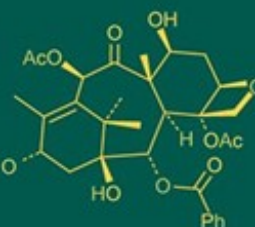
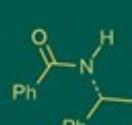


International Journal of Advanced Biochemistry Research



ISSN Print: 2617-4693
ISSN Online: 2617-4707
NAAS Rating (2026): 5.29
Indexing: Embase
IJABR 2026; SP-10(10): 695-699
www.biochemjournal.com
Received: 10-08-2026
Accepted: 27-09-2026
Published: 08-10-2026

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Genetic Engineering Approaches for Enhancing Macronutrient Use Efficiency in Crops

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DOI: <https://www.doi.org/10.33545/26174693.2026.v10.i10Si.10362>

ABSTRACT

Improving nitrogen (N), phosphorus (P), potassium (K), and sulfur (S) use efficiency is central to sustaining crop productivity while reducing fertilizer inputs and environmental impacts. Conventional breeding has achieved partial progress, but nutrient-use efficiency is a complex, polygenic trait strongly influenced by genotype $\times$ environment interactions. Genetic engineering and genome editing enable precise modification of nutrient transporters, metabolic enzymes, transcription factors, and regulatory networks controlling nutrient uptake, assimilation, remobilization, and stress responses. This review summarizes current strategies for enhancing macronutrient-use efficiency through transgenic and genome-editing approaches, highlights key candidate genes and pathways, and discusses opportunities and challenges for deploying nutrient-efficient crops in sustainable agricultural systems.

Keywords: Nutrient-use efficiency, Nitrogen, Phosphorus, Potassium, Sulfur, Genetic engineering, Genome editing, Transgenic crops

Introduction

Global agriculture must increase food production while confronting soil degradation, water scarcity, climate variability, and environmental pollution from excessive fertilizer use. Nitrogen, phosphorus, potassium, and sulfur fertilizers have driven yield gains since the Green Revolution, but a large proportion of applied nutrients is lost through leaching, runoff, volatilization, or immobilization in soil (Khan *et al.*, 2018; Good *et al.*, 2007) [2, 1]. These losses contribute to groundwater contamination, eutrophication, greenhouse-gas emissions, and rising production costs.

Nutrient-use efficiency (NUE) describes the capacity of a plant to acquire nutrients from soil and convert them into biomass or harvestable yield (Nieves-Cordones *et al.*, 2020; Giehl and von Wirén, 2014) [4, 3]. NUE is commonly partitioned into nutrient uptake efficiency (acquisition from soil) and nutrient utilization efficiency (assimilation, remobilization, and allocation to economic yield). Improving NUE is challenging because it involves multiple genes, metabolic pathways, and interactions with environmental factors.

Genetic engineering and genome editing complement conventional breeding by enabling targeted modification of genes controlling nutrient transport, assimilation, signaling, root architecture and stress tolerance. This review focuses on transgenic and genome-editing strategies for improving N, P, K and S use efficiency in major crops.

Nitrogen-use efficiency

1. Nitrogen uptake and transport

Crops absorb nitrogen mainly as nitrate (NO_3^-) and ammonium (NH_4^+). Nitrate uptake is mediated by NRT1/NPF (low- to medium-affinity) and NRT2 (high-affinity) transporters, often in association with NAR2/NRT3 proteins (Feng *et al.*, 2011; Chiba *et al.*, 2015) [6, 5]. Ammonium uptake is mediated by AMT transporters, particularly important in rice (Ranathunge *et al.*, 2014) [7]. Overexpression of *OsNRT2.1* under the *OsNAR2.1* promoter enhanced nitrate uptake and grain yield in rice (Chen *et al.*, 2016) [8]. Expression of *OsNRT2.3b*, a pH-sensitive nitrate transporter, increased nitrogen uptake, agronomic NUE, and grain yield by approximately 40% under specific conditions (Fan *et al.*, 2016) [9]. Overexpression of *OsAMT1.1* improved ammonium uptake, nitrogen assimilation, and yield (Ranathunge *et al.*, 2014) [7]. However, constitutive overexpression of some transporters reduced NUE, underscoring the importance of promoter choice and tissue-specific regulation.

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Nitrogen assimilation and metabolism

After uptake, ammonium is assimilated via the glutamine synthetase (GS)–glutamate synthase (GOGAT) pathway. Overexpression of GS and GOGAT genes improved nitrogen assimilation in several species, although responses varied with tissue, developmental stage, and nitrogen form (Cai *et al.*, 2009; Oliveira *et al.*, 2002) [10, 11].

Alanine aminotransferase (*AlaAT*) links nitrogen and carbon metabolism. Expression of barley *HvAlaAT* in canola, rice, and sugarcane increased biomass and maintained yield under reduced nitrogen supply (Good *et al.*, 2007; Snyman *et al.*, 2015) [12]. The maize transcription factor *ZmDof1* enhanced carbon skeleton production and nitrogen utilization under low-nitrogen conditions (Yanagisawa *et al.*, 2004; Kurai *et al.*, 2011) [14, 13].

Regulatory genes

Transcription factors provide opportunities to modify multiple NUE-related processes simultaneously. TaNAC2-5A in wheat increased root growth, nitrogen accumulation, and grain yield (He *et al.*, 2015) [15]. *OsMADS25*, *NLP7*, *DEP1*, *HY5*, and *MYB61* regulate nitrogen uptake, assimilation, root development, and yield (Yu *et al.*, 2015; Yu *et al.*, 2016; Sun *et al.*, 2014; Gao *et al.*, 2020) [16, 17, 18, 19]. These regulators are attractive targets but require careful evaluation of pleiotropic effects.

Phosphorus-use efficiency

1. Phosphate uptake and transport

Phosphorus is absorbed mainly as inorganic phosphate (Pi), but availability is limited by immobilization in acidic and alkaline soils (Bar-Yosef, 1991; Holford, 1997) [20, 21]. High-affinity phosphate uptake is mediated by PHT1 transporters, while PHO1 proteins facilitate long-distance transport to shoots (Hamburger *et al.*, 2002; Liu *et al.*, 2011) [22, 23].

Overexpression of *OsPHT1* and *OsPT6* increased phosphate accumulation, tiller number, and seed yield in rice and soybean (Seo *et al.*, 2008; Yan *et al.*, 2014) [24, 25]. NtPT1 and TaPT2 enhanced phosphate content, photosynthesis, and biomass under phosphate deficiency (Park *et al.*, 2010; Guo *et al.*, 2014) [27, 26].

Organic-acid secretion and phosphatases

Plants can increase phosphate availability by secreting organic acids that solubilize soil phosphate. Overexpression of bacterial citrate synthase increased citrate secretion,

phosphate acquisition, and biomass by 25–35% in tobacco (Lopez-Bucio *et al.*, 2000) [28]. Enhanced malate secretion also improved phosphate uptake and tolerance to deficiency (Lu *et al.*, 2012) [29].

A substantial fraction of soil phosphorus occurs in organic forms. Engineering acid phosphatases and phytases (e.g., *PAP1*, *PAP3*, *PAP15*, *GmACP1*) improved hydrolysis of organic phosphorus and increased biomass (Wang *et al.*, 2009; Wasaki *et al.*, 2009; Zhang *et al.*, 2014; Kuang *et al.*, 2009) [31, 32, 33, 30].

Potassium-use efficiency

Potassium is essential for enzyme activation, osmotic regulation, photosynthesis, and stress tolerance. Potassium-use efficiency (KUE) depends on efficient uptake, transport, and redistribution.

Potassium uptake involves HAK/KUP/KT transporters, Shaker channels, tandem-pore channels (TPK), and regulatory kinases (Wang *et al.*, 2013; He *et al.*, 2017) [35, 34]. The AKT1–CIPK23–CBL module is central to high-affinity potassium uptake under deficiency (Xu *et al.*, 2006; Wang *et al.*, 2011) [37, 36]. Overexpression of *AtCIPK23* improved potassium accumulation, root growth, and deficiency tolerance (Xue *et al.*, 2016) [38]. *AtHAK5* and *OsHAK5* enhanced high-affinity potassium uptake and shoot translocation (Nieves-Cordones *et al.*, 2010; Yang *et al.*, 2014) [39, 40].

Overexpression of *OsTPKb* improved potassium homeostasis and tolerance to potassium deficiency and drought (Ahmad *et al.*, 2016) [41].

Expression of *ApKUP3* in rice increased potassium accumulation, chlorophyll content, photosynthesis, and drought tolerance (Song *et al.*, 2014) [42]. These results highlight the close link between potassium nutrition and abiotic-stress resilience.

Sulfur-use efficiency

Sulfur is absorbed mainly as sulfate and is required for synthesis of cysteine, methionine, glutathione, and various secondary metabolites. Sulfur-use efficiency (SUE) depends on sulfate uptake, transport, assimilation, and remobilization.

Sulfate uptake is mediated by SULTR transporters. SULTR1;1 and SULTR1;2 function in root uptake, while SULTR1;3 contributes to vascular transport (Yoshimoto *et al.*, 2002, 2003; Rae and Smith, 2002) [43, 44]. Overexpression of *GmSULTR1;2b* increased sulfate uptake, biomass, and seed weight in tobacco (Ding *et al.*, 2016) [45].

Sulfate assimilation involves adenosine-5'-phosphosulfate reductase (APR) and sulfite reductase (SiR). Expression of bacterial APR increased cysteine and glutathione levels (Tsakraklides *et al.*, 2002) [46]. Overexpression of maize SiR enhanced sulfite reduction and stress tolerance (Xia *et al.*, 2018) [47]. Expression of the tomato sulfate transporter LeST1.1 in *Brassica juncea* improved sulfur status, chlorophyll, protein content, and biomass under sulfur deficiency (Abdin *et al.*, 2011) [48].

Engineering sulfur-rich storage proteins can improve nutritional quality. Expression of a sulfur-rich sunflower seed albumin in *Lupinus angustifolius* increased seed methionine content (Molvig *et al.*, 1997) [49], although similar approaches in rice were less effective (Hagan *et al.*, 2003) [50].

Genome editing for macronutrient-use efficiency

Genome editing, particularly CRISPR/Cas systems, enables targeted modification of endogenous genes without necessarily introducing foreign DNA (Urnov *et al.*, 2010; Dangol *et al.*, 2019; Bharat *et al.*, 2020; Tiwari *et al.*, 2020) [52, 53, 51, 54].

Nitrogen

CRISPR/Cas9 knockout of *MIR396f* in rice increased grain size, panicle branching, and biomass under nitrogen-deficient conditions (Zhang *et al.*, 2020) [55]. Base editing of NRT1.1B introduced nucleotide substitutions associated with improved NUE (Lu *et al.*, 2017) [56]. Editing of *MYB61* clarified its role in nitrogen utilization and interaction with *GRF4* (Gao *et al.*, 2020) [16].

Phosphorus

CRISPR-mediated modification of *OsACS* and *OsDOF15* revealed their roles in ethylene biosynthesis, lateral-root development, and primary-root elongation under phosphate deficiency (Lee *et al.*, 2019; Qin *et al.*, 2019) [57, 58]. These studies highlight the potential to modify root architecture to enhance phosphate acquisition.

Potassium

Genome editing has been used to investigate genes involved in potassium and phosphate efficiency, including *OsHKT1;1*, *OsHKT1;4*, *OsHAI*, and *OsPRX2* (Mohammed, 2018; Karunarathne *et al.*, 2020; Mao *et al.*, 2018) [60, 59]. Disruption of *OsPRX2* impaired potassium-deficiency tolerance, indicating its role in potassium nutrition and stress adaptation.

8. Opportunities and Challenges Opportunities Direct modification of genes with known functions in nutrient transport, assimilation, and regulation. Faster validation of candidate genes compared with conventional breeding alone. Potential to combine multiple traits (e.g., transporters, enzymes, transcription factors) through gene stacking.

- Ability to generate nutrient-efficient varieties with reduced fertilizer requirements.
- Precision modification of regulatory sequences using base editing and prime editing.

- Integration with genomic selection, marker-assisted breeding, and precision agronomy.

Challenges

- Strong genotype × environment interactions affecting trait stability.
- Differences between controlled-environment and field performance.
- Possible trade-offs between nutrient efficiency, yield, and quality.

- Metabolic imbalances from excessive transporter or enzyme expression.
- Transformation and regeneration constraints in many crops.
- Regulatory requirements and public acceptance of genetically modified and genome-edited crops.
 - Potential ecological effects on soil microbes and nutrient cycling (Good *et al.*, 2007; Khan *et al.*, 2018) [1, 2].

Comparative summary of candidate genes

Nutrient	Candidate gene or pathway	Crop or plant system	Main reported outcome
Nitrogen	OsNRT2.1/OsNAR2.1	Rice	Enhanced nitrate uptake and grain productivity (Chen <i>et al.</i> , 2016)
Nitrogen	OsNRT2.3b	Rice	Improved nitrogen uptake, agronomic NUE, and yield (Fan <i>et al.</i> , 2016)
Nitrogen	HvAlaAT	Rice, canola, sugarcane	Improved biomass and yield under reduced nitrogen (Good <i>et al.</i> , 2007)
Nitrogen	OsGS1;1 / GOGAT	Rice and other crops	Enhanced ammonium assimilation (Cai <i>et al.</i> , 2009)
Nitrogen	TaNAC2-5A	Wheat	Increased root growth, nitrogen accumulation, and yield (He <i>et al.</i> , 2015)
Phosphorus	OsPHT1/OsPT6	Rice and soybean systems	Increased phosphate acquisition and seed production (Seo <i>et al.</i> , 2008; Yan <i>et al.</i> , 2014)
Phosphorus	PHO1	<i>Arabidopsis</i> and crops	Improved phosphate loading and shoot translocation (Hamburger <i>et al.</i> , 2002)
Phosphorus	Citrate synthase	Tobacco and other crops	Enhanced organic-acid secretion and phosphate mobilization (Lopez-Bucio <i>et al.</i> , 2000)
Phosphorus	PAP/phytase genes	Soybean, <i>Arabidopsis</i> , and crops	Improved utilization of organic phosphorus (Kuang <i>et al.</i> , 2009; Zhang <i>et al.</i> , 2014)
Potassium	AKT1–CIPK23 pathway	<i>Arabidopsis</i> and crops	Improved potassium uptake under deficiency (Xu <i>et al.</i> , 2006)
Potassium	AtHAK5/OsHAK5	<i>Arabidopsis</i> and rice	Enhanced high-affinity potassium uptake (Nieves-Cordones <i>et al.</i> , 2010; Yang <i>et al.</i> , 2014)
Potassium	OsTPKb	Rice	Improved potassium homeostasis and stress tolerance (Ahmad <i>et al.</i> , 2016)
Sulfur	SULTR1;1/SULTR1;2	<i>Arabidopsis</i> and crops	Enhanced sulfate uptake (Yoshimoto <i>et al.</i> , 2002)
Sulfur	GmSULTR1;2b	Tobacco	Increased sulfate accumulation and biomass (Ding <i>et al.</i> , 2016)
Sulfur	APR/SiR	Transgenic plant systems	Enhanced sulfur reduction and glutathione production (Tsakraklides <i>et al.</i> , 2002; Xia <i>et al.</i> , 2018)
Sulfur	LeST1.1	<i>Brassica juncea</i>	Improved sulfur status, protein content, and growth (Abdin <i>et al.</i> , 2011)

Future progress will depend on integrating tissue-specific promoters, gene stacking, multiplex genome editing, multi-omics analysis, root-system engineering, field-based phenotyping, and precision nutrient management (Brown *et al.*, 2021; Sattar *et al.*, 2019; Kaul *et al.*, 2020) [61, 62, 63].

Conclusion

Transgenic and genome-editing approaches provide powerful tools for improving macronutrient-use efficiency in crops. Manipulation of nitrate and ammonium transporters, nitrogen-assimilatory enzymes, and regulatory genes can enhance nitrogen acquisition and utilization. Phosphorus-use efficiency can be improved through phosphate transporters, organic-acid secretion, acid phosphatases, and phytases.

Potassium-use efficiency depends on coordinated regulation of HAK/KUP/KT transporters, Shaker channels, tandem-pore channels, and regulatory kinases. Sulfur-use efficiency can be enhanced by targeting sulfate transporters, sulfur-assimilation enzymes, and sulfur-rich storage proteins.

The most effective strategies will likely combine tissue-specific expression, genome editing, gene stacking, root-system engineering, and precision nutrient management. Importantly, improvements should be validated under realistic field conditions and assessed using agronomic, environmental, and nutritional indicators. Nutrient-efficient crops that maintain yield and quality with lower fertilizer input can contribute to sustainable agricultural production and environmental protection.

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How to cite this article: Vemula S, Anil D. Genetic Engineering Approaches for Enhancing Macronutrient Use Efficiency in Crops. *International Journal of Advanced Biochemistry Research*. 2026;SP-10(10):695-699. doi: <https://www.doi.org/10.33545/26174693.2026.v10.i10Si.10362>