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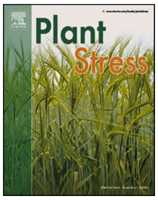

Review

Advances in genomics-assisted breeding strategies for enhancing nutrient uptake and use efficiency in cereals: A pathway toward sustainable agriculture

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ABSTRACT

Staple cereals such as rice, wheat, and maize are key to food security by providing the bulk of calories consumed worldwide. However, cereal productivity is often limited by inefficient uptake and utilization of essential nutrients, including N, P, Fe, and Zn especially under stress conditions. Enhancing nutrient uptake efficiency (NutrUE) in staple crops is crucial to reducing fertilizer inputs, supporting sustainable agriculture, and securing food and nutrition for future generations. The present review discusses recent advancements in genomics-assisted breeding (GAB) aimed at improving nutrient uptake (NU) in major cereals. This review delineates the biochemical and molecular underpinnings of NU, emphasizing how genomics tools such as QTL mapping, GWAS, GS, and CRISPR/Cas9 enable the dissection and targeted improvement of multifactorial NU and NutrUE-related traits. Additionally, it also explored the high-throughput phenotyping (HTP) and genotyping (HTG) platforms, including imaging techniques like MRI, X-Ray CT, and UAV-based RGB/Multispectral imaging, aligned with next-generation sequencing which enable precise and rapid characterization for NU and NutrUE-related traits. Furthermore, the review addresses how multi-omics approaches (genomics, transcriptomics, proteomics, and metabolomics) contribute to the identification of candidate genes and regulatory pathways associated with NU. Ultimately, this integrated approach provides valuable strategies and insights for researchers, breeders, and policymakers working in accelerating the development of NU and NutrUE cereal cultivars, thereby supporting agricultural sustainability and global hunger prevention.

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1. Introduction

Global challenges like climate change, population growth, resource depletion, and urbanization require an increase in crop productivity to ensure food and nutritional security (Bakala et al., 2020; Saini et al., 2020). Among the cereals rice (*Oryza sativa* L.), wheat (*Triticum aestivum* L.), and maize (*Zea mays* L.), are the major food crops as they provide the majority of caloric intake in human diet (Gudi et al., 2022; Singh et al., 2024a). Abiotic stresses like heat, cold, drought, and salinity threaten crop productivity under climate change (Arif et al., 2025a; 2025b; Bakala et al., 2024; Singh et al., 2025). These stresses often impair nutrient acquisition and metabolism. Crop productivity heavily depends on efficient uptake and utilization of nutrients such as nitrogen (N), phosphorus (P), potassium (K), iron (Fe), zinc (Zn), calcium (Ca), cadmium (Cd), copper (Cu), and magnesium (Mg) (Sandhu et al., 2021). The NU in plants is a complex trait governed by polygenes and it highly influenced by environmental factors and shows continuous variation. The NU from rhizospheric zone mainly influenced through root system architectural (RSA) traits such as phenotypic plasticity, root length and density, number of root hairs and length, absorption capacity, depth of roots, and plant growth and developmental stages and other environmental factors such as soil type, nutrient dynamics, soil microbe flora, availability of light and temperature, humidity and rainfall/water availability at root zone of plants (Lynch, 2005; Shahzad and Amtmann, 2017). Plant roots play a crucial role in the NU from the rhizosphere *via* direct or indirect ways. The uptake/absorption of nutrients into plant root cells facilitate through specific type of transporters for particular mineral elements (Sasaki et al., 2016). In the rhizosphere zone, arbuscular mycorrhizal fungi (AMF) play a key role in enhancing NutrUE and activating plant defense, with genetic variation affecting mycorrhizal responsiveness and disease resistance (Hohmann and Messmer, 2017). Contribution of plant growth promoting microbes (rhizosphere zone) in soil plant nutrient management expands NU and biofortification in staple crops and is a long-term solution to the problem of micronutrient deficiencies, builds crop resilience, and promotes food and nutritional security in various cropping systems (Jalal et al., 2024).

Modern era of agriculture, it's necessary to use advanced breeding and genomics techniques for the identification of genetic factors associated with uptake and their assimilation of nutrients in crops. Fundamental approaches to understand the basic mechanism of NU by genetics, breeding, and physiological approaches, is essential for crop improvement. Understanding of the physio-biochemical pathways linked with NU and their transport, assimilation and source to sink relationship through GAB techniques would lead to targeted improvement in NutrUE under nutrient-limited conditions (Mitra, 2015; Wahab et al., 2024). GAB can be highly effective in improving NU in cereals by utilizing genomic tools like genomic selection (GS), marker-assisted selection (MAS), and genome-wide association studies (GWAS) (Varshney et al., 2021). These techniques allow breeders to identify and select genes linked to efficient with NU, such as nitrogen use efficiency (NUE) and phosphorus use efficiency (PUE), early in the segregation generation of breeding process. NutrUE in plants is closely associated with quantitative trait loci (QTLs) related to RSA (Sandhu et al., 2016, 2015).

Among the various genomic tools GWAS and GS have proven valuable in improving complex traits, including NutrUE in cereals by targeting functional adaptive traits including RSA, symbiotic relationships, and physiological mechanisms (Mallikarjuna et al., 2022). Additionally, advancements in HTP techniques coupled with GWAS and GS have facilitated the identification of candidate genes associated with NutrUE and other adaptive traits. These developments provide insights into the underlying mechanisms that can improve major NutrUE in cereals. Proteomics and metabolomics provide insights into nutrient pathways, and computational modeling helps predict gene interactions, leading to the development of nutrient-efficient for crop production (Moshood et al., 2025). Multi-omics approaches offer a strong framework for uncovering the complex regulatory networks involved in NU in cereals, thus leading to advancements in crop improvement (Saini et al., 2024). Continued advancements in multi-omics technologies and data integration methods will enhance researchers' ability to decipher complex regulatory networks in cereals (Mahmood et al., 2022).

Validating and fine-tuning GWAS associations for NU in cereals is achieved through candidate gene approaches, transcriptomic analysis, metabolomics, and genome editing tools which offer deeper insights and precision in gene-function studies (Ashraf and Ahmad, 2023). Candidate gene approaches involve investigating genes with possible roles in NU and NutrUE, based on their functions or expression profiles under different nutrient conditions (Pflieger et al., 2001). Transcriptomic techniques such as RNA sequencing (RNA-Seq) and quantitative PCR (qPCR) measure gene expression levels involved in NU under different conditions, thus providing insights into how genes respond to varying nutrient availability in cereals (Fu et al., 2023; Imadi et al., 2015; Kaur et al., 2022). Proteomics and metabolomics are pivotal for elucidating gene functions associated with NU in cereals, offering molecular insights beyond genomics by characterizing the proteome (all expressed proteins) and metabolome (small molecule metabolites), which directly reflect gene function and environmental interactions (Raza et al., 2024; Singh et al., 2024b). Recent progress in delivery systems and genome editing technologies, such as CRISPR/Cas (clustered regularly interspaced short palindromic repeats) system, have further enhanced the efficiency and applicability of RNAi (RNA interference) in crop improvement programs.

Overall, GAB will support more precise and effective strategies in future for improving NU and efficiency performance in rice, wheat, and maize. Understanding the regulatory networks involved in NU allows for the development of targeted breeding strategies and genetic modifications. Integration of multi-omics approaches would be helpful in better understanding of the genetic basis of NU in cereals. Which may lead to the development of improved crop cultivars in a better responsive way for decreasing the environmental footprints of chemical fertilizers for agricultural practices in a sustainable manner. Despite the increasing use of genomic tools in cereal breeding, a comprehensive integration of multi-omics approaches specifically targeting NU mechanisms in major cereals remains limited. This study uniquely synthesizes current genomic-assisted strategies with HTP and genome editing to address NutrUE in rice, wheat, and maize under nutrient-limited conditions. Keeping all these aspects, this article is conceptualized to explore the fundamental physio-biochemical and molecular mechanisms behind the uptake of major (N and P) and minor (Fe and Zn) nutrients in three major cereals: rice, wheat, and maize. Also focusing on HTP and HTG approaches for the identification of diverse parents for introgression of NutrUE traits and generation of mapping populations. The multi-omics approaches and genome editing techniques would be useful in dissecting the genetic loci associated with NutrUE traits and development of improved cereal cultivars.

2. Role of plant breeding in NU

NU efficiency is critical for plant growth and development as well as defence mechanism against biotic and abiotic stresses. Efficient NU in plants is important for low input agricultural while maintaining the yield and quality of the product to support the nutritional requirements of the consumers (Jyoti et al., 2024). However, most of the breeding efforts in major crops have been focused on developing high-yielding varieties (HYVs) that require intensive cultivation including the higher application of fertilizers. Only a fraction of the fertilizers applied is taken up and utilized by the improved varieties exhibiting reduced impact of N fertilization on yield improvement (Hu et al., 2023; Tilman et al., 2022), thus signifying the need for enhancing the NU efficiency. The genetic and molecular mechanisms underlying NU and transport in cereals, including diverse transporter proteins and signaling networks, offer valuable insights into improving NutrUE through targeted genetic manipulation (Messmer et al., 2012).

Genetic improvement of the NU and utilization in major crops is gaining increasing interest to reduce demand for agricultural inputs while maintaining high yield (Hu et al., 2023). There is significant variation in NU and utilization capacity among germplasm collections of wheat, maize, and rice (Saini et al., 2022; Petroli et al., 2023). Despite the presence of this variation, however, conventional plant breeding strategies for NU have been challenging and showed limited success (Ferrante et al., 2017). Before starting breeding program for NU efficiency precise phenotyping is very important. Phenotyping for NU has been challenging but started benefiting from recently developed high-throughput platforms for measuring multiple ion-uptake rates in rice, wheat, and maize (Griffiths et al., 2021). But NU is a complex multi-genic trait involving myriads of genes, transport of the macro and micro-nutrients and some environment such as soil physical and chemical properties, these all factors regulating the plant growth and development. Micronutrients interactions and chemical similarities lead to competition for plant transport proteins and other uptake mechanisms thus impacting their absorption and bioavailability to plants (Griffiths et al., 2021). Moreover, continued yield gains have significantly reduced grain Zn and Fe and declines in micronutrient concentrations in rice, wheat, and maize (Fan et al., 2008; Guttieri et al., 2015).

Limited understanding of the genetic basis of NU hampers the development of nutrient-efficient cultivars. To understand the genetic basis of NU, several mapping populations are developed and QTLs linked to NU were identified in wheat (Liu et al., 2019; Saini et al., 2021), maize (Gallais and Hirel, 2004; Xu et al., 2022a), and rice (Navea et al., 2023). Exploring diverse germplasm by allele mining to uncover natural variation, which facilitates the identification of alleles associated with yield and stress resilience (Singh, 2025). For example, natural allelic variation in the *DNR1* locus creates natural variants that mediate auxin involvement in regulating N uptake and metabolism with the *indica* allele having increased NUE and yield in rice (Zhang et al., 2021a). Recent advances in sequencing and genotyping technologies, increasing genomic resources as well as molecular biology tools have enabled the identification of genomic regions and genes and functionally validate their role in NU. The identification of high-density single-nucleotide polymorphism (SNPs) in diverse germplasm (Liu et al., 2019; Manjunath et al., 2023), which are distributed across the genome, support developing genetic markers and applying MAS for enhancing NutrUE in crops (Heidari et al., 2024).

Considering the complexity of NU traits, traditional breeding strategies through cross-hybridization is less effective for utilizing the existing diverse germplasm. The development of nutrient-rich, HYVs adapted to diverse climatic conditions requires the strategic use of advanced breeding tools to screen thousands of germplasm accessions and establish a core collection for targeted hybridization. Recently, GAB strategy emerged as a modern breeding approach for facilitating the breeding process for improving complex traits such as efficient NU in plants (Varshney et al., 2021). GAB involves the GS for selecting potential genotypes; MAS for introgression and pyramiding of the traits into high-yielding genotypes, speed breeding for reducing the life cycle applies, omics techniques to dissect regulatory networks for NU, and the application of genome editing for NutrUE traits in an integrated manner (Dhanyalakshmi et al., 2024; Varshney et al., 2021).

3. Biochemical factors involved in NU

NU in cereals involves complex mechanisms, including specific transport systems, root exudation, chelation, and microbial interactions (Dakora and Phillips, 2002; Lynch, 2019). N is primarily acquired through nitrate and ammonium transporters (e.g., NRT and AMT families) (Sandhu et al., 2021), whereas P uptake largely occurs *via* phosphate transporters (PHT family) (Wang et al., 2021). K is absorbed through specialized channels and transporters, such as HAK/KUP family (Wang and Wu, 2017). Micronutrients like Fe and Zn are obtained through mechanisms involving phyto-siderophore secretion, organic acid-mediated chelation, and specific transporter proteins (e.g., ZIP and YSL families) (Ajeesh Krishna et al., 2020; Yamagata et al., 2022). These uptake processes are fundamentally governed by complex biochemical pathways that modulate nutrient availability, mobilization, and assimilation within plants. Understanding these biochemical processes is important, as they directly influence the efficiency with which plants absorb, translocate, and assimilate nutrients. Biochemical factors such as root exudates, enzyme activities, transporter proteins, and hormonal regulation play significant roles in determining NutrUE (Fig. 1)(Giehl and von Wirén, 2014; Jia et al., 2022; Wang and Wu, 2017). The following sections deal with major biochemical factors governing the NU in cereals:

3.1. Root exudates and their role

Root exudates, comprising a diverse range of organic compounds such as organic acids (citrate, malate, oxalate), phenolics, phytosiderophores, amino acids, and extracellular enzymes, significantly influence nutrient availability and uptake in cereals (Ma et al., 2022). These exudates alter the chemical and biological properties of the rhizosphere, thereby enhancing the mobilization and subsequent uptake of nutrients like P, Fe, Zn, and other micronutrients (Dakora and Phillips, 2002). Organic acids secreted by cereal roots play a key role in the mobilization of P, particularly under P deficient conditions. Citrate and malate can effectively solubilize phosphate by chelating metal ions (e.g., Aluminum, Fe, and Ca), which otherwise immobilize P in the soil (Lynch, 2019). Fe and Zn uptake, critical for plant growth and human nutrition, is significantly enhanced by specialized root exudates known as phytosiderophores. Cereals (wheat, barley, maize, and rice) synthesizing and releasing phytosiderophores like mugineic acids (MAs) under Fe-deficient conditions. These phytosiderophores chelate Fe^{3+} ions in the soil that forms soluble complexes that can subsequently be absorbed by roots through specific transporters, such as Yellow Stripe-Like (YSL) proteins (Yamagata et al., 2022).

Genetic variations in phytosiderophore secretion among different cereal genotypes significantly affect their capacity to tolerate nutrient-limited soils which makes this trait a promising target for GAB. Phenolic compounds, amino acids, and extracellular enzymes also play supporting roles in nutrient availability. Phenolic exudates contribute to nutrient mobilization by facilitating metal chelation and altering microbial communities, while extracellular enzymes like phosphatases and phytases hydrolyze organic P compounds, enhancing P availability to plants (Giehl and von Wirén, 2014). Root microbiomes and rhizosphere are essential in the promotion of NutrUE by boosting nutrient acquisition, mobilization, and signals that enhance plant growth and survival in diverse agriculture systems. Modern breeding and domestication of maize and barley have changed root traits and rhizosphere microbiome, which commonly diminished plant-microbiome interactions that are essential to NU/acquisition under low-input regimes (Schmidt et al., 2016; Kindtler et al., 2024). These aspects of microbial relationships can be explained and utilized to enhance the aspect of sustainable crop production and resource utilization efficiency. Recent advances in plant-microbiome research highlight the vital role of the rhizosphere microbiome in enhancing nutrient uptake and NUE in cereals. AMF, plant growth-promoting rhizobacteria (PGPR), and associative diazotrophs contribute to nutrient solubilization, mobilization, and biological nitrogen fixation (BNF). Diazotrophic bacteria such as *Azospirillum, Herbaspirillum*, and *Gluconacetobacter* establish loose associations with cereal roots and can fix atmospheric N, especially under low-input conditions, providing a sustainable source of N. Additionally, rhizosphere microbes enhance P and Fe mobilization through organic acid secretion and siderophore production. The selection and breeding of cereal varieties capable of recruiting beneficial microbial consortia (termed microbiome-assisted breeding), is emerging as a complementary strategy to GAB. Understanding host-microbiome interactions can

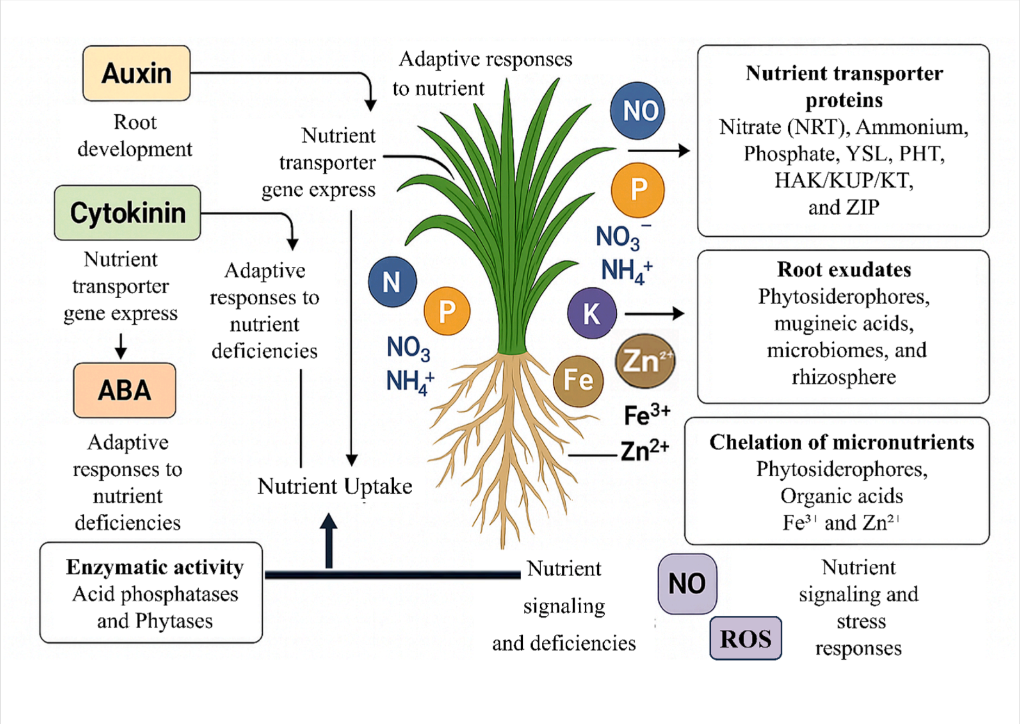

Fig. 1. Role of biochemical factors such as hormones and signaling molecules nutrient uptake in cereals. The diagram illustrates how plant hormones (e.g., auxin, cytokinin, ABA) and signaling molecules (e.g., nitric oxide [NO], reactive oxygen species [ROS]) regulate root development, nutrient transporter gene expression, and adaptive responses to nutrient deficiencies. Root enzymatic activities (acid phosphatases, phytases), root exudates (organic acids, amino acids, phytosiderophores), and chelation processes aid in mobilizing and acquiring key nutrients (e.g., N, P, K, Fe, Zn). Specific transporter proteins (e.g., NRT, PHT, HAK/KUP, ZIP, YSL) facilitate uptake, while coordinated hormonal signaling integrates nutrient sensing with stress responses to optimize plant growth under variable nutrient conditions.

inform trait selection for root exudation, rhizosphere colonization, and stress resilience, thus enhancing nutrient acquisition and sustainability (Ahmad et al., 2025; Ullah et al., 2025).

3.2. *Nutrient transporter proteins*

Nutrient transporter proteins play an essential role in NU by facilitating the efficient absorption and internal transport of both macronutrients (NPK) and micronutrients (Fe and Zn) in cereals. These transporter proteins are predominantly located in root epidermal and cortical cells that regulate nutrient influx from the soil solution into the plant roots, thus determining overall plant nutrient efficiency and productivity (Wang and Wu, 2017; Zelazny and Vert, 2014). N uptake, primarily in the form of nitrate (NO^{3-}) and ammonium (NH^{4+}), involves specialized transport proteins such as nitrate transporters (NRT) and ammonium transporters (AMT). The nitrate transporter families *NRT1* and *NRT2* mediate nitrate uptake across a broad concentration range, with NRT1.1 and NRT2.1 being critical regulators of nitrate uptake efficiency in cereals (Feng et al., 2020; Sandhu et al., 2021). Similarly, AMT facilitates ammonium absorption which is crucial under low-nitrate conditions (Hao et al., 2020). P uptake is mediated primarily by phosphate transporters belonging to the PHT1 gene family. These transporters actively transport phosphate ions from the rhizosphere into root cells. Genetic variation in PHT1 transporter expression has been documented in rice and wheat, thus influencing phosphate acquisition under P-deficient conditions (Poirier et al., 2021; Wang et al., 2021). Thus, identifying genotypes with efficient phosphate transporter expression offers valuable targets for GAB strategies. K uptake involves several transporter families, including HAK/KUP/KT transporters and specific K channels. Members of the HAK/KUP/KT transporter family regulate K absorption, under low-K conditions and enhances NutrUE in cereals (Cai et al., 2021; Li et al., 2018; Wang and Wu, 2017). Micronutrient transporters significantly impact the bioavailability of these critical nutrients. Fe uptake in cereals involves YSL and ZIP (Zinc-regulated transporter/Iron-regulated transporter-like Protein) families, which facilitate the transport of Fe-phytosiderophore complexes into root cells. Similarly, ZIP family transporters play a vital role in Zn uptake and internal redistribution within the plant (Ajeesh Krishna et al., 2020; Yamagata et al., 2022).

3.3. *Role of hormones and signaling molecules*

Plant hormones and signaling molecules significantly influence NU by regulating root architecture, transporter gene expression, and biochemical processes involved in nutrient assimilation. Key phytohormones such as auxins, cytokinins, abscisic acid (ABA), and ethylene modulate root development (Fig. 1), root hair proliferation, and lateral root formation, thereby directly affecting nutrient acquisition capacity in cereal crops (Kiba et al., 2011; Zhao et al., 2021). Auxin regulates growth and development by influencing cell elongation, root formation, and tillering, while also enhancing NUE and stress resistance through genes like *DNR1* and *OsARF18* in rice. Understanding auxin signaling and transport aids in optimizing yield and adaptability for sustainable rice cultivation (Hou et al., 2025). Cytokinins, on the other hand, regulate nutrient transporter gene expression, especially influencing nitrate and phosphate transporters. These hormones maintain an optimal balance between root and shoot growth based on nutrient availability, thus signaling plants to adjust growth patterns to enhance NutrUE (Gu et al., 2018; Sakakibara, 2021). ABA and ethylene are involved in adaptive responses to nutrient deficiencies. Under nutrient-limiting conditions, ABA and ethylene signaling pathways are activated to regulate the expression of specific nutrient transporter genes and enhance root exudation processes that mobilize nutrients in the rhizosphere (Müller, 2021). Furthermore, signaling molecules such as nitric oxide (NO) and reactive oxygen species (ROS) play a critical role in nutrient signaling and stress responses. These molecules act as secondary messengers and modulate the transcriptional regulation of nutrient transporter genes and root morphological adaptations under nutrient-stressed environments (Hong et al., 2024).

3.4. Enzymatic activity in roots

Root enzymatic activity significantly influences nutrient mobilization and availability in cereals. Various extracellular enzymes secreted by roots play key roles in the solubilization, mineralization, and acquisition of critical nutrients including N and P (Cao et al., 2024). Among these enzymes, acid phosphatases, phytases, and nitrate reductase (NR) are especially important under nutrient-deficient conditions. Acid phosphatases (APases) released by cereal roots hydrolyze organic phosphate compounds present in the rhizosphere into inorganic phosphate (Pi), enhancing its availability for NU. Genetic variability in APase activity has been observed across cereal genotypes that makes this trait an attractive target for GAB strategies aimed at improving PUE (Bhadouria and Giri, 2022). Phytases specifically hydrolyze phytate, a major form of organic P in soils, releasing Pi accessible to plant roots. Enhanced phytase activity has been linked to improved P acquisition in maize and wheat, thus highlighting the importance of selecting genotypes with naturally higher root phytase activity for breeding nutrient-efficient varieties (Singh and Satyanarayana, 2011). NR, an essential enzyme involved in N assimilation, reduces nitrate absorbed by roots into nitrite, subsequently converted into ammonium and assimilated into amino acids. Variability in NR activity among cereal varieties is closely associated with differences in NUE which makes it a valuable biochemical marker for breeding programs targeting enhanced N acquisition and utilization (Sandhu et al., 2021).

3.5. Chelation and bioavailability of micronutrients

Chelation is a critical biochemical process through which plants enhance the bioavailability of essential micronutrients such as Fe, Zn, Cu, and Mg. Cereals utilize specific organic compounds such as phytosiderophores and organic acids, to chelate micronutrients in the rhizosphere, forming soluble complexes that are efficiently absorbed by roots (White and Broadley, 2009). Phytosiderophores, primarily synthesized and secreted by graminaceous plants, including rice, wheat, and maize, are highly effective in mobilizing Fe under Fe deficient conditions (Römheld, 1991). These phytosiderophores (MAs) possess strong affinity for ferric iron (Fe^{3+}), forming soluble Fe^{3+} phytosiderophore complexes that are subsequently taken up via specific root transporters, particularly YSL transporters (Yamagata et al., 2022). Variability in phytosiderophore production and secretion among cereal genotypes significantly impacts their ability to acquire Fe efficiently, thus highlighting this biochemical trait as a promising target for GAB. In addition to phytosiderophores, organic acids like citrate, malate, and oxalate released from roots are crucial in enhancing micronutrient bioavailability (Cakmak et al., 1996). These organic acids facilitate micronutrient uptake by chelating metal ions, particularly Zn^{2+} and Mn^{2+}, rendering them soluble and bioavailable for absorption through root transporter proteins, including members of the ZIP family. Cereals exhibiting higher organic acid exudation often display improved Zn and Mg uptake efficiency, making organic acid secretion an important biochemical characteristic for nutrient acquisition (Ajeesh Krishna et al., 2020; Dakora and Phillips, 2002; Gupta et al., 2016).

Integrating biochemical insights with advanced genomic tools accelerates the selection process, enabling breeders to efficiently develop nutrient-efficient cultivars, ultimately helping to sustainable agriculture.

4. Molecular mechanisms of NU in cereals

The plant genome regulates gene expression to maintain cellular homeostasis under different stresses to ensure nutrient and water availability for crop growth and development (Mitra, 2018). High-affinity transporters facilitate uptake of N and P under low nutrient conditions, while low-affinity transporters operate at higher concentrations. Specific transporters also regulate the uptake of secondary and micronutrients during both low and high-nutrient stress. Schematic overview of the transporters and genes operating for the uptake, assimilation, translocation, and remobilization of macro (N and P) as well as micronutrients (Zn and Fe) from soil rhizospheric zone to cereal grains is provided in Fig. 2. The following section focuses on the molecular mechanism of major and minor NU in cereals:

4.1. Nitrogen (N)

N play a significant role in plant growth and development. The photosynthesis process in plant cells is mostly dependent on the most abundant protein Rubisco. N mostly accumulated in the plant leaves regulated by the Rubisco enzyme for photosynthesis, so it is observed that the under limited N conditions negatively affect Rubisco resulted in decreases photosynthetic activity that directly affects plant yield (Guo et al., 2019). Absorption of N is mainly in the form of nitrate and ammonium ions in the plants. The assimilation of N involves different enzymes to channelize nitrate into amino acids and proteins. Nitrate and nitrite are the primary source of N in cereals, both elements can be targeted for improvement in the efficient uptake and transport through GAB in future. Nitrate converted into nitrite through *NAD(P)H*-dependent enzyme NR inside the cytoplasm and further nitrite reduced into ammonia by nitrite reductase (Sétif et al., 2009). Ammonia is channelized by the synthesis of amino acid glutamate acting as primary receiver of ammonia, this reaction consecutively catalyzed through two enzyme glutamine synthetase and glutamate synthase (*GOGAT*). Glutamine synthetase has two isoforms i.e., *glutamine synthetase1* expressed in cytosol of leaves, roots, and phloem cells, whereas the second isofrom *glutamine synthetase2* expressed in plastids of chloroplast, roots, and etiolated tissues (Lea and Miflin, 2011). *GOGAT* also exist in two isoforrms, i.e., GOGAT ferredoxin-dependent (*Fd-GOGAT*) and GOGAT-NADH dependent (*NADH-GOGAT*), and play an important role in N assimilation/recycling (Lea and Miflin, 2011). Glutamate and glutamine are the primary amino acids essential for protein synthesis. The partial fraction of ammonia also associated with the arginine metabolism through carbamoyl phosphate (C-skeleton). In addition to the primary N metabolism, secondary N sources (nitric oxide, nitrous oxide, nitroalkane, nitrile, hydrazine, and formamide) also contribute to the N metabolism (Sandhu et al., 2021).

N absorption by plant roots occurs in the form of nitrate in aerobic soils, while ammonium is more commonly absorbed in acidic soils and wetlands. The transport of N from soil to root and to other different plant parts is through plasma membrane localized protein (transporters). It regulate mobilization of nutrients from source to sink (Fan et al., 2017). Based on availability of N, plants evolved two systems for uptake of N; when N availability is adequate, plants use a low-affinity transport system (LATS), whereas under limited availability of N use high affinity transport system (HATS). Plants have two low-affinity and two high-affinity transporters for nitrate (*NRT1*-LATS and *NRT2*-HATS) and ammonium (*AMT1*-LATS and *AMT2*-HATS). Majority of the cereal uptake N in the form of NO^{3-}, whereas rice uses both the N form i.e., NO^{3-} and NH^{4+}. The transport of nitrate involved four nitrate transporter families namely *NPF, NRT2, CLC*, and *SLAC1/SLAH.* The first NO^{3-} transporter *NRT1.1* was identified in *Arabidopsis* (Tsay et al., 1993). The *NRT1* (rename as *NPF*) transporter family is the largest family; it is classified into eight subfamilies. The *NPF* transporters are well characterized into 52 members in *Arabidopsis*, 88 members in rice and 292 members in wheat (Kumar et al., 2022; Von Wittgenstein et al., 2014).

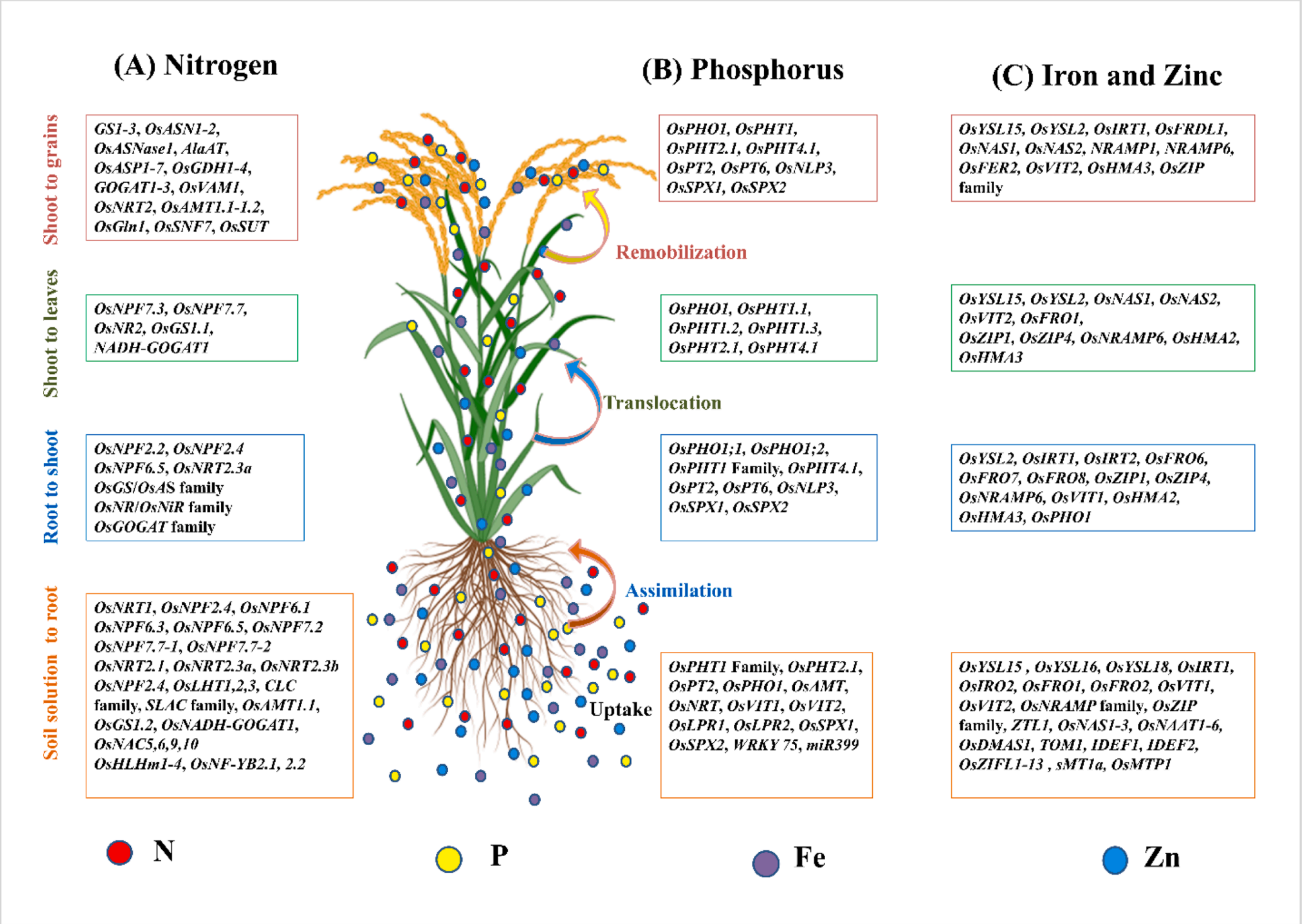

Fig. 2. Schematic representation of transporters and genes involved in nutrients uptake (absorption of nutrients from the soil by root), assimilation (conversion of absorbed nutrients into useful compounds in the plant), translocation (movement of nutrients from roots to other parts of the plant) and remobilization (redistribution of stored nutrients to growing or needy tissues) in plant systems. Transporters and genes associated with nitrogen (A); phosphorus (B); and iron and zinc (C). Here red, yellow, violet, and blue points on plant indicate nitrogen, phosphorus, iron zinc movement, respectively.

The high affinity nitrate transporters *NRT2* family having 7, 4 and 46 transporters in *Arabidopsis*, rice, and wheat, respectively (Feng et al., 2011; Kotur et al., 2012; Kumar et al., 2022; Yan et al., 2011). *Chloride channel* (*CLC*) family of nitrate transporters associated with vacuolar transport of nitrate. *Arabidopsis*, rice, and wheat having 6, 7, and 34 *CLC* genes involved in nitrate and chloride homoeostasis (Jossier et al., 2010; Kumar et al., 2022; Zifarelli and Pusch, 2010). The fourth family *SLAC1/SLAH* transport nitrate in guard cells and roots, having 4, 8, and 40 members in *Arabidopsis*, rice, and wheat, respectively (Kumar et al., 2022). This study reported 412 nitrate transporters in hexaploid wheat, out of those 12 genes were only root specific, 11 root-shoot and 17 genes for grain/spike specific identified. These four transporter families play a significant role together in nitrate uptake and utilization in plants. Generally, *indica* rice cultivars more efficiently uptake nitrate than *japonica*, thus *indica* rice more successfully grown under aerobic or upland conditions. Gene *NRT1.1B/NPF6.5* utilized to check polymorphism between *japonica* and *indica* cultivars for nitrate uptake (Chen and Ma, 2015; Hu et al., 2015). By integrating key genes, root traits, and plant microbe interactions, to understanding the genetic, molecular, and microbial regulation of N uptake and improve NUE in maize (Li et al., 2025).

Transporter *AtNRT1.9* increase uptake of NO^{3-} in root phloem, *AtNRT1.11* and *AtNRT1.12* redistributes phloem N to youngest tissues in *Arabidopsis* (Hsu and Tsay, 2013). The transporters *NPF6.1, NPF7.4*, and *NPF7.7* increase uptake of NO^{3-}; *AMT1;1* increases NH^{4+} uptake and also showed homeostasis with K in rice (Tang et al., 2019). A major QTL designated as *Gpc-B1* showed 66 % phenotypic variation, present on wheat chromosome 6BS controlling grain protein content has been cloned (Uauy et al., 2006). The five transporters (*TaNRT 2.1*, Ta*NRT 2.2*, Ta*NRT 2.3*, Ta*NAR 2.1*, and Ta*NAR2.2*) regulate HAT system in wheat, though activation of the transporters in absence of nitrate (Cai et al., 2007). Nitrate transporters are the main player for the uptake of N in most plants but in certain case ammonium form is predominant in the soil. Rice having ten-member family *AMT* transporters, broadly classified into HATs and LATs. The three *OsAMT1* family members belonged to HATs group whereas three *OsAMT2*, three *OsAMT3* and one *OsAMT4* members falling in LATs group (Li et al., 2017; Loqué and von Wirén, 2004). In rice, *OsNR1, OsNR2, NiR, OsGS1.1, OsGS1.2, OsGS1.3, OsGS2, OsNADH-GOGAT1, OsNADH-GOGAT2, OsFd-GOGAT, OsASN1,*and *OsATG8b* genes involved in assimilation and remobilization of N (Nazish et al., 2021; Sandhu et al., 2021). Transcription factors (TFs) like *WRKY1* play a major role in regulation of N network in plants, which can be targeted for GAB. The *AMT* transporters more efficiently enhanced NUE in ammonium, loving rice cultivars than nitrate transporters. The increased uptake of N also has synergetic effects on uptake of P, K, Ca, Cu, Fe, and Zn in plants. Thus, advanced genotyping technologies can be efficiently utilized for the improvement of NUE in wheat and maize by targeting only nitrate transporters through marker and GAB programs. And these transported also has a significant role in the varietal development of rice, specially breed for direct seeded cultivation system where nitrate uptake is predominant.

4.2. Phosphorus (P)

P is an important element for better root establishment and plant growth. Most of the plant's uptake P *via* Pi forms i.e., $H_2PO_4^-$ and HPO_4^2, depending on pH of soil. Under Pi deficit conditions, plants root growth and architecture are adversely affected. The plasma membrane localized to phosphate transporter (*PHT1/PT*) family mainly responsible for the uptake of P from soil solution to root cells (Sasaki et al., 2016). Plants also have both low and high affinity phosphate transporters; the high affinity phosphate transporters are localized in plasma membrane of root hairs, induced under Pi deficit conditions whereas affinity phosphate transporters are expressed in Pi sufficient conditions and predominantly presents in entire plant. Some TFs, namely *PHR1* (*phosphate starvation response 1*), *OsPTF1,* and *WRKY 75* are also responsible for Pi uptake under Pi starvation conditions in rice and maize (Lin et al., 2013). Maize *ZmPT7* regulates Pi uptake and redistribution; it is expressed in roots and leaves under Pi deficiency (Wang et al., 2020). *Arabidopsis* has four Pi transporter families i.e*., PHT1, PHT2, PHT3,* and *PHT4* (Lin et al., 2009). The members of *PHT1* gene family located at plasma membrane of root epidermal cells (Lin et al., 2009), *PHT2* gene family located at chloroplasts (Versaw and Harrison, 2002), *PHT3* in mitochondria (Poirier and Bucher 2002) and of *PHT4* in golgi apparatus (Guo et al., 2008). Under Pi-deficiency, the up-regulation of *TPSI1/Mt4/At4* gene families indicate the importance at early stage of plant adaptation to low P availability (Hammond et al., 2004). In rice, genes *PT4* and *PT8* are expressed only in roots whereas *OsPT2* and *OsPT6* in both root-shoot tissues (Zhang et al., 2015). TFs *PHR1* had two homologues in rice namely *OsPHR1* and *OsPHR2* (Zhou et al., 2008). Over-expression of *OsPHR2* gene in transgenic rice increased accumulation of Pi in roots and helped to root elongation and root hair purification. Micro RNAs also play an important role in Pi uptake; under P-deficit conditions *miR399* was up-regulated in plants (Bari et al., 2006; Fujii et al., 2005). In maize under Pi-deficiency increased the colonization of AMF and reported that induction Pi transporter gene *ZmPHT1;6* and *ZmPt9* by formation of mycorrhiza (Willmann et al., 2013). The *Arabidopsis* and rice *PHT1* genes are mostly expressed in roots, *AtPHT1;5* and *OsPHT1;8* (*OsPT8*) genes are involved in source to sink distribution of phosphate. Thus, the P uptake can be improved in rice, wheat and maize by targeting majorly *PHT* family, *PHO* and *NLP* transporters through GAB.

4.3. Uptake of Fe and Zn

The uptake of micronutrients is a very complex process; it is also governed by polygenes and many complex biochemical pathways. The uptake of Fe in plants is *via* two strategies (strategy-I and -II). The strategy-I involves proton release into the rhizosphere to solubilize Fe^{3+} into soil, reduction of Fe^{3+} through Fe^{2+} chelate reductase, and resulted transport of Fe^{2+}into root cells. The mechanism strategy-I of Fe uptake utilized the chelation-based strategy by releasing Fe^{3+}specific phytosiderophores and uptake of Fe^{3+}phytosiderophores complexes through specific transporters (Colangelo and Guerinot, 2006). Most of the graminaceous family plant use chelation strategy (strategy-II) for uptake of metal ions (Fe, Zn, and Cu etc.). The graminaceous plants secrete MAs family phytosiderophores in the rhizosphere for solublization of the Fe^{3+} ions and develop Fe^{3+}phytosiderophores complexes (Colangelo and Guerinot, 2006). The biosynthesis of the MAs involved various enzymatic processes and genes that encode for different enzyme/by-products. The methionine is the precursor of MAs, in this process L-methionine first adenosylated by S-adenosylmethionine synthetase resulted converted into S-adenosylmethionine (SAM). The enzyme nicotianamine synthase (NAS) plays very important role in Fe and Zn uptake mechanism in wheat and rice, it converts SAM into nicotianamine (Johnson et al., 2011; Kamaral et al., 2022). The nicotianamine associated with Fe^{2+} and Fe^{3+} directly involved in uptake of Fe. Nicotianamine aminotransferase (NAAT) enzyme converts nicotianamine into 3'’-oxo form and subsequently converted into 2′-deoxymugineic acid (DMA) through deoxymugineic acid synthase (DMAS) (Kobayashi et al., 2008; Ogo et al., 2007). DMA is a one type of MAs directly involved in uptake of Fe. DMA finally converted into MAs, epiHDMA, HMA and epiHMA with the help of IDS2 and IDS3 (IDS: Fe-deficiency-specific clone). These MAs binds with Fe^{3+} ions in the rhizosphere and absorbed by the root cells (Kobayashi et al., 2008, 2001; Ogo et al., 2007).

Rice use both strategies for Fe uptake, under submerged condition uptake in the form of Fe^{2+} ions through *FRO* (Fe^{3+} chelate reductase) genes family, iron regulated transporters (*IRT*) and ZIP (ZRT IRT-like protein) families (Colangelo and Guerinot, 2006; Ishimaru et al., 2006). The *FRO* genes are eight-member gene family (*FRO1–8*), the FRO2 (*OsFRO2* in rice) expressed in epidermal cells of roots, and some other expressed specifically in shoot tissues i.e., *FRO6, FRO7* and *FRO8* (Colangelo and Guerinot, 2006) under Fe-deficit conditions. The transport of Fe^{2+} ions takes place through *IRT1*, a ZIP family transporter (Eide et al., 1996). Under Fe-deficient condition, transporters *OsIRT1* and *OsIRT2* expressed in rice roots, and also transport Zn (*OsIRT1*) (Ishimaru et al., 2006).

Under the aerobic condition most of the cereal's uptake Fe in the form of Fe^{3+} through chelation strategy. The transport of Fe-PS complexes involved mainly through YS1 transporters. YS1 defective mutant (*ys-1*) in maize unable to uptake Fe-PS and had interveinal chlorosis (Curie et al., 2001). In rice 18 *YS1 like* (*YSL*) putative candidate genes were identified. The gene *OsYSL2* expressed in encode for Fe^{2+}-NA and Mn^{2+}-NA, whereas *OsYSL15* and *OsYSL16* expressed in root tissues (Inoue et al., 2008; Kobayashi et al., 2005) under Fe-deficiency. *OsYSL2* works like *OsIRT1* in transport of Fe^{2+}-NA and also provide binding core site to *IDEF2*, helped in Fe homeostasis (Ogo et al., 2008). *OsYSL15* a dominant transporter of Fe^{3+} ions and play an important role in Fe ions transport form root to phloem tissues during early vegetative stage in rice (Inoue et al., 2008). *OsYSL15* is also expressed in developmental stages of flower, seed and embryo in rice. The *OsYSL16* transcripts present in root epidermis and vascular bundles of phloem had an important role in for allocation of Fe^{3+}-DMA (Kakei et al., 2012). And the *OsYSL18* transports only Fe^{3+}-DMA but not Fe^{2+}-NA, Zn^{2+}-DMA, Zn^{2+}-NA (Aoyama et al., 2009). The *OsFRDL1* a citrate transporter, mainly involves in Fe translocation into rice grains (Yokosho et al., 2009).

The expression pattern of MAs synthesis genes was triggered under Fe-deficient condition in rice *OsNAS1–3, OsNAAT1–6* and *OsDMAS1* (Inoue et al., 2008), and in maize *ZmNAS1–3* (Inoue et al., 2008; Mizuno et al., 2003). Under Zn-deficiency barley roots absorb more Zn-DMA and less Zn^{2+}, but rice absorb more Zn^{2+} than Zn-DMA (Ishimaru et al., 2011). The *OsNAS1* and *OsNAS2* genes responsible for long distance transport of Fe, these are expressed in roots and leaves while *OsNAS3* expressed only in roots under Fe-deficit condition in rice (Inoue et al., 2003). The overexpression of *OsNAS1, OsNAS2* and *OsNAS3* increases the concentration of Fe-NA and Zn-NA in rice. *OsNAS2* potentially contribute towards higher Fe and Zn concentration in polished rice grains (Johnson et al., 2011). The up-regulation of *HvNAS1, HvNAAT-A, HvNAAT-B, HvIDS2,* and *HvIDS3* in barley under Zn deficient roots (Suzuki et al., 2006). The genes *TOM1* and *HvTOM1* are the PS-efflux transporters of DMA in rice and barley, respectively. These genes showed high expression in roots under Fe-deficiency and overexpression positively associated with Fe-deficiency tolerance (Nozoye et al., 2011). Thus, the identification of the Fe-deficiency inducible aldo-kito reductase genes facilitate the cloning of DMA synthase genes i.e. *OsDMAS1, TaDMAS1*, and *ZmDMAS1* in rice, wheat and maize, respectively (Bashir et al., 2006; Inoue et al., 2008). Under Fe-deficiency responsive cis-elements (*IDE1, IDE2)* of *IDS2* promoter induce higher expression in roots and leaves tissues in rice (Kobayashi et al., 2003). Another *cis* element/trans factor interactions functionally associated with the Fe-deficiency response in plants (Kobayashi et al., 2007). The MAs secretion in rhizosphere also regulated by TFs protein i.e., *bHLH* (Ogo et al., 2007). Overexpression of the *bHLH* gene *OsIRO2* in rice significantly increased the secretion of MAs (Ogo et al., 2007). The TFs *IDEF1* and *IDEF2* bind at *IDE1* and *IDE2*, respectively (Kobayashi et al., 2007), and both are present in root and leaves of rice. *IDEF1* regulates *OsIRO2* which is associated with Fe-deficiency tolerance whereas *IDEF2* regulates *OsYSL2* associated with Fe homeostasis in plants (Kobayashi et al., 2007; Ogo et al., 2008).

The transports of Zn also use chelation strategy like Fe. The intracellular and intercellular transports of Fe and Zn takes placed through *NRAMP* (natural resistance associated macrophage protein) and *YSL* family transporters in rice and other cereals (Colangelo and Guerinot, 2006). The *NRAMP* transporters are evolutionarily conserved ubiquitous metal transporters. Across the rice genome eight *NRAMPs* are present, out of six *OsNRAMP1, OsNRAMP4, OsNRAMP5, OsNRAMP6, OsNRAMP7,* and *OsNRAMP8* responsible for transmembrane transport of Fe and Zn ions and play important role in metal homeostasis (Liu et al., 2021; Sperotto et al., 2010). Plant vacuoles are also an important for storage of excess Fe. Two orthologs of *Arabidopsis VIT1* (Vacuolar Iron Transporter) in rice i.e., *OsVIT1* and *OsVIT2* that transport Fe^{2+}, Zn^{2+} and Mn^{2+} ions from tonoplast into vacuoles has been identified (Zhang et al., 2012). *OsVIT1* and *OsVIT2* enhanced translocation of Fe and Zn between sink and source and resulted in higher accumulation of Fe and Zn ions in rice seeds (Zhang et al., 2012). The *YSL* family gene also transports Zn-PS complexes under Fe-deficit conditions but not detectable under Zn-deficiency, it indicates *YSL* proteins mainly for Fe transporter.

The *ZIP* family metal transporters are mainly involved in Zn transport using strategy-II. Several *ZIP* proteins characterized in rice, wheat and maize (Colangelo and Guerinot, 2006; Kamaral et al., 2022) under Zn-deficit conditions. The mobilization of Zn ions from xylem to phloem mainly depends on *ZIP* transporters in wheat (*TaZIP3, TaZIP7*) and rice (*OsZIP1, OsZIP3, OsZIP4, OsZIP5, OsZIP7, OsZIP8, OsZIP9, OsZIP10*, and *OsZIP11*) (Ishimaru et al., 2011; Kamaral et al., 2022; Liu et al., 2021). *OsZIP1, OsZIP3,* and *OsZIP4* showed higher expression in roots while *OsZIP4* in shoot under Zn-deficiency (Chen et al., 2008). These all-ZIP transporters are suitable candidates for targeting improvement in Zn tolerance cultivars using GAB approaches. The ZIFL (Zinc-Induced Facilitator-Like) family transporters also involved in Zn homeostasis, and rice having 13 paralogs *OsZIFL1–13* is present (Ricachenevsky et al., 2011). It is also reported that under Zn-excess and Fe-deficiency the accumulation of *OsZIFL4, OsZIFL5, OsZIFL7*, and *OsZIFL12* transcripts. The *OsMT1a* (type 1 metallothionein) is expressed in root under water stress conditions and it is associated with Zn homeostasis and drought tolerance in rice (Yang et al., 2009). The overexpression of endogenous ferritin genes (*OsFER2*) in the endosperm specific GlutelinA2 (*OsGluA2*) promoters increases Fe and Zn accumulation in rice grains (Paul et al., 2012). The metal transporter protein transporter (*OsMTP1*) is localized in the membrane of cells. It has significant role in uptake of Zn and Cd to maintain the ion homeostasis. The OsMTP1 also reduce Zn toxicity in rice when crop grown under Zn excessive conditions (Yuan et al., 2012). The *HMA* (*Heavy Metal ATPase*) family transporters also transport Zn from root to shoot in rice i.e., *OsHMA, OsHMA2,* and *OsHMA3* are orthologs of *Arabidopsis HMA* genes for Zn homeostasis (Liu et al., 2019; Takahashi et al., 2012). The overexpression of the *OsNAS2, OsNAS3, Osfer2* could be the potential target genes to increase Fe and Zn concentration rice and wheat grains (Abbai et al., 2019; Kamaral et al., 2022).

Future breeding efforts should focus on key genes involved in phytosiderophore biosynthesis and metal ion transport, such as *OsNAS1/2/3, OsDMAS1*, and *OsYSL15*, which play pivotal roles in Fe and Zn acquisition and long-distance transport. Additionally, genes like *OsIRT1, OsZIP4*, and *OsNRAMP5* can be targeted for enhancing root-mediated uptake under micronutrient-deficient conditions. The TFs *OsIRO2, IDEF1*, and *IDEF2* also represent critical regulators for coordinated expression under Fe-deficiency and can serve as targets for improving stress tolerance and NutrUE.

5. High-throughput phenotyping and genotyping for NU

The conventional low-throughput phenotyping and genotyping has mostly led to false positives during statistical analysis (Tuberosa, 2012). The precision and accuracy of a large number of sample size is a prerequisite for any research experiment, including NU, which can be efficiently facilitated by HTP and HTG platforms (Fig. 3). Both high throughput platforms are now being used to facilitate the faster evaluation of phenotypic traits and genetic profiling of large populations. Nevertheless, they have become popular choices for efficient MAS and GS by GAB, which enabling rapid and precise improvement of breeding populations (Bhat et al., 2020).

5.1. Imaging platforms for shoot and root phenotyping

HTP makes use of advanced imaging and remote sensing technologies to collect extensive phenotypic data efficiently and non-invasively in cereals crops to enhance the NU (Table 1). For instance, multispectral imaging platforms can be used to measure plant health, growth rates, and nutritional status in real-time, allowing breeders to make educated choices based on empirical data (Hilli, 2022). The high-throughput root phenotyping technique plays a major role in significantly enhancing our understanding of RSA and its relationship with NU efficiency (Maqbool et al., 2022; Sharma et al., 2024).

Currently various root phenotyping platforms have been developed, which involve a growth chamber along with imaging devices such as MRI (magnetic resonance imaging), X-Ray CT (computed tomography), PET (positron emission tomography) and NCT (neutron computed tomography) (Maqbool et al., 2022; Sharma et al., 2024) and various software for characterization of root traits. Another advanced root phenotyping system can be used by 3D laser scanning alongside a transparent gel-based growth medium (Fang et al., 2009). This innovative approach enables the non-destructive capture and modelling of root architecture in rice and soybean, particularly under different P conditions. Image based HTP used for evaluating RSA and biomass-related traits in doubled haploid (DH) population under different P conditions using hydroponic culture and 660K SNP array used for genotyping and found 34 QTLs associated with root morphological and P uptake related traits at seedling stage in wheat (Yang et al., 2021a).

5.2. 3D and deep learning approaches

Dynamic phenotypes obtained from 3D point clouds and VIs (vegetation indices) were utilized in GWAS to identify loci associated with NUE and plant height, such as *Rht12, TaARF12–2B, WPCL1–3A*, and *TaDWF4–3A* in wheat (Chen et al., 2024a). The methodology indicated the capabilities of 3D digital phenotyping in enhancing wheat breeding and facilitating the discovery of NUE genes. A 2-D based hydroponic “Pouch and Wick” HTP platform used to analyze the root architecture of 36 elite wheat genotypes in juvenile stage and concluded that length of lateral roots was associated with grain Zn concentration while root angle was associated with grain Fe content in wheat (Khokhar et al., 2019).

The 4-D MRI is appropriate for investigating the RSA of wheat seedlings during establishment in natural soil conditions (Pflugfelder et al., 2022). Eight parental MAGIC (multi-parent advanced generation inter-cross) population of winter wheat were used for study MRI based phenotyping could accurately measure genotypic diversity in root characteristics, including emergence timing, elongation rates, and angles (Pflugfelder et al., 2022). These traits are essential for comprehending RSA and its influence on seedling establishment and nutrient absorption in cereals. X-ray micro-computed tomography (micro-CT) system utilizing for the three-dimensional reconstruction and quantitative assessment of metaxylem vessels within maize root systems (Pan et al., 2017). A systematic image processing protocol was established, aimed at segmenting and analyzing the metaxylem vessels across the

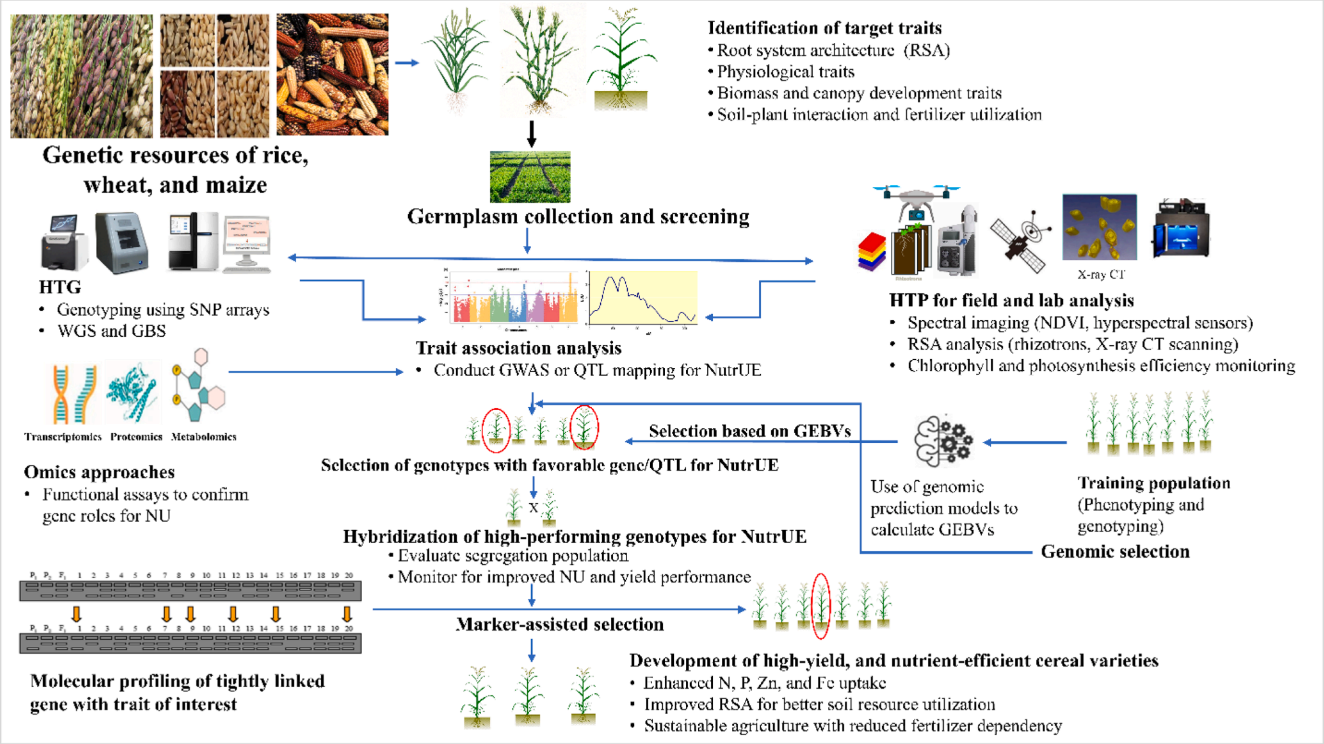

Fig. 3. A modern breeding scheme for enhanced NutrUE in cereals by using high-throughput phenotyping and genotyping techniques. NutrUE= Nutrient use efficiency, NU= Nutrient uptake, GWAS= genome wide association study, QTL= quantitative trait loci, HTP= high-throughput phenotyping, HTG= high-throughput genotyping, WGS= whole genome sequency, GBS= genotype by sequency.

first to sixth whorl of maize crown roots, confirming the precision of their approach by comparing it with scanning electron microscopy (SEM) results. This experiment offers valuable insights into NU by delivering comprehensive 3D anatomical data regarding root structures, especially the metaxylem vessels, which play a vital role in the transport of water and nutrients. Examining the spatial arrangement and interconnectivity of these vessels can enhance our comprehension of the impact of root structure on water transport and nutrient absorption efficiency, which is crucial for advancing crop varieties that exhibit improved drought resilience and NutrUE. Similarly, a study explored how wheat roots may use soil macropores to circumvent layers of compact soil using X-Ray CT and imaging revealed that roots adjust their development path to intersect with pores (Zhou et al., 2021). Macropores provide low-resistance pathways for wheat roots to grow deeper into the soil. This enables roots to reach nutrient-rich layers that are otherwise difficult to access. MRI produces high-resolution, 3-D models of root systems, thus enabling researchers to examine root development patterns, length, branching, and dispersion within soil. This knowledge is essential for learning how roots navigate the soil to get nutrients such as N, P, and K. The red, green, and blue (RGB) color imaging technology has been used in sorghum to determine various plant traits which are associated with performance of the crop underwater and N stress (Neilson et al., 2015).

5.3. UAV-based RGB indices

RGB imaging in sorghum suggested that AMF significantly enhanced biomass and P, Zn and Fe bioavailability, indicating the potential of HTP in revealing hidden traits that contribute to nutrient efficiency in cereals (Watts-Williams et al., 2022). High-resolution images are also used for barley canopies which were captured using RGB cameras, both from ground-based and UAV (unmanned aerial vehicle) platforms, to calculate VIs such as relative green area (GA) and greener area (GGA) (Kefauver et al., 2017). The indices obtained from RGB images successfully monitored N-related performance and showed a correlation with grain yield, highlighting their effectiveness in evaluating NUE in barley (Kefauver et al., 2017). Similarly, RGB imaging was used in rice to non-destructively evaluate geometric characteristics such as the minimal enclosing circle, convex hull, and calliper length under low P. These characteristics facilitated the identification of P-efficient genotypes *via* the assessment of plant architecture and foliar modifications (Bhatta et al., 2021). The method facilitated the preliminary assessment of tolerant cultivars, contributing to enhanced NutrUE in rice breeding initiatives.

The RGB image was successfully used to assess NUE in wheat at the seeding stage, the study results showed high correlations between shoot biomass and leaf area at seven weeks after sowing under low N conditions, indicating that vegetative phenotypic screens should focus on selecting wheat varieties under low N conditions (Nguyen et al., 2019). UAVs with remote sensing technologies (Aziz et al., 2025) offer an efficient, non-destructive method for assessing crop water use efficiency (Yadav et al., 2024) and NUE. UAV-based multispectral indices to predict water use efficiency and NUE in wheat, using field trials with varying water and N treatments across three wheat genotypes and results revealed RNDVI (red normalized difference vegetation index) was better in predicting the phenotypic variations for NUE calculated from N contents of plant samples with high R^2 (0.72–0.94), while NDRE (normalized difference red-edge index) was consistent in predicting both NUE N-content and NUE grain yield by 0.73–0.84 with low root mean square errors (Yang et al., 2020). Remote sensing, specifically RGB indices and UAV-based HTP, to assess maize yield under low N conditions, RGB indices like hue and GGA showed strong correlations with grain yield, with UAV measurements providing the best results and SPAD values also correlated well, especially during the vegetative stage (Buchaillot et al., 2019). These findings highlight the value of remote sensing in improving maize breeding and yield predictions under varying N conditions. UAV-based RGB imaging also have been used to study NutrUE in rice (Khose and Mailapalli, 2024; Shi et al., 2021) wheat

(Nguyen et al., 2019; Zhai et al., 2025) and maize (Ghazal et al., 2024; Uddin et al., 2021).

Table 1
High-throughput phenotyping tools for nutrient uptake related traits in cereal crops.

S. No.	HTP tools/ platforms	Uses for phenotyping traits	Crop name	References
1	Pouch and wick hydroponic-based HTP system imaging by DSLR camera	Root vigour, root length, and root diameter	Wheat	(Atkinson et al., 2015)
2	RGB digital cameras	Crop growth, phenology, yield components, and vegetation indices for NUE	Grass species, sorghum, wheat, rice, and maize	(Araus and Kefauver, 2018; Bhatta et al., 2021; Nguyen et al., 2019; Poiré et al., 2014; Uddin et al., 2021)
3	Crop Circle	NDVI	Wheat	(Nguyen et al., 2016)
4	SPAD meter	SPAD unit	Wheat and rice	(Bhatta et al., 2021; Nguyen et al., 2016)
5	NIR imaging/ Hyperspectral imaging	Greenness of the leaves	Sorghum and wheat	(Moshood et al., 2025; Neilson et al., 2015)
6	RhizoFlux	HTP of multiple ion-uptake rates in maize-particularly macronutrients nitrate, ammonium, potassium, phosphate, and sulfate	Wheat	(Griffiths et al., 2021)
7	Plant phenotyping platform for plant and microorganism interactions (4PMI) HTPP	RSA phenotyping; Rhizotrons suitable for plant growth in controlled conditions and non-invasive image acquisition of plant shoot and root systems (RhizoTubes)	Wheat	(Colombo et al., 2022; Jeudy et al., 2016)
8	GrowScreen-Rhizo1 phenotyping platform	Root system traits including visible total root length, visible main root length, visible lateral root length, visible root system width, and depth	Wheat	(Nagel et al., 2021)
9	WinRhizo	Root morphology traits and leaf area	Wheat	(Rossi et al., 2024)
10	UAVs with multispectral camera	Canopy spectral reflectance information, anthocyanin reflectance index, green chlorophyll index, and ratio vegetation index	Wheat and Rice	(Kaushal et al., 2024; Liang et al., 2021)
11	TraitFinder digital phenotyping system-multispectral 3D laser scanners (Phenospex Ltd., Heerlen, Netherlands)	It allows obtaining time-series of both geometry traits, such as leaf area, and spectral vegetation indices of plants under controlled environment	Wheat	(Bazhenov et al., 2023)

*HTP=High-throughput phenotyping, RGB= Red-Green-Blue, NDVI=Normalised difference vegetation index, RSA=Root system architecture, UAVs=Unmanned Aerial Vehicles.

Furthermore, UAV-based 3D imaging alongside deep learning techniques (PointNet++) used to assess wheat canopy height and VIs under various N treatments (Chen et al., 2024a). Digital RGB imaging method is strongly correlated to important NUE traits of wheat varieties (Nguyen et al., 2019). HTP using UAV and terrestrial robotic systems coupled with machine learning (ML) algorithms is revolutionizing our comprehension of phenotyping and significantly influencing genetic research (Singh et al., 2016).

5.4. HTG combined with HTP for NU in cereals

Regarding HTG, it involves state-of-the-art technologies which can rapidly analyze genetic variations across numerous individuals mostly by using SNPs and various other genetic markers (Fig. 3). It has become an indispensable tool in molecular breeding programs due to facilitation of proper identification of genetic variants coupled with selection for superior traits. Diversity arrays technology (DArT) and genotyping by sequencing (GBS) have emerged as leading approaches owing to their efficiency and cost-effectiveness (Appleby et al., 2019). DArTseq enables comprehensive genome profiling and the targeting of genomic regions, essential for elucidating the genetic basis of various traits of interest in cereals (Ganal et al., 2019; Gawroński et al., 2016). GBS technique has gained attention in cereal research, and it facilitates the identification of SNPs across several populations, hence aiding in MAS (Milczarski et al., 2016). The efficiency of GBS in generation of dense genetic maps has been reported to be valuable for crops such as barley and wheat, where comprehending genetic interactions is crucial for enhancing production and stress resilience (Puglisi et al., 2021). Furthermore, the integration of GBS with sophisticated ML models has shown potential in forecasting grain production and other essential features in diverse cereal populations (Puglisi et al., 2021).

Plant genomics has been evolving faster due to advancements in next-generation sequencing (NGS) technologies that provide HTG and permit rapid and precise marker genotyping at elevated densities. These advancements need to go hand in hand with the fast acquisition of concrete phenotypic data with enough resolution for the appropriate use of genetic data. It has been observed that accuracy in the identification of marker-trait associations (MTA) along with estimation of GEBV (genomic estimated breeding value) relies on precise genotyping and phenotyping analysis, which ultimately affects the effectiveness of GAB. Semi-automated HTP platform fitted with spectrometers to analyze spectral reflectance of wheat canopy and further genotyping was carried out by using the TaBW280K SNP array (Jiang et al., 2019). It is reported that a *cfn0652917* QTL in the *PPD-D1* region played a major role in the wheat plant's response in an N optimal and N-deficient environment (Jiang et al., 2019). High throughput root phenotyping used for PUE along with 35K wheat-breeders-affymetrix-SNP-array genotyping for 304 wheat association panels and reported 10 highly significant MTA and 22 potential candidate genes identified which associated with PUE-related traits (Rajamanickam et al., 2024). WinRHIZO Pro 2013e used root scanner and energy dispersive x-ray fluorescence (EDXRF) methods to study various root traits and seed Fe content of Bengal and Assam Aus rice association panel at seedling stage under Fe-deficiency conditions (Panda et al., 2024). GWAS analysis revealed four candidate genes *OsFLA, OsBIDK1, OsHPL3,* and *AKR2B* (*XBOS252*) in rice which are associated with various traits associated with plant's response in Fe-deficiency conditions (Norton et al., 2018). High throughput sequencing used to genotype CSSL (chromosome segment substitution lines) of rice developed by crossing between 9311 and Nipponbare (Zhou et al., 2017). In this study, six new QTLs (*qNUE2.1, qNUE4.1, qNUE6.1, qNUE6.2, qNUE10.1,* and *qNUE10.2*) were identified for NUE, while seven QTLs (*qNUP2.1, qNUP3.1, qNUP6.1, qNUP8.1, qNUP10.1, qNUP11.1,* and *qNUP11.2*) were identified for N-uptake in rice (Zhou et al., 2017). The 6K SNP array used for genotyping of 230 BC_1F_5

introgression lines (ILs) derived by crossing of Weed Tolerant Rice 1 and Hao-an-nong (Jewel et al., 2019). The ILs were phenotyped for various NutrUE traits. It was reported that four QTL hotspot regions (QTL harbor-I to IV) on certain chromosomes were associated with various NUE-related traits in rice (Jewel et al., 2019). Phenotyping for PUE performed using a rice panel of 292 different accessions *via* a hydroponic system and 44K SNPs used for GWAS to identify many genomic regions linked with PUE on chromosomes 1, 4, 11, and 12 (Wissuwa et al., 2015). Further expression studies revealed functional alterations in two anticipated nucleic acid-interacting proteins, which are probable causative reasons for the observed haplotype-associated differences in PUE (Wissuwa et al., 2015). UAV-based HTP and whole genome sequencing based study to understand the responses of maize across 233 inbred lines by using the time-series data on canopy coverage and VIs (Rodene et al., 2022). Further, genome-wide association mapping revealed 29 distinct genomic regions associated with traits derived from image analysis, thus highlighting a candidate gene (*Zm00001d031997*) associated with the assembly of photosystem II under both N applied and unapplied conditions (Rodene et al., 2022).

GS is another potential domain apart from GWAS for the use of HTG data. The standard GS procedure involving a training population that has gone through both HTP and HTG is used to construct a ML model which can predict the phenotypic values of non-genotyped individuals (Wang et al., 2018). An average improvement of 12 % in model accuracy was observed by inclusion of canopy temperature and normalized difference vegetation index from HTP platforms in GS models (Crain et al., 2018). These procedures integrating GS and HTP data have significant potential for enhancing accuracy and efficacy in selection within breeding programs by approaching GAB. The precision of GS in maize for root attributes evaluated under N and P stress using 41 single-cross hybrids and it found by analyzing hybrid data that the genomic prediction scheme (RR-BLUP) showed more accuracy than phenotypic selection for every trait (Fritsche-Neto et al., 2012). Five classical GS models for various characters in maize were evaluated under low P (0 kg/ha P_2O_5) and normal P (120 kg/ha P_2O_5) conditions (Xu et al., 2018). It was observed that characters which showed high heritability had high prediction accuracy. Furthermore, it determined that a moderate density of SNP markers (8000 SNPs) is sufficient for achieving accurate predictions regarding low P tolerance traits in maize (Xu et al., 2018).

In summary, HTP and HTG have addressed major challenges in collecting precise phenotypic data and accurate genetic profiles, respectively, enabling deeper genomic investigations into key genes and their regulatory mechanisms involved in NU in cereal crops. Moving forward, integrating these technologies with ML and multi-omics approaches holds great promise for accelerating the development of nutrient-efficient crop varieties.

6. Identification of genomic regions associated with NU in cereals

Advancements in genomic technologies, computational tools, HTP, and HTG are continually improving researchers' ability to identify and utilize the genetic determinants of NU traits in cereals (Fig. 3). Identifying genomic regions, QTLs, and genes associated with NU in cereals is a critical aspect of agricultural genetics and crop improvement. This knowledge is vital for developing crops that are more efficient in nutrient use, which is crucial for meeting the growing global food demands. Key root-related traits can be identified through genomic techniques that pinpoint specific genomic regions associated with the target trait in cereals. To understand the NU complexity requires sophisticated experimental designs and large datasets to accurately identify associated genetic factors (Ferrante et al., 2017). Different kinds of germplasm accessions may have varying genetic backgrounds, which can affect the generalizability of findings. To identify genomic regions related to NU, researchers first developed recombinant population for linkage and QTL mapping to track genetic markers associated with traits and GWAS to explore associations across the genome (Table 2).

Linkage mapping involves constructing a genetic map (Jansen et al., 2001) by analyzing recombination frequencies between genetic markers and then identifying genomic regions associated with NU traits through segregation analysis. QTL mapping identifies genomic regions that correlate with variations in quantitative traits, such as NU efficiency, by linking phenotypic differences (e.g., nutrient levels) to genetic variation (e.g., markers) to locate specific QTLs (Table 2).

A genetic linkages map developed using 153 markers from a population of backcross recombinant inbred lines (BILs) for QTL mapping from a cross between *O. sativa* L. and *O. rufipogon* Griff (Luo et al., 2017). This analysis identified 21 of 231 BILs as tolerant to low P, offering important data for the cloning and utilization of P-deficiency tolerance genes from *O. rufipogon* (Luo et al., 2017). Another study to identified QTLs for NUE and its components using a recombinant inbred line (RIL) population, which derived from Nipponbare × OM052 cross, with 159 F_3 individuals grown under low and high N conditions (Bai et al., 2021). A high-density linkage map was created with 2707 SLAF (specific length amplified fragment sequencing) markers. Further this study QTL analysis revealed four significant QTLs on chromosomes 1, 6, and 11, explaining 2.96–11.11 % of the phenotypic variance, which aids in identifying potential NUE candidate genes for rice improvement (Bai et al., 2021). The high-density genetic map developed with 184 RILs from the 'Tainong 18 × Linmai 6′ cross revealed 121 QTLs identified for seedling related traits and 130 QTLs for maturity traits, contributing significantly to large-scale NUE improvements in wheat breeding (Zhang et al., 2019). DH population from Yangmai 16 × Zhongmai 895 was assessed for root architecture and biomass traits in wheat under varying P conditions and 34 QTLs with positive effects under low P were identified (Yang et al., 2021a). A study uncovered 17 QTLs for root related traits in an F_8 maize recombinant inbred population across different N levels, with a major QTL identified on chromosome 1 explaining 43.7 % of the variation in average axial root length under low N, which could aid in developing N-efficient maize (Liu et al., 2008). 67 F_2 segregation population derived from L354 × L585, and 24 SSR markers revealed seven QTLs for P efficiency on chromosome 5, with the nearest QTL is *PeSB-5* and *PeSB-7* which closest to marker umc2136 at 11.7 cM, highlighting the need for more precise mapping and potential for P-limited maize breeding (Chibesa and Tembo, 2020).

A major QTL associated with enhanced P uptake under low P conditions, *Pup1* (*Phosphorus uptake 1*), that was identified by QTL mapping of NU in rice. The gene contained by this locus is called *OsPSTOL1* (*Phosphorus Starvation Tolerance 1*) and it enhances early root growth, biomass enhancement and improve PUE (Gamuyao et al., 2012). Introgression of *Pup1* into elite rice varieties has led to great improvements in yield under P-deficient soils. Recent experiments also established that it remains stable and effective in different environments and among different genetic backgrounds (Duppala et al., 2025; Mishra et al., 2025b) and is useful in MAS and GAB to enhance NutrUE.

Conducting GWAS to explore genome-wide associations with NU in cereals involves specialized steps due to the trait's complexity, which is influenced by genetic, environmental, and agronomic factors. GWAS identifies genetic variants associated with NU traits by scanning the genome for relevant SNPs, helping to understand the NU variability in cereals. GWAS revealed 10 significant MTAs and 25 QTLs across 39 traits, with SNPs explaining 8–84 % of the phenotypic variance in rice (Sandhu et al., 2019). Grain yield positively correlated with seedling-establishment, root architecture, NU, and yield traits, which promote the importance of root traits for improving the NU and yield in dry directed seeded rice, and promising progenies with these QTLs may benefit GAB (Sandhu et al., 2019). Understanding the basis of genetic for macronutrient accumulation in wheat under K-deficiency is vital for improving nutritional quality. Recently a study evaluated 111 wheat accessions screened under moderate and low K treatments, revealing significant macronutrient reductions under low K and GWAS identified 31 SNP markers linked to Mg, Ca, K, and P these findings can guide

Table 2
Mapping population and germplasm accessions used for nutrient uptake traits in cereals.

Crops	Sequencing approach/ Platform	Mapping population/Germplasm	Target traits	Significant outcomes	References
Rice	RFLP markers	Nipponbare × Kasalath (NIL)	P uptake	Four putative QTLs detected on chromosome 2, 6, 10, and 12 with 5.8–27.9 % PVE	(Wissuwa et al., 1998)
	RFLP markers	Nipponbare × Kasalath (NIL)	P uptake	Identified one major QTL (*Pup1*) on chromosome 12 explaining 78.8 % PVE	(Wissuwa et al., 2002)
	SSR analysis	85 Introgression line developed from elite *indica* cultivar Teqing and the wild rice (*O. rufipogon*)		Wild rice contributed favorable alleles for most of the QTLs, and one major effect of QTL for Zn content accounted for the largest proportion of phenotypic variation (11 %–19 %) was detected near the simple sequence repeats marker RM152 on chromosome 8	(Garcia-Oliveira et al., 2009)
	High-throughput genotyping	Kasalath variety used a donor for introgress *Pup1* gene, with suitable marker and further 80 diverse germplasm used to validate this gene	P uptake	Marker-assisted backcrossing approach, *Pup1* was introgressed into two irrigated rice varieties and three Indonesian upland varieties	(Chin et al., 2011)
	RFLP/SSR markers	Zhenshan 97 × Minghui 63	P uptake	Identified three QTLs (*qPUP1, qPUP7*, and *qPUP10*) on chromosome 1, 7, and 10, accounting 13.6 % PVE	(Wang et al., 2014)
	Whole-genome re-sequencing (WGRS)	9311 × Nipponbare (128 CSSLs)	N uptake	Detected two major QTLs (*qNUP6*.1 and *qNUP8*.1) on chromosome 6 and 8 with 11.86–13.99 % PVE	(Zhou et al., 2017)
	RAD-seq	GH128 ×W6827 (262 F_2lines)	N and P uptake-related traits	Identified twenty-one QTLs on 6 chromosomes with 1.20- 8.19 % PVE	(Fu et al., 2019)
	Genotyping-by-Sequencing	Complex mapping population (IR 74,371–70–1–1, UPLRi 7, IRRI 123, Kali Aus, Vandana, and IRRI 148)	N and P uptake-related traits	Identified one QTLs (S2_20,846,594) for N uptake on chromosome 2 and one QTL for P uptake (S5_24,675,892) on chromosome 5	(Sandhu et al., 2019)
	3038,555 SNP markers and RNA-seq for validation	191 rice accessions	PUE	*OsAAD* promising gene for increasing physiological-PUE and grain yield under normal and low-P	(Yan et al., 2023)
	Rice SNP-Seek database	234 genotypes	P-utilization efficiency	Haplotypic combinations identified for important candidate genes like *OsHGSNAT, OsCHLG, OsERTF, OsHSP70, OsSUR2, OsSH* and *OsPAF1* that shown to significantly increase yield and P-utilization efficiency	(James et al., 2024)
Wheat	AFLP, Xgwm, WMC, Xgdm, Xpsp	Double haploid lines (Hanxuan 10 × Lumai 14)	N uptake	Identified 17 QTLs on twelve chromosomes, explaining 5.2–21.9 % phenotypic variance	(An et al., 2006)
	SSR markers	Ye478 × Wu312 (advanced-backcross line population)	N uptake efficiency	Detected 13 QTLs each under high-nitrogen and low-nitrogen level, accounting 7.1 to 35.4 % phenotypic variance	(Li et al., 2015)
	Genotyping-by-sequencing	136 RIL (Yorktown × and VA05W-151) 138 doubled haploids (Yorktown × VA09W-52) population	NUE	Six QTLs associated with NUE and N-related traits, among them two associated with known photoperiod (*Ppd-D1* on chromosome 2D) and disease resistance (FHB-4A) genes. The NUE QTL on 1D, 6A, 7A, and 7D explained 18.1 % PVE	(Brasier et al., 2020)
	90 K SNP array	150 spring wheat diversity panel including landraces, pre-green revolution, post-green revolution, and elite varieties	P utilization efficiency	Two significant loci associated with P utilization efficiency on chromosomes 3A and 4A: *qPE1–3A* and *qPE2–4A*, respectively	(Safdar et al., 2021)
	35K-SNP array	82 bread wheat accessions procured from Australian Winter Cereals Collection (Australia) and CIMMYT (Mexico)	PUE	Six accessions (NI 5439, IC- 534,271, TURACO, CARAZINHO, DL 784–3, and RAJ 3777) identified PUE, future may be included in the breeding programs to develop new cultivars tolerant to low P stress	(Soumya et al., 2021)
	Infinium iSelect 15 K SNP bead array and 135 K Axiom Exome Capture Array	221 winter wheat cultivars	NUE	*NPF2.12* gene indirectly contributes to root growth and NUE by activating nitric oxide signaling under low N conditions in wheat and barley	(Siddiqui et al., 2023)
	SSR markers	Xiaoyan 54 × Jing 411 (RIL)	N uptake	Detected four QTLs for N uptake with 7.6–17.0 % PVE and three QTLs for P uptake explaining 7.1–14.5 % PVE	(Xu et al., 2023)
	Genotyping-by-Sequencing	HUW468 × C306	N uptake efficiency	Detected 13 QTLs on chromosomes 1B, 3A, 4B, 5A, 5D, 6A, and 6D accounting 6.7 to 22.9 % PVE	(Singh et al., 2023)
	660 K Illumina Infinium SNP array	431 cultivars	N, P, and K uptake efficiency	Identified potential SNPs explaining 4.77–12.85, 5.09–10.6, and 5.05–9.24 % PVE for N, P, and K, respectively	(Xu et al., 2024)
Maize	SSR markers	Ye478 × Wu312 (RIL)	P uptake efficiency	Identified two major QTLs (*qPupE07N8–1*, and *qPupE07N8–2*) under normal P condition, explaining 13.7 and 15.9 % PVE	(Gu et al., 2016)
	QuantStudio 12 K Flex Real-Time PCR	B73	Nitrate and ammonium transport	N transporter genes involved in different organs show that a given transporter can be specifically expressed in a tissue and a developmental stage as observed with the expression of *ZmNRT2.1* in the roots or *ZmAMT1.1B* in the silks	(Dechorgnat et al., 2019)
	MaizeSNP56 BeadChip maize array	139 maize inbred lines	N uptake efficiency	Identified *Zm00001d008901* gene (*CBL-interacting serine/threonine-protein kinase 20*) on chromosome 8	(He et al., 2020)
	Illumina HiSeq 2000 system	234 maize doubled haploid lines from six populations	PUE	*Zm00001eb374120* gene related to phosphorus concentration in the soil, under lower P	(Li et al., 2022)

(*continued on next page*)

Table 2 (*continued*)

Crops	Sequencing approach/ Platform	Mapping population/Germplasm	Target traits	Significant outcomes	References
				concentration and see the significant effect on plant growth and development	
	Genotyping-by-Sequencing	132 tropical maize inbred lines	P uptake efficiency	Detected 1 QTN (S3_190,210,784) on chromosome 3, explaining 0.56 to 0.80 % PVE	(Zeffa et al., 2024)
	Full-length sequences of ferredoxin proteins from maize, rice and Arabidopsis were downloaded from Maize GDB	LH244 inbred line was used for transformation	NUE	ZmFd4 interacts and co-localizes with nitrite reductases (ZmNiRs) in chloroplasts to promote their enzymatic activity	(Jia et al., 2025)

*RIL=Recombinant inbred line, NIL=Near inbreed line, PVE= phenotypic variation explained, NUE=Nitrogen use efficiency, and PUE=Phosphorus use efficiency.

breeding programs to develop wheat with enhanced nutrient efficiency (Alqudah et al., 2025). Improving PUE in maize can mitigate global fertilizer dependence, GWAS identified 306 quantitative trait nucleotides and 186 candidate genes associated with PUE, highlighting that integrating these findings could lead to the development of maize cultivars with better PUE (Zeffa et al., 2024).

111 different wheat genotypes used to measure the contents of P, K, Ca, and Mg to detected significant (474 SNP) markers using GWAS to identify the target candidate genes for improved micronutrient accumulation in wheat grains for better human nutrition (Elkelish et al., 2024). *TraesCS1A02G261200* gene was found on chromosome 1A and is responsible for the binding proteins for Ca ions. Moreover, T allele-carrying accessions showed significantly higher accumulations of Ca, P, and Mg as compared to C allele-carrying accessions, thus exploration of the mechanisms for protein regulation is essentially an important technique to improve the nutritional contents of wheat grains. Recently genomic-assisted stacking used for *crtRB1, opaque2*, and *waxy1* genes to enhance amylopectin in biofortified maize (PMI-PV5, and PMI-PV9) to improve nutritional security and industrial utilization (Mishra et al., 2025a). The *waxy1* (*wx1*) mutant improves amylopectin in maize starch. There is 70–75 % starch in conventional maize but the *wx1* allele in waxy maize improves amylopectin to 90–100 %. Researchers introgressed *wx1* allele into parental inbreds of multiple nutrient-rich maize having high pro-vitamin A, tryptophan, and high lysine. Gene-specific markers such as *crtRB1* and *o2* were used to select desirable gene segregants from BC_2F_2, BC_2F_1, and BC_1F_1. Background selection was used with >90 SSR markers. The recurrent parent genome was recovered at a higher rate of 94.8–96.8 % amylopectin increased to 98.4 % as compared to the mean of origin hybrid (72.7 %). Moreover, pro-vitamin A, tryptophan, and lysine contents were also increased. Furthermore, similar grain yield and agro-morphological traits were also observed in the MAS-derived genotypes.

Although numerous QTLs and genomic regions associated with NU have been identified in cereals, their direct application in MAS or GAB remains limited. This gap is primarily due to factors such as genotype × environment interactions, lack of trait validation across diverse backgrounds, and challenges in HTP under field conditions. Only a few loci, like *Pup1* for P uptake in rice, have been successfully deployed in breeding programs. Future integration of validated genomic regions using GS and genome editing holds promise for accelerating NutrUE improvement in cereals.

7. Genomic selection (GS) for NU in cereals

GS is offering revolutionary approaches for improving NU efficiency in plants. Utilizing advanced statistical models and HTG enables the prediction of genetic potential for nutrient absorption and utilization. GS causes significant acceleration of this process and helps for early selection of individuals with potential nutrient efficiency/acquisition traits. GS has successfully improved nutrient efficiency in maize, wheat and rice (Voss-Fels et al., 2019). GS integration with other omics technologies offers even more potential to refine nutrient efficiency traits. Additionally, artificial intelligence (AI) and ML are even improving the efficiencies of GS prediction models for better use of GS technologies in NU. A panel of 441 maize lines was used for genomic prediction, which demonstrated moderate to high accuracy, suggesting its strong potential to accelerate the development of N-efficient maize hybrids under low-input conditions (Ertiro et al., 2020). Recently, study highlights that incorporating rhizobiomes into GS improves maize trait predictions, especially under low N conditions, microbiome-enabled model outperformed traditional GS by 3.7 % on average, with larger improvements (8.4–40.2 %) under low N conditions (Yang et al., 2024).

Genome-wide selection enhances MAS by simultaneously using thousands of markers distributed across the genome. In GS, a high-density marker profile is established to ensure genome-wide coverage and linkage with desirable traits. The process occurs in two phases: first, associations between genome-wide genotypes and phenotypes are statistically analyzed within a reference population, generating genomic estimated breeding values (GEBVs) (Goddard and Hayes, 2007). Second, these GEBVs are used to efficiently identify superior individuals in breeding populations. GS significantly improves the precision and speed of selection compared to traditional methods by reducing dependence on repeated phenotypic evaluations, thereby accelerating genetic improvement. GWAS and GS, integrated with advanced phenotyping, enable the identification and improvement of complex NutrUE traits in cereals by uncovering key adaptive genes and pathways (Mallikarjuna et al., 2022). Integrating GS with HTP and multi-environment data in addition will maximize its usefulness in creation of nutrient-efficient cultivars in future.

8. Multi-omics approaches to validating the identified gene function for NU

Multi-omics approaches, integrating genomics, transcriptomics, proteomics, and metabolomics, are essential for uncovering the complex regulatory networks involved in cereals improvements (Saini et al., 2024; Yang et al., 2021b). By combining data from these different layers of biological information, researchers can map out the interactions between genes, proteins, and metabolites that regulate NU processes, which enhance the GAB utilization for crop improvement. This comprehensive strategy enables the identification of key regulatory factors and pathways, thus providing insights into how cereals manage nutrient acquisition and utilization, ultimately guiding the development of improved crop cultivars with enhanced nutrient efficiency. QTL mapping and GWAS enhance the understanding and discovering genes that control the intake and homeostasis of macronutrients and micronutrients. Further advances in gene function analysis (Fig. 4) aid breeding attempts to optimize fertilizer usage, increase yield in low nutrient soils, and improve crop resilience to environmental shocks (Ahakik et al., 2024). Functional validation of genes, such as those implicated in stress response pathways or metabolic networks, permits targeted treatments that improve crop performance under a different

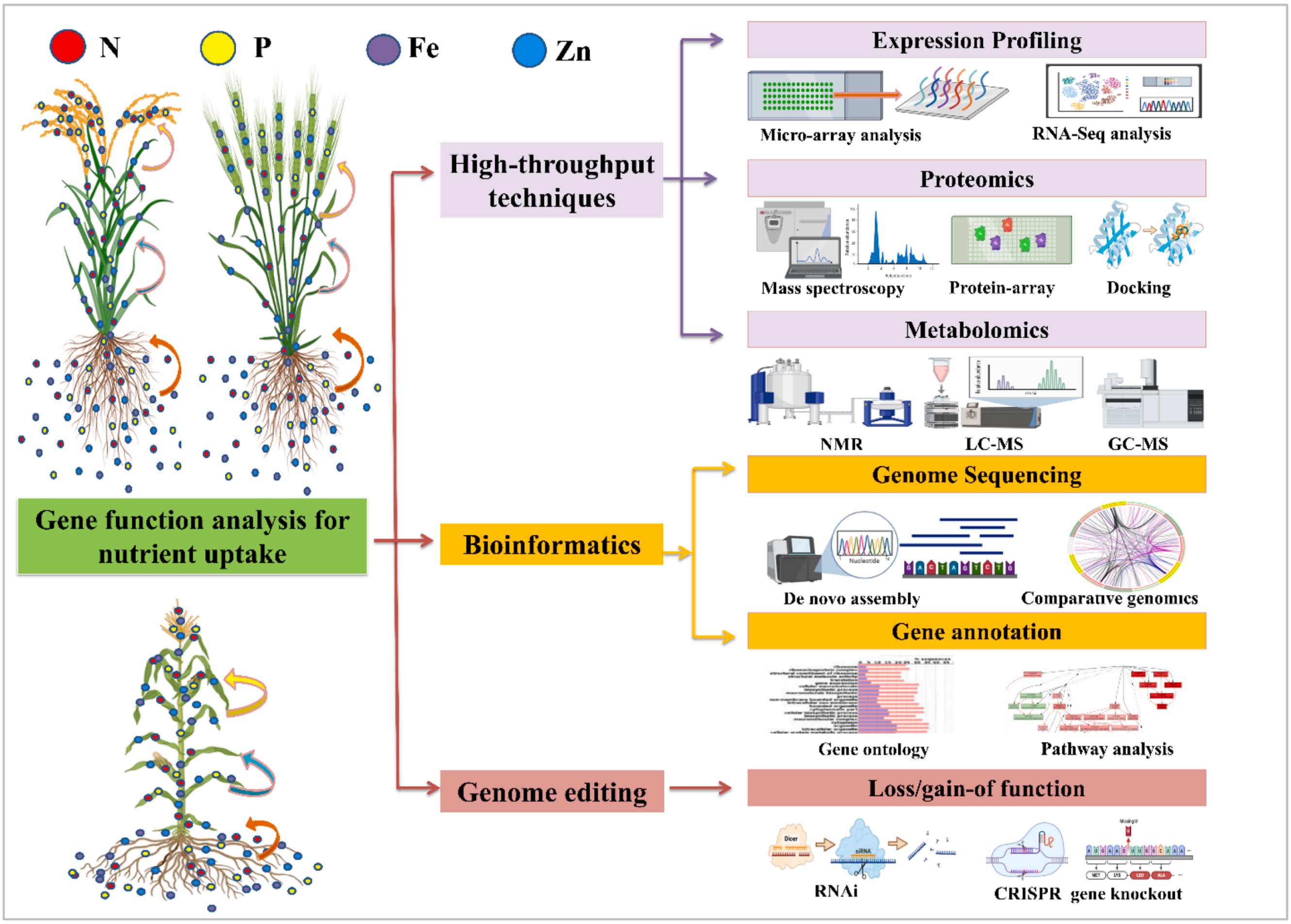

Fig. 4. Gene function analytical tools for nutrient uptake in cereals.

environmental situation. Furthermore, gene functional analysis allows for the detection of off-target effects and undesired phenotypic results, improving the safety and efficacy of genome editing applications (Chapman et al., 2017). The interaction between functional genomics and genetic engineering promotes the translation of fundamental discoveries into practical innovations, such as biofortified crops, disease-resistant varieties, and biotechnological solutions for sustainable development (Nasar et al., 2024). Additionally, the combination of system biology and computer modeling with gene functional analysis has improved our ability to anticipate gene interactions and phenotypic consequences, resulting in advances in synthetic biology and precision breeding (Gayathiri et al., 2023). These approaches enable genome-wide functional assessments that uncover complex trait regulation, facilitating the development of next-generation solutions by GAB for sustainable agriculture.

Genomic data provides the complete sequence information of an organism's DNA, offering insights into genetic variations, gene functions, and potential regulatory elements (Bevan et al., 2017). Comparative genomics can uncover genetic variations between high and low NU cultivars, which helps scientists and breeders to develop nutrient-efficient crops that enhance growth, yield, and environmental sustainability. Comparative genomics study identifies and classifies 1154 basic helix-loop-helix (bHLH) genes across rice, maize, wheat, and *Arabidopsis*, revealing their diverse roles in growth, development, and stress responses, and provides novel insights into their evolutionary relationships, expression patterns, and functional significance (Wei and Chen, 2018).

By analyzing RNA-seq data, researchers can identify genes that are upregulated or downregulated during NU, thus providing clues about regulatory mechanisms and pathways involved. RNA-Seq analysis in rice demonstrates specific gene expression changes in response to ammonium levels, revealing distinct metabolic adjustments in roots and shoots that reflect adaptation to varying N supplies (Yang et al., 2015). Transcriptomic analysis measures gene expression levels by profiling RNA transcripts helps in understanding how gene expression changes in response to different nutrient levels or stress conditions (Imadi et al., 2015). Transcriptomic analysis revealed 288 up-regulated and 179 down-regulated genes under mixed provision of ammonium and nitrate ratio with significant involvement in N metabolism and other key processes, contributing to better NU and seedling growth in rice (Fu et al., 2023). Chronic N deficiency during grain filling disrupts durum wheat growth and yield, with transcriptomic analysis revealing 4626 DEGs (differentially expressed genes), particularly in roots, and providing key processes in N metabolism, carbon metabolism, which could inform future strategies for improving NUE (Curci et al., 2017). Another study identified the key candidate genes involved in maize root growth as well as development under K-deficiency, revealing 5972 DEGs and several potential targets with homology to *Arabidopsis* regulators, which could inform strategies for enhancing maize yield and stress tolerance (Guo et al., 2023).

Transcriptome sequencing analysis of maize roots under N, P, and K-deficiencies identified 1255, 1082, and 324 DEGs, respectively, with 575 shared DEGs; genes like *MRP2, bZIP77*, and *bZIP53* could be key regulators of root growth under nutrient stress (Ma et al., 2020). The RNA-seq analysis identified 2406 DEGs in the wheat cultivars under N stress, revealing that the N-efficient "PBW677" exhibits distinct adaptive mechanisms and gene expression patterns compared to the N-inefficient "PBW703", contribution potential targets for improving NUE in PAU

(Punjab Agricultural University) wheat breeding programs (Kaur et al., 2022). Additionally, carbon metabolism genes implicated in glycolysis, the TCA cycle, and gluconeogenesis were differentially regulated. RNA-Seq combined with transcriptomic profiling performed to analyze the gene expression patterns that influence nutrient accumulation during rice grain growth (Ren et al., 2023). A total of 27,992 genes were categorized into 20 temporal expression profiles, each representing a different pattern of essential and harmful element accumulation. Three notable expression trends emerged: early reaction (13,715 genes), mid response (2888 genes), and persistent rise (2888 genes). Gene ontology (GO) and KEGG analysis found enrichment in nutrition transport, hormone signaling, and secondary metabolism. Key transporters, such as *OsYSL2* (Fe), *OsZIP5* (Zn), and *OsSWEET14* (sucrose), showed stage-specific expression, indicating nutrient mobilization. These findings advance researchers understanding of gene-mediated elemental translocation in rice grain. Furthermore, microarray analysis has considerably increased the understanding of the molecular processes underpinning nutrition transport, absorption, and stress adaptation (Wang et al., 2021). For example, in rice, microarray research revealed *OsPHR1* and *OsPHR2* as master regulators of the phosphate starvation response. These TFs modulate the expression of downstream genes, including *OsPHT1* family transporters, enhancing phosphate acquisition under low P conditions (Wang et al., 2021).

Proteomics involves the large-scale study of proteins, including their functions, structures, and interactions (Pandey and Mann, 2000). In NU regulatory networks, proteomic data identifies and quantifies proteins involved in transport, signaling, and metabolism, while also revealing post-translational modifications and protein-protein interactions that regulate NU. Proteomics leverages advanced mass spectrometry (MS) techniques, quantitative methods like iTRAQ and TMT, and bioinformatics tools to provide a comprehensive view of the proteins involved in NU (Yan et al., 2022). Proteomics based on iTRAQ revealed that *OsNRT2.1* and *OsNRT2.4* in rice which is essential for nitrate absorption and translocation. TFs like *NIN-LIKE PROTEIN* (NLP) was found to regulate their expression levels and correlate them with nitrate availability (Nazish et al., 2021). Likewise, in barley, proteomic research revealed elevated enzymes in stress signaling and ROS detoxification under Zn-deficient condition, linking ZIP transporters to systemic reactions (Harmanjit and Neera, 2021). Proteomic analysis of rice under different Fe concentrations reveals distinct protein responses to Fe-deficiency and excess, revealing distinct pathways such as phenylpropanoid biosynthesis and ribosome function, and offering insights for improving rice Fe homeostasis through genetic breeding (Zhang et al., 2022). By identifying 104 differentially abundant proteins and highlighting TaHAK1–4A as a key player in K uptake under low K stress and root growth, this research has valuable insights into wheat's molecular response to K-deficiency and suggests avenues for enhancing K uptake efficiency (Xu et al., 2022b). Through proteomic analysis study reveals that the QXN233 maize genotype effectively manages long-term P stress by modulating 681 and 1374 differentially abundant proteins in leaves and roots, respectively, and highlighting key phosphate transporters and ion transporters that contribute to growth under K-deficiency and excess (Sun et al., 2018).

Metabolomics involves the detailed study of metabolites in a biological system to support crop improvement efforts by identifying metabolic changes that enhance growth, disease resistance, and NutrUE (Singh et al., 2024b). Metabolomics provides a snapshot of cellular metabolic states, offering insights into the biochemical pathways regulated by nutrient-related genes by GC–MS, LC-MS and NMR techniques (Wishart, 2019). In cereals, metabolomics provides insights into how nutrient deficiencies and environmental stress alter metabolite profiles, offering valuable information for improving nutrient efficiency and stress tolerance in breeding programs. Metabolomic profiling of P-deficient maize reveals increased di and trisaccharides and amino acids, providing valuable insights for developing strategies to improve PUE (Ganie et al., 2015). Metabolomics identified key metabolic markers for PUE in rice, showing that efficient cultivars sustain CO_2 assimilation even with reduced leaf P, with sinapate, benzoate, and glucoronate emerging as notable indicators (Watanabe et al., 2020). Seed inoculation with AMF and plant growth-promoting rhizobacteria increases N uptake efficiency and it significantly alters root metabolome in maize with a strong correlation between microbial communities and metabolomic profiles (Ganugi et al., 2022). The metabolomic analysis of wheat under different P conditions identified critical metabolic shifts in carbohydrate and amino acid pathways, providing insights into how wheat adapts to phosphate scarcity and showed key metabolites that could enhance PUE (Cuyas et al., 2023). OM052 rice genotype exhibits superior NUE compared to Huanghuazhan, showing enhanced glutamate dehydrogenase activity and differential metabolite accumulation under varying N level, providing insights into optimizing carbon and N metabolism for improved NUE (Ruan et al., 2023). Metabolomics profiling reveals that combining N with Zn significantly enhances Zn availability in soil by increasing cis-aconitic acid secretion in winter wheat which is linked to upregulated citrate synthase and cis-aconitase activities and reduced isocitric acid levels (Nie et al., 2023).

Modern genetic engineering advancements are now essential for clarifying and improving the mechanisms of nutrient absorption in cereal crops by allowing for the exact functional study of genes involved in the acquisition, transport, and digestion of nutrients. Transgenic cereals like rice, wheat, and maize with enhanced NutrUE have been made possible by technological developments in RNAi delivery, such as agrobacterium-mediated transformation and particle bombardment (Saurabh et al., 2014). Increased phosphate absorption and decreased reliance on P fertilizers have also been shown by RNAi-derived knockdown lines that target genes *OsPT2* in rice (Liu et al., 2010). RNAi-mediated silencing of lysine-poor α-zeins mimics the opaque kernel phenotype of the *o2* mutant, along with high lysine content, this study suggests that a decrease in α-zein is directly correlated with higher lysine content, thereby enhancing its nutritional quality (Houmard et al., 2007). RNAi technology has also been utilized to biofortify rice with iron by reducing the phytic acid concentration (Ali et al., 2013). RNAi was used to silence the *IPK1* gene using a seed-specific oleosin18 (*Ole18*) promoter, and transgenic rice showed a 3.9-fold down-regulation in *IPK1* transcripts in transgenic seeds, correlating to a 1.8-fold greater iron accumulation in the endosperm, without affecting the plant's growth and development (Ali et al., 2013). For mining the candidate genes for improving NUE in maize, 66.7 % of identified candidate genes were reported to be involved in N metabolic processes (He et al., 2020). *Zm00001d025831* encoded ammonium transporter 1 and *Zm00001d004633* encoded transmembrane amino acid transporter family protein for better NUE. The identified molecular markers in this study can be target GAB approach by MAS for breeding higher NUE maize varieties. Over-expression of cytokinin oxidase 5 (*OsCKX5*) gene in root-specific *RCc3* promoter, showed positive enhanced root traits and NU in rice (do Nascimento et al., 2022).

Integrating multi-omics data gives a complete perspective on the regulatory networks involved in NU (Ashraf and Ahmad, 2023). Systems biology approaches and computational tools integrate with genetic, multi-omics datasets to map interactions and identify key regulatory nodes, signaling pathways, and metabolic networks that affect NU efficiency. For instance, integrated transcriptomic and metabolomic analyses reveal how N levels regulate carbon and N metabolism, guiding new strategies to enhance NUE in rice (Xin et al., 2019). The integration of proteomics, metabolomics, and physiological analyses revealed that applying high N levels prior to drought stress can enhance both yield and stress resilience in rice (Du et al., 2020). The integrated transcriptomic and microRNA analyses identified important regulators and candidate genes involved in NUE in rice suggesting their important roles for developing NUE by GS and molecular breeding techniques (Barbadikar et al., 2025). Multi-omics study of *Pup1*-expressing NIL-23 reveals that *Pup1* confers P-deficiency tolerance through integrated regulation of gene expression, nutrient transport, metabolic reprogramming, and epigenetic mechanisms to enhance PUE in rice (Vinod et al., 2025). Integrative omics analysis shows that transcriptional and translational regulation play roles in maize response under low N, result showed combining responsive genes, open chromatin, and TFs networks to low N which helps guide strategies to advance NUE in maize (Fang et al., 2024). Integrated transcriptomic and metabolomic study revealed the N levels affecting aphid resistance in wheat through the modulation of carbon and N pathways and defense networks that contribute to enhanced NUE and insect resilience in wheat breeding program (Wang et al., 2025). Integrated omics analysis identified the important genetic and metabolic responses to K-deficiency tolerance in the wheat genotype KN9204 that have the different regulatory mechanisms and offered the important candidate genes to enhance K absorption and utilization efficiency (Zhao et al., 2020). Such studies exemplify the potential of integrated omics in prioritizing candidate genes for genome editing and marker development, accelerating NutrUE variety development in cereals. These all-advanced tools help to identify TFs that regulate gene expression, proteins that interact with these TFs, and metabolites that modulate protein activity or gene expression, all of which contribute to the regulation of NU networks.

9. CRISPR/Cas9: precision editing challenge and limitation for enhancing NU in cereals

CRISPR/Cas9 technology has revolutionized gene function analysis for NU in cereals by enabling precise and efficient genome editing. This system allows targeted knockouts, knock-ins, base editing, and transcriptional regulation of genes involved in nutrient acquisition, transport, and metabolism (Chen et al., 2024b). By using CRISPR/Cas9 to create gene knockouts and RNAi to decrease gene expression in cereals, researchers can efficiently investigate the roles of individual genes in NU mechanisms. CRISPR/Cas9 providing precision in boosting mineral nutrient utilization and stress tolerance through the targeted modulation of nutrient metabolism regulators to enhance crop quality and resilience (Sathee et al., 2024). Similarly, gain-of-function strategies, such as CRISPR activation (CRISPRa) and base editing, have been used to enhance the expression of genes like *Pstol1* and *OsNAS2* in rice, improving P acquisition and micronutrient biofortification (Sathee et al., 2024). Recently, CRISPR-Cas9 mediated modification of the *OsNAS2* promoter has successfully elevated Zn concentrations and grain yield in rice, showing a promising strategy for addressing micronutrient deficiencies; however, further field validation and investigation into the spikelet number enhancement are needed (Ludwig et al., 2024). Through loss-of-function approaches, CRISPR elucidates the roles of key transporters (e.g., nitrate transporters *OsNRT1.1B* and phosphate transporters *OsPHT1.8*), revealing their necessity in N and P uptake in rice (Ludwig et al., 2024). CRISPR/Cas9-mediated mutagenesis of *TaARE1* homoeologs in wheat has led to enhanced NUE, delayed senescence, and increased the grain yield under N-limiting conditions, demonstrating the promise of gene editing for developing high-yield, N-efficient wheat (Zhang et al., 2021b). CRISPR/Cas9 system providing a more efficient and effective method than meganucleases, ZFNs (zinc-finger nucleases), and TALENs (transcription activator-like effector nucleases) for improving both agronomic and NU traits in maize (Farooq et al., 2023). The combination of modern techniques like as CRISPR/Cas systems, RNAi and synthetic biology with gene functional investigations has transformed our capacity to edit genomes with unprecedented precision (Chaudhary et al., 2024).

CRISPR also uncovers regulatory networks controlling NU, including TFs and hormonal pathways, enabling deeper insights into complex traits. Targeted disruptions of negative regulators (LBD37, CIPK23, SPL9) enhance N signaling, while CRISPR/dCas9-mediated promoter engineering and base editing (ABE/CBE) fine-tune P and K homeostasis, advancing crop resilience and genetic improvement (Sathee et al., 2022). Targeted knockouts of MIR396ef, OsIRO3, and OsZIP9 have improved NU and stress resilience. Base editing (ABE, CBE) and CRISPR/dCas9-mediated transcriptional modulation optimize nutrient homeostasis without inducing double-strand breaks (Yağız et al., 2022). Disruptions in *OsNRAMP5* (Cd transport), *OsVIT2* (Fe sequestration), and *OsNRT1.1B* (nitrate transport) demonstrate the promise of CRISPR for biofortification and sustainable agriculture. CRISPR interference and CRISPRa are two types of technology in which TFs are fused with dCas9 to inhibit or boost transcription *via* RNA polymerase and so upregulate or downregulate the expression of a gene of interest. Researchers may leverage their understanding of genes that regulate nutrient homeostasis in plants, as well as improved genome editing tools, to build plants with desired features. The creation of resource-efficient, high NUE plants using CRISPR-Cas technology will accelerate genetic improvement for yield. Precise genome editing programs should prioritize major genes, such as *OsNRT1.1B, OsPHT1.8, OsNAS2,* and *TaARE1*, as well as the regulators, such as *LBD37* and *CIPK23*, to improve NutrUE and develop multi-stress resilient cereal crops in the future. This approach facilitates functional genomics and accelerates the development of higher NU cereal varieties under limited resources, hence providing sustainable agriculture and food security.

While genome editing technologies such as CRISPR/Cas systems have been heralded for their precision and speed in plant breeding, their application in improving polygenic traits such as NutrUE remains limited. NutrUE traits are governed by complex interactions among numerous genes, making single-gene edits insufficient in most cases. Only in specific cases where a few genes critically impact a metabolic pathway may genome editing prove effective. Furthermore, several other challenges still exist, such as poor in vitro regeneration rates efficiency (particularly in cereals which are often recalcitrant to tissue culture), limited field tested of edited lines, and slow progress on lab to commercial level varieties (Mao et al., 2019; Vora et al., 2023; Hackfort, 2024). Validation of genome-edited lines under greenhouse and field conditions is also essential, yet often overlooked. To date, only a limited number of genome-edited cereal varieties have reached the market. The promise of precision technologies in transforming agriculture must be matched by policies that ensure equitable access, ownership rights, and benefit-sharing among farmers, breeders, and consumers (Hackfort, 2024). Furthermore, the issues related to intellectual property and patent limits becoming problems of dependencies of farmers to multinational industries or private players, possibly limiting the small breeders and government-based programs and also challenging the principles of seed sovereignty and open-access science (Jiang, 2020). Genome-edited crop regulations are still being debated in several countries. For example, in Europe and Switzerland, oversight remains uncertain, especially on how such crops are to be separated in relation to regular GMOs (Vora et al., 2023; Marone et al., 2023). In Australia, recent legal frameworks have clarified the status of certain genome-edited plants, exempting some from GMO regulation (Thygesen, 2024). Likewise, India has come up with detailed policy guidelines on genome editing but the bigger policy debates are an ongoing process (Ghoshal, 2024). Importantly, genome editing and other genetic engineering technologies are not permissible in organic agriculture systems, which restricts their application in low-input and agroecological farming (Nuijten et al., 2016). These bottlenecks should be overcome using open innovation platforms, transparent regulatory systems, and validation in fields to have an equitable and sustainable impact of genome editing on nutrient-efficient crop improvement.

10. Challenges and future prospectives

GAB for improved NU in cereals presents significant opportunities, yet numerous challenges remain. NU traits, including essential macro and micronutrients are complex, controlled by multiple genes, transporter proteins, root exudation processes, and interactions with environmental conditions. This genetic complexity complicates with traditional breeding approaches, limiting rapid improvement. A significant challenge is balancing yield stability with NutrUE. Conventional breeding typically prioritizes yield, often inadvertently neglecting nutrient efficiency, resulting in reduced fertilizer use efficiency. Addressing this requires careful balance, and use of genomic insights without sacrificing yield productivity. Furthermore, the polygenic nature and high genotype-environment interaction of these traits complicate their precise genetic mapping. Advanced genomic tools like QTL mapping, GWAS, GS, and MAS are promising, yet their accuracy heavily depends on robust phenotypic data and high-density genetic markers. Achieving efficient, precise phenotyping through HTP remains essential but demands substantial resources and standardized protocols.

Therefore, future progress lies in integrating HTP and HTG approaches, enabling rapid, accurate trait characterization and improved selection accuracy for NU. The use of GS, multi-omics integration, and AI-driven predictive modeling (UAV-based) will likely revolutionize NU breeding programs by enabling targeted, efficient, and early-stage selection. Emerging genome editing techniques, including CRISPR/Cas9 and RNAi, offer precise modifications to nutrient transporters and RSA traits, promising improved nutrient absorption, and use efficiency in major cereals like rice, wheat, and maize. In the future, interdisciplinary integration of genomic tools, multi-omics data, computational biology, and targeted gene editing technologies will facilitate precise, sustainable improvements in cereal NutrUE, productivity, and climate resilience.

12. Conclusions

NU is a complex trait governed by polygenes, transporters, biochemical pathways, and environmental interactions. This article emphasizes the crucial roles of specific transporters and biochemical pathways; key genomic regions associated with NU and NutrUE for cereal improvement. Phenotypic approaches for dissecting NU-related traits are limited to more accuracy and speed, necessitating HTP and HTG tools for more precise characterization. GAB methods such as GWAS, MAS, GS, and genome editing show immense potential for developing genetic resources with enhanced nutrient absorption efficiency and improved yield. Integrating omics tools with AI-based predictive models can significantly enhance the understanding of complex molecular networks underpinning NU acquisition. It will be helpful if applying advanced analytical methods, including AI-based modeling combined with GS approaches would facilitate precise selection for key traits linked to NutrUE, NU, stress resilience, and yield improvement in cereals. Thus, integrating modern genomics and biotechnology tools presents a robust pathway for developing cereal cultivars for enhanced NU, thus offering solutions to global nutritional security challenges and contributing significantly to sustainable agriculture.

CRediT authorship contribution statement

Gurjeet Singh: Writing – original draft, Methodology, Formal analysis, Conceptualization. **Om Prakash Raigar:** Writing – original draft, Formal analysis. **Simardeep Kaur:** Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Ruchi Bishnoi:** Writing – original draft. **Kinjal Mondal:** Writing – original draft. **Kibrom B. Abreha:** Writing – original draft, Visualization. **Amrit Kumar Nayak:** Writing – original draft. **Tabinda Athar:** Writing – review & editing, Writing – original draft. **Vinay Sharma:** Writing – review & editing, Writing – original draft. **Danishta Aziz:** Writing – original draft. **Santosh Gudi:** Writing – review & editing, Validation, Investigation. **Pawan Saini:** Writing – review & editing, Writing – original draft. **Amit Kumar:** Writing – review & editing, Validation, Project administration, Funding acquisition. **Rakesh Bhardwaj:** Writing – review & editing, Supervision. **Amritbir Riar:** Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

No data was used for the research described in the article.

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