged as powerful tools for accelerating wheat quality improvement and biofortification by enabling precise manipulation of genes involved in nutrient uptake, transport, metabolism, and grain composition. Unlike conventional breeding, these approaches allow the direct modification or introduction of target genes, facilitating the simultaneous improvement of grain iron (Fe) and zinc (Zn) concentrations, starch composition, carotenoid content, and the reduction of anti-nutritional compounds such as phytic acid (Wang *et al.*, 2018; Ni *et al.*, 2023; Yigider *et al.*, 2023). A notable example is the genetic transformation of the wheat cultivar *Bobwhite* with the bacterial carotenoid biosynthetic genes phytoene synthase (crtB) and carotene desaturase (crtI). While the expression of either gene alone resulted in only modest increases in carotenoid accumulation, their combined expression markedly enhanced grain carotenoid content, producing darker yellow to red grains with improved provitamin A potential (Umar *et al.*, 2019). Such studies demonstrate the capacity of transgenic approaches to simultaneously enhance the nutritional and functional quality of wheat.

The advent of CRISPR/Cas genome-editing systems has further transformed wheat improvement by enabling precise, efficient, and multiplex modification of homoeologous genes without introducing extensive foreign DNA. Compared with conventional transgenic approaches, CRISPR-based editing provides greater precision and flexibility for improving complex traits associated with grain quality, nutritional value, and stress adaptation (Ma *et al.*, 2024; Qian *et al.*, 2025). One important application has been the modification of starch biosynthesis pathways, where enzymes such as starch synthases and starch-branching enzymes regulate the balance between amylose and amylopectin. Targeted disruption of starch synthase IIa (SSIIa) genes has been shown to increase amylose content, whereas RNA interference (RNAi)-mediated suppression of starch-branching enzymes has generated high-amylose wheat lines with significantly elevated resistant starch levels (Yamamori *et al.*, 2000; Regina *et al.*, 2006; Konik-Rose *et al.*, 2007). These modifications improve starch functionality while enhancing nutritional quality by increasing resistant starch, which contributes to improved glycemic regulation and gut health.

Recent advances have further expanded the genome-editing technology beyond CRISPR/Cas9. The CRISPR/Cas12a (Cpf1) system recognizes T-rich protospacer adjacent motif (PAM) sequences and generates staggered DNA breaks, enabling efficient targeting of genomic regions that are less accessible to Cas9 while facilitating multiplex editing with reduced off-target effects. In wheat, Cas12a has been successfully applied for the simultaneous editing of multiple genes associated with agronomic and quality traits, demonstrating its potential for complex trait improvement (Zheng *et al.*, 2025). Similarly, base editing enables precise single-nucleotide substitutions without creating double-strand DNA breaks, making it particularly valuable for generating beneficial allelic variants controlling grain quality and disease resistance. Prime editing further extends this capability by introducing targeted nucleotide substitutions, insertions, and deletions without the need for donor DNA templates, thereby providing exceptional flexibility for precision breeding. In addition, DNA-free genome editing, achieved through the delivery of CRISPR ribonucleoprotein (RNP) complexes, enables the production of transgene-free edited plants that may encounter fewer regulatory constraints in several countries. Collectively, these biotechnological innovations are reshaping wheat breeding by enabling precise manipulation of genes controlling nutritional quality, processing characteristics, and agronomic performance. Nevertheless, their large-scale deployment remains constrained by challenges including genotype-dependent transformation and regeneration efficiency, variable editing frequencies in elite cultivars, and evolving regulatory frameworks and public acceptance concerning genome-edited crops (Zheng *et al.*, 2025; Gao *et al.*, 2025). Integrating these technologies with genomic selection, high-throughput phenotyping, and conventional breeding is expected to further accelerate the development of

nutritionally enriched, high-quality, and climate-resilient wheat cultivars.

8. Phenotyping and high-throughput technologies

The successful deployment of advanced breeding and genome editing strategies relies on precise and efficient phenotyping of complex quality traits. High-throughput phenotyping platforms have therefore become essential tools for accelerating wheat improvement. Technologies such as near-infrared spectroscopy (NIRS), imaging systems, and automated analyzers enable rapid and non-destructive assessment of grain composition and physical traits, significantly enhancing selection efficiency (Ma *et al.*, 2021; Desta and Ortiz, 2014). In parallel, ionomic and metabolomic approaches provide detailed insights into mineral composition and metabolic pathways, facilitating accurate evaluation of biofortification traits and identification of underlying genetic determinants (Razzaq *et al.*, 2021; Kassem, 2025). The integration of digital phenotyping with artificial intelligence (AI) and machine learning (ML) has transformed wheat quality research by enabling rapid, high-throughput, and non-destructive assessment of complex traits. Digital phenotyping platforms equipped with RGB, hyperspectral, thermal, and near-infrared (NIR) imaging sensors can capture detailed information on grain morphology, canopy architecture, physiological status, and spectral characteristics associated with grain protein content, starch composition, and micronutrient accumulation. AI and ML algorithms, including random forest, support vector machines, and deep learning models, analyze these large and multidimensional datasets to identify complex genotype–phenotype relationships that are often difficult to detect using conventional statistical approaches (Che *et al.*, 2026). For example, hyperspectral imaging combined with deep learning has been successfully used to accurately predict grain protein content and classify wheat quality classes, while ML-assisted genomic prediction models have improved the prediction accuracy of complex traits such as grain yield, protein content, and grain hardness by integrating genomic, phenotypic, and environmental data. Furthermore, AI-driven multi-omics integration facilitates the identification of candidate genes and quantitative trait loci (QTLs) associated with wheat quality, thereby accelerating marker-assisted selection and genomic selection for the development of nutritionally enriched and high-quality wheat cultivars (Crossa *et al.*, 2025; Reynolds *et al.*, 2025). Together, advances in biotechnology and high-throughput phenotyping are converging toward a more precise and data-driven breeding paradigm, enabling the efficient development of nutrient-dense and high-quality wheat cultivars.

9. Emerging directions

The future of wheat quality improvement and biofortification is moving toward integrated breeding strategies that combine nutritional enhancement with yield stability, climate resilience, and practical deployment. However, translating genetic gains into consistent nutritional and agronomic performance remains challenging because quality and nutritional traits are controlled by complex genetic architectures and are strongly influenced by environmental conditions. Therefore, future progress will depend not only on developing nutrient-dense genotypes but also on improving trait stability, validating performance across environments, and strengthening the pathway from breeding programs to farmers and consumers.

9.1. Climate-resilient, nutrition-dense wheat ideotypes

Future wheat improvement increasingly aims to develop ideotypes that combine stable yield and stress adaptation with enhanced grain nutritional quality. This objective is particularly important because heat, drought, and other climatic stresses can alter grain filling and nutrient accumulation, potentially reducing the nutritional advantage of otherwise superior genotypes (Gupta *et al.*, 2025). Recent genetic analyses in CIMMYT wheat populations have highlighted the complexity of simultaneously improving grain zinc, iron, and yield-related traits, emphasizing the importance of identifying favorable combinations rather than selecting these traits independently (Zhang *et al.*, 2026). However, the simultaneous improvement of yield, stress tolerance, and micronutrient density remains difficult because these traits may show unfavorable genetic relationships and substantial genotype × environment interactions. Nutrient concentration can also fluctuate with soil fertility, temperature, water availability, and grain-filling conditions, reducing the consistency of biofortification across locations and seasons (Gupta *et al.*, 2021). A further challenge is that selection based solely on nutrient

concentration may identify genotypes that perform well under experimental conditions but fail to maintain their nutritional advantage in farmers' fields. These limitations can be addressed through multi-environment testing, selection for trait stability, use of diverse donor germplasm, and evaluation of nutritional traits together with yield, disease resistance, and end-use quality. Thus, the next generation of wheat ideotypes should be selected not simply for maximum nutrient concentration, but for stable nutritional value under realistic production environments while maintaining competitive yield and quality (Bhardwaj *et al.*, 2022).

9.2. Policy support and global biofortification initiatives

Scientific advances alone cannot ensure the nutritional impact of biofortified wheat; their benefits ultimately depend on successful varietal release, seed multiplication, farmer adoption, and consumption. International initiatives such as HarvestPlus and collaborative national breeding programs have demonstrated the feasibility of developing and disseminating iron- and zinc-enriched wheat, providing an important foundation for large-scale nutritional improvement (Shewry, 2025). In India, for example, policy initiatives and partnerships have increasingly supported the production and dissemination of zinc-biofortified wheat, while Bihar and Odisha have undertaken efforts to integrate biofortified crops into broader nutrition and agricultural programs. Nevertheless, the transition from successful breeding lines to widespread impact remains constrained by several practical challenges, including lengthy varietal evaluation and release procedures, inadequate availability of quality seed, weak dissemination systems, variable farmer acceptance, and limited consumer awareness. In addition, nutritional traits may receive lower priority than yield, disease resistance, or market-preferred characteristics when farmers make cultivar choices (Qaim, 2020). These challenges require coordinated solutions across the breeding-to-consumption pipeline. Stronger collaboration among breeding institutions, national agricultural programs, seed systems, policymakers, nutrition agencies, and farmers can facilitate faster testing, multiplication, and dissemination of biofortified cultivars. Participatory varietal selection and farmer-oriented demonstrations can improve adoption by ensuring that biofortified varieties also meet local requirements for yield, adaptation, disease resistance, processing quality, and market value (Roy *et al.*, 2022). At the policy level, incorporating nutritional traits into varietal evaluation and release criteria could help move biofortification from a specialized objective toward a routine component of cultivar development. This transition is already emerging in national programs; recent CGIAR–HarvestPlus efforts have emphasized embedding nutritional criteria into new variety development and release processes rather than treating biofortification as a separate intervention (Sun *et al.*, 2024). At the consumer level, nutrition education and clear communication of health benefits can strengthen acceptance, while monitoring grain nutrient concentration and bioavailability after varietal release can help determine whether breeding gains translate into meaningful nutritional benefits. Ultimately, stronger seed systems, supportive policies, participatory breeding, and sustained monitoring will be essential for converting biofortified wheat from successful breeding products into widely adopted nutritional interventions (Ma *et al.*, 2024). Overall, the future of wheat biofortification will depend on moving beyond the development of nutrient-dense genotypes toward an integrated breeding–seed–farmer–consumer pipeline. The major challenge is to ensure that nutritional gains remain stable under climate variability while maintaining yield, processing quality, farmer preference, and market competitiveness (Lawrenson *et al.*, 2024). Addressing these challenges through multi-environment validation, selection for nutritional stability, coordinated seed systems, supportive policy frameworks, and stronger stakeholder engagement will be essential for translating advances in wheat improvement into measurable and sustainable gains in food and nutritional security.

10. Conclusion

Despite substantial progress in wheat quality improvement and biofortification, key challenges remain in simultaneously enhancing end-use quality, micronutrient density, and yield stability. Complex genotype × environment interactions, pleiotropic gene effects, and a limited understanding of micronutrient bioavailability, especially the role of phytic acid and the grain matrix, continue to limit breeding efficiency. In addition, the lack of rapid and cost-effective phenotyping across diverse environments hampers large-scale trait evaluation.

Addressing these gaps will require integrative multi-omics approaches, functional validation of candidate genes, and genomic selection for multi-trait improvement, along with greater use of diverse germplasm. While biofortification offers a sustainable solution to hidden hunger and has shown promising success, its full potential depends on integrating genetic improvement with agronomic and processing strategies. Ultimately, stronger collaboration among breeders, nutritionists, policymakers, and stakeholders will be essential to develop climate-resilient, nutritionally enriched wheat varieties that support global food and nutritional security.

Authors contributions

Jagdeep Singh Randhawa: Original draft, conceptualisation, planning, monitoring, Manuscript writing; Arshvir Kaur Boparai: editing, writing, revisions; Dr. Lenika Kashyap, Dr. Satinder Singh, Dr. Satinder Kaur and Dr. Achla Sharma: Conceptualisation, planning, monitoring, review of the draft.

Conflict of interest statement

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

Ethical compliance statement

NA

Declaration on the use of Generative AI or AI-assisted technologies

The authors declare that no generative AI or AI-assisted technologies were used in the preparation of this manuscript. All text, data interpretation, and analysis were conducted entirely by the authors.

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