

NITROGEN ASSIMILATION IN MONOCOT CROPS UNDER BIOTIC AND ABIOTIC STRESS: A COMPARATIVE PERSPECTIVE WITH *ARABIDOPSIS THALIANA*

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ABSTRACT

Nitrogen (N) is the most critical macronutrient governing plant growth, development, and yield, forming the elemental backbone of amino acids, proteins, nucleic acids, chlorophyll, and hormones. The primary assimilatory pathway sequential reduction of nitrate (NO_3^-) by nitrate reductase (NR) and nitrite reductase (NiR), followed by ammonium (NH_4^+) incorporation via the glutamine synthetase/glutamate synthase (GS/GOGAT) cycle is conserved across higher plants but shows remarkable diversity in gene family size, regulation, and tissue specificity between the dicot model *Arabidopsis thaliana* and economically dominant monocot crops such as rice (*Oryza sativa*), maize (*Zea mays*), wheat (*Triticum aestivum*), sorghum (*Sorghum bicolor*), and barley (*Hordeum vulgare*). These cereals feed over half the world's population yet use only 30-50% of applied N fertilizer, motivating intensive study of nitrogen use efficiency (NUE). Biotic stresses (pathogen infection, herbivory, nematodes) and abiotic stresses (salinity, drought, heat, cold, nitrogen starvation) each disrupt distinct nodes of N metabolism through enzyme inactivation, transporter downregulation, hormonal reprogramming, and metabolic flux redirection. This review systematically examines: (i) the core N assimilation enzymes across *Arabidopsis* and major monocots; (ii) the nitrate transporter (NPF/NRT1, NRT2) and ammonium transporter (AMT) gene families; (iii) the impact of individual and combined abiotic stresses on N metabolism in cereals; (iv) the crosstalk between biotic stress and N nutrition; (v) regulatory networks including NIN-like protein (NLP) and Dof transcription factors, calcium signaling, reactive oxygen species (ROS), nitric oxide (NO), polyamines, phytohormones, and TOR kinase; and (vi) biotechnological and breeding strategies to improve NUE under stress. The ureide pathway, NH_4^+ toxicity, CLE peptide N signaling, and the NLP-NIGT1 feedforward loop receive special attention as monocot-relevant topics underexplored by the *Arabidopsis* model.

KEYWORDS: Nitrogen assimilation; monocots; rice; wheat; maize; GS/GOGAT; nitrate reductase; NRT transporters; AMT; biotic stress; salinity; drought; temperature; nitrogen starvation; NUE; *Arabidopsis*

1. INTRODUCTION

Nitrogen is the mineral nutrient required in the greatest quantity by plants and is a primary limiting factor for agricultural productivity worldwide (Crawford and Forde, 2002; The et al., 2021). Plants acquire N predominantly as inorganic NO_3^- and NH_4^+ from the soil, integrating these forms into the organic N pool through a tightly regulated assimilatory cascade (Tsay and Chiu, 2007; Vidal et al., 2020). Despite its elemental abundance in the atmosphere, fixed N availability constrains the growth of most terrestrial ecosystems, and over 108 million metric tons of synthetic N fertilizers were applied globally in 2019, with projections exceeding 236 MMT by 2050 (Zhao et al., 2023; Liu et al., 2022). Yet NUE in cereals remains disappointingly low: rice, wheat, and maize recover only 30–50% of applied N, with the remainder lost to leaching, denitrification, and volatilization, contributing to eutrophication, greenhouse gas emissions, and soil degradation (Curci et al., 2017; Han et al., 2015; Yadava et al., 2020).

Arabidopsis thaliana, as the foremost dicot model, has provided mechanistic insight into nitrate transport (Krapp et al., 2014; Xu et al., 2024; Remans et al., 2006), the primary nitrate response (Konishi and Yanagisawa, 2013; Maeda et al., 2018; Ueda and Yanagisawa, 2023), ammonium transport regulation (Rawat et al., 1999; Loqué and

von Wirén, 2004), N signaling (Frungillo et al., 2014; Li et al., 2021), and N-hormone crosstalk (Zhang et al., 2023; Fang et al., 2021). These discoveries established the canonical framework of plant N biology. However, *Arabidopsis* diverges from monocot crops in fundamental ways: it preferentially uses NO_3^- as N source whereas paddy rice thrives predominantly on NH_4^+ (Chen and Guo, 2013; Ding et al., 2015); it lacks C4 photosynthetic N concentration mechanisms found in maize and sorghum; it possesses smaller gene families for N assimilation enzymes compared to cereals (Liu et al., 2022); and it faces limited salinity and flooding tolerance compared to rice grown in paddy conditions (Mann et al., 2023).

The practical consequence of these differences is that mechanisms elucidated in *Arabidopsis* cannot always be directly extrapolated to crop systems, necessitating dedicated research in rice, wheat, maize, and sorghum. This is urgent given that these crops face escalating threats from climate change driven abiotic stresses drought (Jeong et al., 2010; Casartelli et al., 2018; Alamillo et al., 2010), salinity (Sathee et al., 2021; Yao et al., 2008; Nam et al., 2015), heat (Hungria and Kaschuk, 2014; Kaushal et al., 2016; Alsamir et al., 2021), and cold (Gong et al., 2025; Howarth and Ougham, 1993) as well as from biotic stressors including pathogens, insects, and nematodes that alter plant N status in complex ways (Wang et al., 2025; Farjad et al., 2018; Paschalidis et al., 2019).

This review provide a comprehensive, comparative analysis of N assimilation in monocot crops under stress, explicitly benchmarked against *Arabidopsis*. We cover the biochemistry of the core assimilatory pathway, the transporter gene families, the diverse stress impacts, and the regulatory networks that integrate N metabolism with stress responses, concluding with biotechnological strategies to enhance NUE in cereals.

2. Core N Assimilation Enzymes: From Arabidopsis to Monocots

2.1 Nitrate Reductase (NR) and Nitrite Reductase (NiR)

The first committed step of inorganic N assimilation is the cytosolic, NADH-dependent reduction of NO_3^- to NO_2^- by nitrate reductase (NR), a molybdenum-cofactor enzyme encoded by NIA genes (Crawford and Forde, 2002; Liu et al., 2022). *Arabidopsis* encodes two NR genes (AtNIA1, AtNIA2), with AtNIA2 contributing ~90% of total NR activity; rice similarly has OsNIA1 and OsNIA2, with OsNIA2 dominant in leaves (Sathee et al., 2021). Gene family expansion in cereals three NR genes in rice and wheat, four in maize suggests differential tissue-specific and stress-responsive regulation not fully captured by the *Arabidopsis* two-gene model (Liu et al., 2022). NR is post-translationally regulated by 14-3-3 proteins and phosphorylation of Ser534 (in *Arabidopsis*), and its activity is exquisitely sensitive to N status, light, and carbon supply (Crawford and Forde, 2002). Under multiple abiotic stresses, NR activity declines as photosynthate supply is disrupted, creating a bottleneck that limits the entire downstream pathway.

Nitrite (NO_2^-) produced by NR is immediately transported to plastids where nitrite reductase (NiR) reduces it to NH_4^+ using ferredoxin as the electron donor. NiR requires siroheme as a prosthetic group; its biosynthesis depends on uroporphyrinogen III methyltransferase (UPM1). Overexpression of AtUPM1 in *Arabidopsis* elevated NiR and NR gene expression and protein levels, increased total protein and chlorophyll, enhanced photosynthetic electron transport, and conferred tolerance to N and S deficiency, establishing siroheme biosynthesis as a critical upstream determinant of N assimilation capacity (Garai and Tripathy, 2018). *Arabidopsis* encodes one NiR gene, while rice, maize, and wheat each possess two to three NiR genes, again suggesting stress-specific functional diversification in crops (Liu et al., 2022).

2.2 GS/GOGAT: The Central Cycle of Ammonium Assimilation

Ammonium from nitrate reduction, direct root uptake, photorespiration, or amino acid catabolism is incorporated into organic form by the GS/GOGAT cycle, the primary route of inorganic N incorporation in all plants (Crawford and Forde, 2002; Bernard and Dietrich, 2005). Glutamine synthetase (GS) uses ATP to incorporate NH_4^+ into glutamate (Glu), generating glutamine (Gln). Two GS isoforms exist plastidic GS2 reassimilates photorespiratory NH_4^+ in chloroplasts, while cytosolic GS1 isoforms operate in roots for primary assimilation and in senescing leaves for N remobilization (Masclaux-Daubresse et al., 2010; Tegeder and Masclaux-Daubresse, 2018).

Arabidopsis encodes five GS1 genes (AtGLN1.1-1.5) and one GS2 (AtGLN2); rice has three GS1 genes (OsGS1;1, OsGS1;2, OsGS1;3) and one OsGS2; maize encodes five GS1 genes (ZmGLN1.1-1.5) and one GS2; wheat has three GS1 (TaGS1.1-1.3) and one TaGS2 (Liu et al., 2022). Overexpression of OsGS1;1 in rice improved grain yield under low N, while disruption of OsGS1;1 reduced tillering demonstrating that cytosolic GS1 is rate-limiting for vegetative growth and N use efficiency under restricted N supply (Liu et al., 2022). OsNADH-GOGAT1 is specifically expressed during grain filling and its loss-of-function causes chalky grains with reduced N content, establishing it as essential for grain quality in rice (Liu et al., 2022). By contrast, AtNADH-GOGAT1 in *Arabidopsis* is primarily involved in N remobilization during senescence a mechanistic divergence with significant implications for breeding grain quality traits.

Glutamate synthase (GOGAT) catalyzes the reductive transfer of the amide group from Gln to 2-oxoglutarate (2-OG), regenerating two molecules of Glu. Ferredoxin-GOGAT (Fd-GOGAT) in chloroplasts handles photorespiratory NH_4^+ , while NADH-GOGAT in non-photosynthetic plastids carries out primary and grain-filling assimilation. Rice has one Fd-GOGAT (OsFd-GOGAT) and two NADH-GOGAT (OsNADH-GOGAT1 and OsNADH-GOGAT2) genes. Salt stress at the reproductive stage in rice significantly suppresses transcript levels of OsGLN1.1, OsGLN1.2, OsGLN2, OsFd-GOGAT, and OsNADH-GOGAT in flag leaves, with tolerant genotypes maintaining higher enzyme activity (Sathee et al., 2021). Cold stress during the tillering stage in japonica rice similarly impairs N-metabolizing enzyme activities (NR, GS, GOGAT), with cold-tolerant varieties maintaining higher root enzyme homeostasis linked to better yield outcomes (Gong et al., 2025).

2.3 Asparagine Synthetase, GDH, and the N Remobilization Network

Beyond the GS/GOGAT cycle, asparagine synthetase (ASN) transfers the amide group of Gln to aspartate, producing asparagine (Asn) a preferred long-distance N transport form in many species due to its high N:C ratio (Bernard and Dietrich, 2005; Masclaux-Daubresse et al., 2010). In wheat, ASN plays a pivotal role in N remobilization from senescing vegetative tissues to developing grains, making it a key target for improving grain protein content (Zhao et al., 2023). Glutamate dehydrogenase (GDH) in mitochondria catalyzes reversible amination of 2-OG under high NH_4^+ conditions and stress, contributing to ammonium detoxification rather than primary assimilation; it is upregulated under N starvation and salinity stress as a backup assimilation route (Curci et al., 2017). Under salinity stress, tolerant rice genotypes upregulate GDH activity, contributing to higher proline synthesis and osmotic adjustment (Sathee et al., 2021). High-temperature stress in *Phaseolus vulgaris* nodules reduces GS and GOGAT activities while affecting nitrogenase and NR, demonstrating that symbiotic N fixation and primary assimilation share thermal sensitivity (Hungria and Kaschuk, 2014).

3. N Transporter Gene Families: Arabidopsis vs. Monocots

3.1 The NPF/NRT1 Family and Dual-Affinity Sensing

Four transporter families mediate N uptake and distribution: the Nitrate Transporter 1/Peptide Transporter Family (NPF, formerly NRT1), the high-affinity NRT2 family, chloride channels (CLC), and slow anion channel-associated homologs (SLAC/SLAH) (Krapp et al., 2014; Tsay and Chiu, 2007; L  ran et al., 2014). The unified NPF nomenclature (L  ran et al., 2014) clarified the enormous diversity of this family: *Arabidopsis* encodes 53 NPF members, only a subset of which have characterized nitrate transport function. The founding member NPF6.3 (NRT1.1/CHL1) is a dual-affinity nitrate transporter that switches between high and low-affinity modes through phosphorylation of Thr101 by the kinase CIPK23 (Ho et al., 2009). Critically, NRT1.1 functions not only as a transporter but also as a nitrate sensor: it perceives external NO_3^- concentration and transmits this signal to the ANR1 transcription factor to promote lateral root elongation in NO_3^- -rich patches, enabling foraging root behavior (Remans et al., 2006; Ho et al., 2009). Mutations in NRT1.1 abolish this root-foraging response (Remans et al., 2006). The roles of NRT1.1 in abiotic stress resistance extend to modulation of ABA transport, stomatal opening, and ion homeostasis (Fang et al., 2021).

In rice, nitrate uptake under flooded conditions was long underestimated, but it is now established that up to 40% of total N uptake may occur as NO_3^- , nitrified in the rhizosphere from NH_4^+ (Yan et al., 2011; Feng et al., 2011). The xylem loading of nitrate in *Arabidopsis* is mediated by NRT1.5 (Lin et al., 2008), which is specifically expressed in root pericycle cells adjacent to xylem; orthologous mechanisms in rice await characterization. NRT1.5 knockout in *Arabidopsis* impairs root-to-shoot nitrate transport and reveals a regulatory loop between nitrate and potassium at the xylem loading step (Lin et al., 2008), suggesting broader mineral crosstalk at the vascular interface.

3.2 High-Affinity NRT2 Family and the NAR2 Partnership

High-affinity nitrate transport (HATS) requires the NRT2 family, members of which form obligate two-component complexes with NAR2 (NRT3) accessory proteins in both *Arabidopsis* and rice. In *Arabidopsis*, AtNRT2.1 is the dominant HATS component; its expression is induced by nitrate, repressed by ammonium and downstream N metabolites, and regulated by the NLP-NIGT1 transcriptional cascade (Ueda and Yanagisawa, 2023; Maeda et al., 2018; Xu et al., 2024). The NIGT1 repressors form a feedforward loop with NLP activators: under nitrate induction, NLPs activate both NRT2.1 expression and NIGT1 expression, and NIGT1 then represses NRT2.1, acting as a rheostat that stabilizes nitrate uptake amplitude across a wide range of external NO_3^- concentrations (Ueda and Yanagisawa, 2023; Maeda et al., 2018). Furthermore, phosphorus (P) starvation activates PHR1, which induces NIGT1 genes, creating a direct link between P and N nutritional signaling through this feedforward module (Maeda et al., 2018).

In rice, four NRT2 genes and two NAR2 genes have been identified (Feng et al., 2011). OsNAR2.1 interacts with OsNRT2.1, OsNRT2.2, and OsNRT2.3a to enable both high- and low-affinity nitrate uptake (Yan et al., 2011). Knockdown of OsNAR2.1 simultaneously suppresses all three OsNRT2 partners, abolishing both HATS and LATS, a striking demonstration of the obligate nature of this partnership (Yan et al., 2011). Spatial expression analysis revealed that OsNAR2.1 is confined to root epidermal cells, while the five OsNRT2 genes show distinct cell-type expression patterns (Feng et al., 2011). Importantly, OsNRT2.1, OsNRT2.2, and OsNRT2.3a are upregulated by nitrate and suppressed by NH_4^+ and high root temperature (37  C), while OsNRT2.4 responds uniquely to auxin supply-indicating distinct physiological roles for each NRT2 isoform and differential N-C-hormone regulatory pathways (Feng et al., 2011). The functional analyses of the *Arabidopsis* NRT2 family have been comprehensively updated by Xu et al. (2024), who confirm that different AtNRT2 members play non-redundant roles in nitrate uptake, remobilization, and signaling under varying N conditions.

3.3 Ammonium Transporters: The AMT Family in Rice vs. Arabidopsis

Ammonium transport is mediated by the AMT/MEP/Rh superfamily, with plant AMT1 and AMT2 subfamilies being the primary root uptake systems (Loqu   and von Wir  n, 2004). In *Arabidopsis*, AtAMT1.1 is the dominant high-affinity NH_4^+ transporter in roots, regulated by N status through a feedback loop involving glutamine accumulation (Rawat et al., 1999). AtAMT1 mRNA and NH_4^+ influx are inversely correlated with N provision; critically, the feedback signal is not NH_4^+ itself but the downstream metabolite glutamine demonstrated by the sustained high AtAMT1 expression when NH_4^+ assimilation is blocked with methionine sulfoximine (Rawat et al., 1999). AMT transport is regulated at multiple levels: transcriptional, post-translational (trans-inhibition by

cytoplasmic NH_4^+), and allosteric (C-terminal regulatory domain), and AMT transporters are subject to complex local root-portion and whole-plant N sensing (Loqué and von Wirén, 2004).

In rice (*Oryza sativa* ssp. *indica*), three OsAMT1 genes (OsAMT1.1, OsAMT1.2, OsAMT1.3) show distinct regulatory responses (Kumar et al., 2003). OsAMT1.1 is rapidly up-regulated under N starvation and repressed by high NH_4^+ , responding most strongly to N status changes. OsAMT1.3 displays a pronounced diurnal pattern upregulated late in the photoperiod suggesting coupling to light-driven photosynthate supply; this diurnal regulation is less prominent in *Arabidopsis* AMTs (Kumar et al., 2003). Since paddy rice grows predominantly in NH_4^+ -rich anoxic soils, the OsAMT gene family is of proportionally greater importance for rice N nutrition than in *Arabidopsis*. NH_4^+ toxicity in rice is linked to futile NH_4^+ cycling across the root plasma membrane; high-NUE rice cultivars show lower NH_4^+ efflux and less futile cycling than low-NUE cultivars, connecting NUE directly to the efficiency of AMT-mediated ammonium transport and retention (Chen and Guo, 2013). Ammonium-grown rice seedlings also show enhanced drought tolerance compared to nitrate-grown seedlings, mediated through increased aquaporin (AQP) expression that improves root hydraulic conductivity and water use a N-form-specific interaction with water relations relevant to paddy management under water deficit (Ding et al., 2015).

3.4 Nitrite Transport and GOSZ Promoter Activity in Monocots

Nitrite (NO_2^-), the transient intermediate between NR and NiR, can also be taken up directly by roots. Kotur et al. (2013) characterized a nitrite-specific plasma membrane transporter in *Arabidopsis* using $^{13}\text{NO}_2^-$ fluxes in NAR2.1 mutants unable to perform sustained high-affinity nitrate uptake. This transporter shows saturable kinetics ($K_m \sim 185 \mu\text{M}$) and is constitutively active but downregulated by ammonium suggesting functional relevance under N-limited conditions where nitrite may accumulate. The extent of nitrite uptake in rice under flooded conditions warrants investigation. The rice GOS2 gene promoter evaluated as a constitutive expression tool drives high-level gene expression across diverse monocot tissues and reproductive organs (de Pater et al., 1992; Park et al., 2010), providing a practical tool for expressing N-metabolism transgenes in rice and other monocots.

4. Impact of Abiotic Stress on N Assimilation in Monocot Crops

4.1 Salinity Stress

Soil salinity affects over 20% of irrigated land worldwide and impairs N metabolism through dual mechanisms: osmotic stress (reducing water potential and stomatal conductance, limiting CO_2 for C-skeletons needed in amino acid synthesis) and ionic toxicity (Na^+ displacing K^+ and disrupting metalloenzyme function) (Ye et al., 2022; Ullah and Ali, 2025; Zayed et al., 2023). In rice, reproductive-stage salinity stress at 10 dS m^{-1} (NaCl) significantly decreased transcript levels of OsNIA (NR), OsNiR, OsGLN1.1, OsGLN1.2, OsGLN2, OsFd-GOGAT, and OsNADH-GOGAT in flag leaves (Sathee et al., 2021). The osmotic stress-tolerant genotype Shabhagidhan (SD) maintained higher leaf nitrate, ammonium content, and enzyme activity than the sensitive genotype Pusa Sugandh-5 (PS5), and showed higher GDH activity that indirectly supported proline accumulation and osmotic adjustment, identifying induction of GDH as a key adaptive response in salt-tolerant rice (Sathee et al., 2021).

In tomato a model system with clear cereal relevance salt stress (75 mM NaCl) significantly decreased LeNRT1.1 and LeNRT1.2 transcript levels, reducing nitrate uptake capacity; LeNRT2.1 was also downregulated, while LeNRT2.3 showed a slight transient increase at 12 h, indicating transporter-class-specific salt sensitivity (Yao et al., 2008). These patterns are consistent with observations in rice where salinity disrupts the proton motive force needed for H^+/NO_3^- symport (Zayed et al., 2023).

In ryegrass (*Lolium multiflorum*) a monocot forage crop salinity increased xanthine dehydrogenase (XDH) and aldehyde oxidase (AO) activities and elevated ureide concentrations (allantoin, allantoic acid) in roots, especially in NH_4^+ -grown plants (Sagi et al., 1998). The salinity-induced increase in XDH activity enhances ureide production, providing N-efficient organic transport forms with low C:N ratios, while AO upregulation promotes ABA biosynthesis, connecting N metabolism to stress hormone production (Sagi et al., 1998). Nitric oxide (NO) has been identified as a mediator of plant responses to salt stress, modulating N transporter expression and GS/GOGAT enzyme activity; S-nitrosothiols (SNOs) regulate both nitrate uptake and reduction by suppressing NRT transporters and NR activity, constituting a feedback loop that fine-tunes nitrate homeostasis (Frunzillo et al., 2014; Zayed et al., 2023).

Nam et al. (2015) studied the role of enhanced ammonium assimilation through transgenic expression of AMT genes in conferring salinity tolerance, while Naresh Kumar et al. (2024), Hafeez et al. (2020), Saddhe et al. (2020), and Rathinapriya et al. (2025) collectively reviewed the genetic resources in halophytes for salt-tolerance genes and their introgression into cereal crops. Halophytes employ Na^+ compartmentalization, ion transporter upregulation (SOS1, NHX), and metabolic adjustments that maintain N assimilation capacity under saline conditions; co-expression of SpSOS1 and SpAHA1 from the halophyte *Sesuvium portulacastrum* in transgenic *Arabidopsis* improved salinity tolerance by maintaining favorable K^+/Na^+ ratios and protecting the plasma membrane from oxidative damage (Fan et al., 2019). Transferring such mechanisms into rice or wheat backgrounds represents a viable strategy to maintain N uptake under salinity.

4.2 Drought Stress

Drought limits N assimilation through reduced mass flow of nitrate to roots, stomatal closure limiting CO_2 availability for amino acid C-skeletons, and direct enzyme inactivation (Alamillo et al., 2010; Ullah and Ali, 2025). Transcription factor (TF)-mediated regulation of root architecture is a primary adaptive response: in rice, overexpression of OsNAC10 (a drought-inducible NAC-domain TF) under the root-specific promoter RCc3

enlarged root diameter by 1.25-fold through expanded stele and cortex, enabling access to deeper soil water and N under field drought, yielding grain yield increases of 25-42% compared to controls (Jeong et al., 2010). This outcome contrasts with constitutive expression under the GOS2 promoter, which did not improve field drought performance demonstrating the essential role of spatial precision in stress-responsive TF engineering (Jeong et al., 2010; Park et al., 2010).

Metabolomic profiling of aus-type rice landraces (Dular, N22) under severe drought revealed higher accumulation of N-rich metabolites amino acids, allantoin, and uridine in shoots of tolerant varieties versus sensitive irrigated varieties (IR64, IR74) (Casartelli et al., 2018). Allantoin ($C_4H_6N_4O_3$), a purine catabolism product and ureide-class compound, accumulated preferentially in drought-tolerant genotypes, providing N storage with ROS-scavenging capacity (Casartelli et al., 2018; Kaur et al., 2022). In contrast, raffinose an abiotic stress compatible solute accumulated more in drought-sensitive varieties, suggesting metabolic channeling differences between tolerance and sensitivity strategies. These N-rich metabolite signatures constitute valuable biomarkers for drought tolerance breeding in rice.

The ureide allantoin has been extensively reviewed as a stress-protective compound. Kaur et al. (2022) demonstrated that allantoin functions as a signaling molecule that activates stress-responsive genes (including P5CS for proline synthesis) and ROS-scavenging antioxidant enzymes, regulates ABA-JA cross-talk, and maintains ion homeostasis by increasing putrescine and spermine accumulation. Importantly, overexpression of Ureide Permease 1 (OsUPS1) in rice under N-limited field conditions increased allantoin accumulation in shoots, enhanced N uptake and remobilization, and improved growth establishing allantoin transport as a tractable target for improving N economy under N limitation and drought (Redillas et al., 2019). In *Phaseolus vulgaris* (common bean a ureidic legume), drought triggers ureide accumulation through transcriptional induction of allantoinase (ALN) and ABA-mediated inhibition of allantoate amidohydrolase (AAH), constituting an ABA-regulated N buffering response independent of nodular N fixation (Alamillo et al., 2010). While *P. vulgaris* is not a monocot, its ureide regulation provides a comparative framework for understanding ureide accumulation in cereals.

In wheat, N starvation during grain filling (studied by Curci et al., 2017) severely impacts grain yield, reducing plant height, tillering, flag leaf area, and total N content. RNA-seq identified 4,626 DEGs in durum wheat under N starvation: most transcriptomic changes occurred in roots (3,270 DEGs), including strong upregulation of NRT2 transporters and amino acid metabolism genes, while photosynthesis, carbon metabolism, and N assimilation genes were predominantly downregulated in leaves and spikes (Curci et al., 2017). N deficiency at anthesis in wheat reduces grain number and weight in a linear relationship with the N deficit, linking N assimilation capacity directly to reproductive output (Zhao et al., 2023).

Ding et al. (2015) demonstrated that ammonium-grown rice seedlings showed enhanced drought resistance compared to nitrate-grown seedlings, and that this advantage was associated with increased aquaporin (AQP) expression, root hydraulic conductivity, and reduced ethylene production revealing a N-form-specific mechanism for drought tolerance with direct relevance for paddy field N management. Under NH_4^+ nutrition, root aquaporin activity helps maintain water flux even under soil drying, while nitrate-grown plants rely more on osmotic adjustment mechanisms that are less effective under severe drought and effect of abiotic stress on nitrogen assimilation in monocot crops are shown in Table 1.

Table 1. Representative research outcomes on the effect of abiotic stress on nitrogen assimilation in monocot crops.

Stress	Genotype	Research outcome	References
Salinity (10 dS m^{-1} NaCl, reproductive stage)	Rice (Shabhadhan vs. Pusa Sugandh-5)	Decreased OsNIA, OsNiR, OsGLN1.1/1.2, OsGLN2, OsFd-GOGAT and OsNADH-GOGAT transcripts in flag leaves; tolerant genotype maintained higher GDH activity, proline synthesis and osmotic adjustment	Sathee et al., (2021)
Drought (root-specific TF overexpression)	Rice (OsNAC10 under RCc3 promoter)	Root diameter enlarged 1.25-fold; 25-42% higher grain yield under field drought vs. controls	Jeong et al., (2010)
Drought (metabolomic profiling)	Rice aus landraces (Dular, N22) vs. irrigated (IR64, IR74)	Drought-tolerant landraces accumulated more N-rich metabolites (amino acids, allantoin, uridine) in shoots	Casartelli et al., (2018)
Nitrogen starvation (grain filling)	Durum wheat	4,626 DEGs identified; NRT2 transporters and amino-acid metabolism genes upregulated in roots, N-assimilation genes downregulated in leaves/spikes	Curci et al., (2017)

Nitrogen limitation (gene overexpression)	Rice (OsUPS1 ureide permease)	Increased shoot allantoin accumulation; enhanced N uptake, remobilization and growth under limited N	Redillas et al., (2019)
N-form comparison under drought	Rice (NH ₄ ⁺ -grown vs. NO ₃ ⁻ -grown seedlings)	Ammonium nutrition enhanced drought tolerance via increased aquaporin expression and root hydraulic conductivity	Ding et al., (2015)
Cold (15°C irrigation, 5–15 days, tillering stage)	Japonica rice (Dongnong 428 vs. Songjing 10)	Cold-tolerant variety maintained higher root NR, GS and GOGAT activity and root biomass, achieving 11.6–20.9% higher yield under prolonged cold	Gong et al., (2026)
Nitrogen starvation (12 h)	Rice	1,650 DEGs identified, with more changes in leaf sheaths (1,158) than roots (492); induced OsNRT2.1, OsAMT1.1 and OsDof1	Yang et al., (2015)

4.3 Temperature Stress: Heat and Cold

Extreme temperatures impair N metabolism at multiple levels. Heat stress directly denatures N-assimilatory enzymes (NR, GS, GOGAT are thermolabile at >35°C), reduces photosynthetic capacity limiting C-skeleton supply, and disrupts protein quality control required for enzyme turnover (Hungria and Kaschuk, 2014; Kaushal et al., 2016; Alsamir et al., 2021; Hayes et al., 2021). In *Phaseolus vulgaris* exposed to high temperature, both GS and GOGAT activities declined significantly alongside NR and nitrogenase in nodules, confirming that heat stress simultaneously disrupts both biological N fixation and primary assimilation pathways (Hungria and Kaschuk, 2014). In tomato, heat stress alters protein abundance and enzyme stability (Alsamir et al., 2021); similar cascades in rice at reproductive stages reduce grain N content and cooking quality. Temperature sensing in plants involves thermosensory photoreceptors (phyB), membrane fluidity changes, and heat shock protein (HSP) induction (Hayes et al., 2021; Howarth and Ougham, 1993); while HSPs protect general cellular machinery, dedicated protection of N-assimilatory enzymes under heat stress is relatively understudied in monocots.

Cold stress at the tillering stage in japonica rice (15°C irrigation water for 5-15 days) severely disrupted root growth, N metabolism, and photosynthesis in a duration-dependent manner (Gong et al., 2025). The cold-tolerant variety Dongnong 428 maintained higher root biomass, stronger NR, GS, and GOGAT activities, and better photosynthetic performance than the cold-sensitive variety Songjing 10, achieving 11.6-20.9% higher yields under prolonged cold stress. Root N-metabolizing enzyme homeostasis under cold was the primary discriminating trait between tolerant and sensitive varieties (Gong et al., 2025). In general, cold reduces membrane fluidity, impairing transporter function and reducing enzyme activities, including AMT and NRT transporters; this reduces N acquisition precisely during early growth stages when N demand is highest. Early gene expression studies by Howarth and Ougham (1993) established that temperature stress induces comprehensive reorganization of protein synthesis and turnover programs, with HSP induction and selective mRNA stabilization governing cellular survival under both heat and cold extremes.

4.4 Nitrogen Starvation

N starvation triggers the most direct disruption of N assimilation pathways, initiating a multi-layered transcriptomic, metabolic, and developmental reprogramming. The primary nitrate response (PNR) in *Arabidopsis* was first characterized by Redinbaugh and Campbell (1991) and subsequently dissected molecularly over three decades (Vidal et al., 2020). The central discovery was that NIN-Like Protein (NLP) transcription factors NLP6 and NLP7 most prominently mediate rapid nitrate sensing: under N-sufficient conditions, NLPs are cytoplasmic, but within minutes of NO₃⁻ addition they translocate to nuclei and activate hundreds of target genes including NRT1.1, NRT2.1, NIA1, NIA2, and genes for C-skeleton supply (Konishi and Yanagisawa, 2013; Vidal et al., 2020).

The NLP-NIGT1 feedforward loop provides regulatory precision: NLPs activate both NRT2.1 and NIGT1 (NITRATE-INDUCIBLE GARP-TYPE TRANSCRIPTIONAL REPRESSOR1) repressor genes; NIGT1 then suppresses NRT2.1, creating a negative feedback that buffers the amplitude of nitrate uptake gene expression over a wide range of external NO₃⁻ (Ueda and Yanagisawa, 2023; Maeda et al., 2018). Mathematical modeling confirms that NIGT1 stabilizes NRT2.1 expression dynamics by adjusting repressor synthesis and promoter affinity parameters (Ueda and Yanagisawa, 2023). In rice, N starvation transcriptomics by Yang et al. (2015) identified 1,650 differentially expressed genes after 12 hr of N deficiency, with more changes in leaf sheaths (1,158 DEGs) than roots (492 DEGs) contrasting with *Arabidopsis* where root responses dominate the N starvation transcriptome. N-starvation-induced genes in rice included OsNRT2.1, OsAMT1.1, genes for lateral root elongation, and the transcription factor OsDof1, which promotes C-N metabolism by inducing phosphoenolpyruvate carboxylase (Yang et al., 2015).

In maize, N starvation during early vegetative stages reduced chlorophyll content, total soluble proteins, and NR activity, with differential expression of genes related to N assimilation and metabolism (Yadava et al., 2020). ZmDof1 (Dof1 transcription factor from maize) enhances carbon metabolism specifically PEPC activity to

provide more 2-OG for the GS/GOGAT cycle; its overexpression in *Arabidopsis* improved growth under N limitation, confirming functional conservation of this monocot N-efficiency TF across taxa (Yang et al., 2015). In durum wheat, chronic N starvation during grain filling upregulates NRT transporters in roots while suppressing photosynthesis genes in leaves and spikes, reflecting a coordinated whole-plant response that prioritizes N acquisition over biomass accumulation (Curci et al., 2017). In *Arabidopsis*, overexpression of UPM1 (siroheme synthase) increased N assimilation capacity under N deficiency by elevating NiR and NR enzyme levels (Garai and Tripathy, 2018) suggesting similar approaches in rice or wheat could improve N capture under N-limited field conditions.

The TOR (Target of Rapamycin) kinase integrates N availability with growth decisions at a systems level (Zhang et al., 2023; Li et al., 2021). Under adequate N and carbon, TOR is active and promotes ribosome biogenesis, protein synthesis, and cell division. Under N limitation, TOR is repressed by SnRK1 (SNF1-Related Kinase 1), triggering autophagy for N recycling from proteins, activating senescence programs for N remobilization from older leaves, and reducing growth (Li et al., 2021; Zhang et al., 2023). Nitrate itself activates TOR in *Arabidopsis* coupling N availability directly to growth providing a molecular rationale for why N-deficient plants show stunted growth even when sugar supply is adequate. Whether OsTOR and ZmTOR function identically in cereals, and how their activity is modulated under combined N and water stress, remains an active area of research.

5. Biotic Stress and N Assimilation: Interactions and Trade-offs

5.1 N Status and Pathogen Susceptibility

The relationship between plant N status and disease susceptibility is complex and pathogen-lifestyle-dependent (Farjad et al., 2018; Wang et al., 2025). High N availability generally increases susceptibility to biotrophic pathogens (requiring living host cells) by promoting lush, rapidly growing tissue rich in amino acids that pathogens exploit, while reducing susceptibility to many necrotrophic pathogens (which kill host cells) by bolstering secondary cell walls and phenylpropanoid defences (Farjad et al., 2018). Wang et al. (2025) comprehensively reviewed how biotic stresses pathogen infections, insect herbivory, and nematode attack disrupt plant nutrient homeostasis by altering transporter expression, root architecture, and N reallocation. Pathogen invasion triggers immune signaling cascades that redirect N-containing metabolites from primary assimilation to defence compound production, including pathogenesis-related (PR) proteins, phytoalexins, glucosinolates, and reactive oxygen species (ROS) mediators all N-requiring processes (Wang et al., 2025).

Farjad et al. (2018) performed a landmark transcriptomic study in *Arabidopsis* examining the interaction between N limitation and infection by the bacterial pathogen *Erwinia amylovora* (Ea). While most Ea-responsive genes were similarly induced or repressed regardless of N status, one-third of transcripts responding to combined N limitation and Ea infection showed responses that could not be predicted from either single stress alone. Critically, many defence-related genes showed prioritization of biotic stress responses over N limitation responses defence programs were maintained even under low N, while N-limitation responses were partially suppressed in infected plants (Farjad et al., 2018). This hierarchical stress prioritization reflects evolutionary programming to preserve immunity under metabolic constraints. Whether this hierarchy is conserved in rice (with its distinct immune system based on NLR resistance proteins and PAMP-triggered immunity) is an open question with significant breeding implications.

5.2 Polyamines, N Metabolism, and Defence

Polyamines (PAs) putrescine (Put), spermidine (Spd), and spermine (Spm) are polycationic aliphatic amines biosynthesized from arginine and ornithine via N-intensive pathways, placing them at the intersection of N metabolism and stress defence (Paschalidis et al., 2019). Glutamate, produced by the GS/GOGAT cycle, serves as the common metabolic hub for proline, arginine, ornithine, and PA biosynthesis, creating a metabolic web that coordinates N partitioning under stress. PAs protect cellular structures (membranes, nucleic acids, proteins) against ionic and oxidative damage through direct electrostatic interactions with negatively charged macromolecules. Their catabolism by diamine oxidase (DAO) and polyamine oxidase (PAO) generates H₂O₂, which contributes to the hypersensitive response (HR) during incompatible pathogen interactions (Paschalidis et al., 2019).

Paschalidis et al. (2019) comprehensively reviewed N-PA interplay in stress responses across diverse plant species. Transgenic rice and maize plants with enhanced PA biosynthesis (overexpressing ADC, arginine decarboxylase; ODC, ornithine decarboxylase; or SAMDC, S-adenosylmethionine decarboxylase) show improved tolerance to drought, salinity, and cold stress simultaneously, making PA metabolism manipulation a uniquely efficient multi-stress strategy. The PA-ethylene interaction is particularly significant: PA catabolism produces ethylene precursors (SAM is shared between PA and ethylene synthesis), and under pathogen attack, PA degradation contributes to the ethylene burst that coordinates systemic defence signaling in cereals (Paschalidis et al., 2019). Ethylene additionally upregulates AMT expression under flooding in rice—a monocot-specific pathway maintaining N acquisition under anaerobic conditions where AMT-mediated NH₄⁺ uptake is the primary N entry route.

5.3 Calcium Signaling: Integration of Biotic and N Responses

Calcium (Ca²⁺) serves as a universal second messenger that integrates both biotic and abiotic stress signals with cellular metabolism. Park and Shin (2022) comprehensively reviewed the roles of Ca²⁺ channels and transporters under biotic and abiotic stresses. Ca²⁺-permeable channels including CYCLIC NUCLEOTIDE-GATED

CHANNELs (CNGCs), HYPERPOLARIZATION-ACTIVATED CALCIUM PERMEABLE CHANNELs (HACCs), GLUTAMATE RECEPTOR-LIKE RECEPTORs (GLRs), and TWO-PORE CHANNELs (TPCs) generate distinct Ca^{2+} signatures (differing in amplitude, duration, and spatial pattern) in response to pathogen attack, drought, salinity, and temperature stress. Resistosomes formed by activated NLR immune receptors have also been identified as Ca^{2+} -permeable channels, providing a direct molecular link between pathogen recognition and Ca^{2+} influx (Park and Shin, 2022). Ca^{2+} efflux by Ca^{2+} -ATPases and $\text{Ca}^{2+}/\text{H}^{+}$ exchangers restores cytoplasmic Ca^{2+} homeostasis and encodes the specificity of the Ca^{2+} signal through its decay kinetics.

At the N metabolism interface, Ca^{2+} -dependent protein kinases (CDPKs) phosphorylate NR, modulating its activity post-translationally under stress (Ullah and Ali, 2025). CIPK23 (a kinase that interacts with CBL calcium sensors) phosphorylates NRT1.1 at Thr101 to switch it from low- to high-affinity mode directly coupling Ca^{2+} signaling to nitrate transport capacity (Ho et al., 2009). CNGC channels activated by pathogen PAMPs generate Ca^{2+} influx that triggers immune responses, but the same channel types are involved in regulating nitrate transporter activity under low-nitrate conditions (Park and Shin, 2022; Ullah and Ali, 2025). This dual role creates a point of crosstalk where pathogen signaling may modulate N transport capacity and vice versa.

5.4 CLE Peptide Signaling and N-Root Development Crosstalk

The CLAVATA (CLV) signaling pathway involving CLE peptide ligands and receptor-like kinases regulates meristem activity and has been connected to N-responsive root development (Araya et al., 2016). CLE peptides modulate lateral root development and systemic autoregulation of nodulation in legumes; recent studies implicate CLE-CLV signaling in adjusting root system architecture in response to N availability in non-legume plants as well (Araya et al., 2016). In rice, N-signaling through the root system involves both local responses to external $\text{NO}_3^-/\text{NH}_4^+$ patches and systemic signals from the shoot reflecting whole-plant N status mechanisms partially analogous to those characterized in *Arabidopsis* via NRT1.1 and the ANR1 MADS-box TF (Remans et al., 2006). Understanding how biotic stress (which modifies root architecture through pathogen-induced defence responses) intersects with N-driven root architectural signaling through CLE peptides represents an emerging frontier in monocot N biology.

6. Regulatory Networks Integrating N Assimilation with Stress Responses

6.1 Transcription Factors

NIN-Like Proteins (NLPs) are the master regulators of the primary nitrate response in *Arabidopsis* (Konishi and Yanagisawa, 2013). NLP7 functions as a nitrate sensor, shuttling between cytoplasm and nucleus in a nitrate-dependent manner; its suppression causes growth retardation on NO_3^- , establishing NLPs as essential for nitrate signaling (Konishi and Yanagisawa, 2013). NLP family proteins bind the conserved nitrate-responsive cis-element (NRE) in promoters of NRT and N assimilation genes. In rice, OsNLP genes are present but their stress-specific regulatory targets remain poorly characterized compared to *Arabidopsis* a significant gap given the importance of NO_3^- signaling even in flooded rice (Yang et al., 2015). The Dof (DNA binding with One Finger) transcription factors represent a monocot-enriched N-regulatory module: ZmDof1 in maize and its rice ortholog activate phosphoenolpyruvate carboxylase (PEPC) to provide 2-oxoglutarate as the amino acceptor for GS/GOGAT, directly connecting C fixation to N assimilation under low-N conditions (Yang et al., 2015; Yadava et al., 2020). The NIGT1 (NITRATE-INDUCIBLE GARP-TYPE TRANSCRIPTIONAL REPRESSOR1) family provides the negative regulatory counterbalance to NLP activation, acting as a repressor hub that also mediates P starvation signals into the nitrate regulatory network (Maeda et al., 2018; Ueda and Yanagisawa, 2023).

NAC transcription factors integrate abiotic stress responses with N remobilization. OsNAC10 (induced by drought, salt, and ABA) modulates root architecture under drought to simultaneously enhance water and N acquisition (Jeong et al., 2010). OsNAC TFs also regulate senescence-associated N remobilization from leaves to grain a critical process for grain protein content in rice that is disrupted under heat and drought stress. In *Arabidopsis*, the epigenetic regulator Polycomb Repressive Complex 1 (PRC1) has been shown to regulate N-responsive gene expression (Marchise et al., 2013), providing a layer of chromatin-based N memory that determines how plants respond to historical N availability. Whether similar epigenetic N memory exists in cereals is unexplored. The promoter of the rice GOS2 gene, which is constitutively active in diverse monocot tissues (de Pater et al., 1992), has been widely used to drive N metabolism transgenes in rice, providing a practical biotechnological platform for validating TF engineering strategies.

6.2 Phytohormones and N-Hormone Crosstalk

Cytokinins (CKs) are synthesized in roots under N-sufficient conditions and transported to shoots as positive signals of N status, where they promote leaf growth and photosynthesis (Tegeder and Masclaux-Daubresse, 2018; The et al., 2021). Absciscic acid (ABA) acts antagonistically: under drought, ABA promotes stomatal closure, reducing CO_2 supply for amino acid synthesis and suppressing N metabolism. ABA also induces ALN expression in *P. vulgaris*, promoting allantoin accumulation as an N-buffering response to drought (Alamillo et al., 2010). Salicylic acid (SA) and jasmonic acid (JA) mediate biotic defence responses; their biosynthesis consumes N-containing precursors (phenylalanine for SA, isoleucine-JA conjugation for JA signaling), creating N resource competition between defence and growth under combined biotic-abiotic stress (Wang et al., 2025; Farjad et al., 2018). Ethylene produced during waterlogging upregulates AMT expression in flooded rice a monocot-specific hormonal mechanism maintaining NH_4^+ uptake under anaerobic conditions (Paschalidis et al., 2019). Nitric oxide (NO), produced from nitrate during N assimilation, regulates its own generation and scavenging through S-

nitrosylation (forming S-nitrosothiols, SNOs) that inhibit both NRT transport activity and NR enzyme activity, providing a sophisticated auto-regulatory NO homeostasis circuit (Frunzillo et al., 2014; Zayed et al., 2023).

6.3 Nutrient Signaling Networks: TOR, SnRK1, and Crosstalk

The TOR-SnRK1 signaling axis is a central integrator of N, carbon, and energy signals (Zhang et al., 2023; Li et al., 2021). TOR is activated by amino acids (especially glutamine a product of primary N assimilation), glucose, and growth factors; it promotes anabolic processes including ribosome biogenesis, protein synthesis, and cell proliferation. SnRK1, the plant homolog of AMPK, responds to energy deficit (low AMP:ATP ratios under stress) by inactivating TOR and activating catabolic programs including autophagy for N recycling and senescence for N remobilization. Li et al. (2021) provided a comprehensive review of dynamic nutrient signaling networks, describing how glucose (via HXK1 and TOR), nitrate (via NLP7, TOR, and SnRK1), and phosphate (via PHR1 and NIGT1) signals are integrated. The NIGT1 hub activated by both nitrate (through NLP) and P starvation (through PHR1) represents a direct N-P signaling integration point that adjusts N uptake in response to P availability and vice versa (Maeda et al., 2018). In rice and wheat, the functional equivalents of these signaling hubs are beginning to be characterized, but the full topology of the N signaling network in cereals under combined stress conditions remains fragmentary compared to *Arabidopsis*.

7. Nitrogen Source-Sink Relations in Monocots: Grain Filling and Stress

Nitrogen source-sink dynamics the partitioning of N between assimilation organs (source leaves, roots) and utilization organs (seeds, meristems, young leaves) determine both yield and quality in cereal crops (Tegeder and Masclaux-Daubresse, 2018). The review by Tegeder and Masclaux-Daubresse (2018) defines a comprehensive framework: N is acquired from the soil in roots, assimilated into amino acids, transported via xylem to source leaves, redistributed in phloem to sinks, and remobilized from senescing tissues for grain filling. Amino acid transporters in the phloem (AAP, UPS, ProT families) control N partitioning toward seeds (Tegeder and Masclaux-Daubresse, 2018). In soybean, overexpression of the ureide permease UPS1 in nodules increased ureide export, stimulating N fixation and improving seed yield (Carter and Tegeder, 2016) demonstrating that N export from source organs is a key bottleneck in seed N accumulation. The allantoin permease (UPS1) strategy in rice (Redillas et al., 2019) parallels this: increasing allantoin export from leaves under N limitation improved N remobilization efficiency and grain quality.

Masclaux-Daubresse et al. (2010) provided a foundational review of N recycling in plants, establishing that GS1 isoforms in cytosol are the primary enzymes of N remobilization during leaf senescence, while Bernard and Dietrich (2005) reviewed asparagine metabolism as central to N export from senescing organs. In monocot crops, the primary form of N transported from senescing flag leaves to developing grain is glutamine and asparagine rather than ureides (as in tropical legumes); the balance between these N forms affects grain protein composition and quality (Zhao et al., 2023). Under drought and heat stress during the grain filling period increasingly common under climate change accelerated leaf senescence shortens the N remobilization window, reducing grain N content and protein yield even when soil N supply is adequate (Zhao et al., 2023; Kaushal et al., 2016).

8. Strategies for Improving NUE in Monocots Under Stress

8.1 Gene Overexpression

Overexpression of GS1 isoforms particularly OsGS1;1 in rice has yielded significant NUE improvements by enhancing primary N assimilation efficiency and N remobilization capacity during grain filling (Liu et al., 2022; Han et al., 2015). Overexpression of OsNADH-GOGAT1 improved grain quality in rice by maintaining amino acid supply during grain filling. In wheat, exploiting natural variation in TaGS1 haplotypes associated with enhanced grain N remobilization offers a molecular breeding approach that avoids transgenic complications (Zhao et al., 2023). Combining GS1 overexpression with elevated GOGAT activity to prevent Gln accumulation without proportional Glu regeneration may maximize N cycling efficiency under low-N stress. Overexpression of AtUPM1 to enhance siroheme biosynthesis and NiR activity represents an upstream engineering strategy that simultaneously improves NR, NiR, S assimilation, and protein synthesis (Garai and Tripathy, 2018), with clear potential for translation to rice and wheat.

8.2 Transcription Factor Engineering

TF-based strategies offer the advantage of simultaneously regulating entire gene networks. Root-specific overexpression of OsNAC10 improves drought tolerance and grain yield through root architectural enhancement with secondary benefits on N acquisition (Jeong et al., 2010). The ZmDof1/OsDof1 approach enhancing C-skeleton supply for N assimilation under low N is directly transferable across monocots (Yang et al., 2015; Yadava et al., 2020). Engineering NLP transcription factors to maintain or enhance their nuclear translocation under stress conditions thereby sustaining N-responsive gene expression is a conceptually attractive strategy awaiting validation in cereals (Konishi and Yanagisawa, 2013). Modulating the NLP-NIGT1 feedforward loop to tune the amplitude of NRT2.1 expression under different N environments could allow precision adjustment of N uptake efficiency across diverse field conditions (Ueda and Yanagisawa, 2023; Maeda et al., 2018).

8.3 Allantoin and Ureide Engineering

The accumulation and transport of allantoin represents an emerging biotechnological target for improving N efficiency under stress. In rice, overexpression of OsUPS1 under N limitation increased allantoin accumulation and improved growth, establishing the ureide permease as a rate-limiting step in allantoin-mediated N economy (Redillas et al., 2019). Kaur et al. (2022) proposed that targeted upregulation of xanthine dehydrogenase (XDH)

the key enzyme producing allantoin via purine catabolism could enhance allantoin levels to provide both N buffering and ROS scavenging during stress. The connections between ureide metabolism, ABA signaling (Alamillo et al., 2010), and PA homeostasis (Paschalidis et al., 2019) suggest that allantoin engineering may have pleiotropic benefits extending beyond N economy to stress hormone regulation. In ureidic legumes (Baral et al., 2016; Duran and Todd, 2012), the ureide pathway is central to N export from nodules; understanding the regulation of allantoinase (ALN) and allantoate amidohydrolase (AAH) in non-legume monocots could reveal untapped N buffering potential and biotechnological and breeding strategies are discussed to improve nitrogen use efficiency (NUE) are shown in Table 2.

8.4 Multi-Omics, GWAS, and Precision Breeding

Genome-wide association studies (GWAS), QTL mapping, and multi-omics integration are accelerating the identification of NUE-related genomic regions in rice, wheat, and maize (Zhao et al., 2023; Han et al., 2015; Liu et al., 2022). CRISPR-Cas9 editing enables precise modification of promoter sequences of NRT2, GS1, and AMT genes to alter their stress-responsiveness without introducing foreign sequences a regulatory-only editing approach with potential for rapid regulatory approval. Transcriptomic datasets from stress-combined experiments (Curci et al., 2017; Yang et al., 2015; Farjad et al., 2018) provide hypothesis-generating resources for identifying novel regulators. Phenomics platforms enabling high-throughput NUE measurement under field stress conditions will accelerate the translation of genomic discoveries into improved varieties (Zhao et al., 2023).

8.5 Rhizosphere Microbiome and Biological N Fixation

Diazotrophic bacteria in the cereal rhizosphere including *Azospirillum*, *Gluconacetobacter*, and *Burkholderia* provide a modest but valuable biological N input (Zayed et al., 2023). Optimizing these associations through inoculant formulation, rhizosphere engineering, or introduction of more effective diazotrophic strains could supplement synthetic fertilizer inputs, particularly under stress conditions when plant N uptake is compromised. The long-term goal of engineering biological N fixation into cereal crops introducing nif genes directly into plants or their associated bacteria remains a significant challenge but would represent a transformative breakthrough for sustainable agriculture (Zayed et al., 2023).

Table 2. Biotechnological and breeding strategies reported to improve nitrogen use efficiency (NUE) under stress in monocots and related species.

Strategy	Species	outcome	Reference
OsGS1;1 (cytosolic glutamine synthetase) overexpression	Rice	Improved grain yield and N remobilization efficiency under low-N conditions	Liu et al., (2022)
Root-specific OsNAC10 (NAC transcription factor) overexpression	Rice	Enhanced root architecture, improved drought tolerance and field grain yield (25-42%)	Jeong et al., (2010)
OsUPS1 (ureide/allantoin permease) overexpression	Rice	Increased allantoin accumulation and improved N economy under N-limited field conditions	Redillas et al., (2019)
AtUPM1 (uroporphyrinogen III methyltransferase, siroheme biosynthesis) overexpression	<i>Arabidopsis thaliana</i>	Elevated NiR and NR activity, increased chlorophyll/photosynthesis, conferred N and S deficiency tolerance	Garai & Tripathy, (2018)
Co-expression of halophyte genes SpSOS1 & SpAHA1	Transgenic Arabidopsis	Improved salinity tolerance via maintenance of favorable K ⁺ /Na ⁺ ratio and reduced membrane oxidative damage	Fan et al., (2019)
Ureide permease UPS1 overexpression (nodules)	Soybean	Increased ureide export from nodules, stimulated N fixation and improved seed yield	Carter & Tegeder, (2016)

9. CONCLUSIONS AND FUTURE PERSPECTIVES

Nitrogen assimilation in monocot crops under biotic and abiotic stress is governed by a multi-layered regulatory architecture that shows both deep conservation with *Arabidopsis* and important crop-specific divergences. The core enzymatic pathway (NR, NiR, GS/GOGAT) is conserved, but monocots have expanded gene families with distinct tissue, stress, and developmental expression patterns particularly at the GS1, GOGAT, NRT2, and AMT levels that enable fine-tuned N economy under agronomic conditions absent from *Arabidopsis* ecology. Key monocot-specific features include: NH₄⁺ dominance as the primary N form in paddy rice (necessitating a

disproportionate role for AMT transporters and tolerance of NH_4^+ toxicity); the N-form-specific drought tolerance mechanism through ammonium enhanced aquaporin expression; cold-tolerant japonica rice varieties maintaining N-metabolizing enzyme homeostasis as a primary cold tolerance mechanism; ureide accumulation in drought tolerant aus-type rice landraces as metabolic N buffering; and the OsDof1 pathway linking C fixation to N assimilation under low N.

Biotic stress imposes a competitive drain on N resources redirected to defence compound biosynthesis; N availability modulates the magnitude of immune responses in a pathogen-lifestyle-dependent manner; and polyamine-N metabolism integration provides simultaneous protection against both biotic and abiotic stresses through ROS-based defence priming. The calcium signaling network (CNGCs, CDPKs, CIPK23) bridges immune responses and N transporter regulation at a single molecular hub. The NLP-NIGT1-PHR1 transcriptional cascade integrates nitrate sensing, N uptake gene expression, and P starvation signals, establishing a nutrient cross-talk network that deserves systematic characterization in cereals. TOR and SnRK1 kinases coordinate N availability with growth and autophagy, modulating N economy under combined C and N limitation.

Critical knowledge gaps for future research include: (1) full characterization of NLP transcription factor networks and their stress-specific targets in rice, maize, and wheat; (2) the molecular basis of cold-dependent suppression of N transporter function in cereals and its genetic basis for breeding; (3) the interaction between biotic stress immune responses and N assimilation gene regulation in rice-specifically whether the defence-prioritization hierarchy characterized in *Arabidopsis* by Farjad et al. (2018) is conserved in NLR-mediated resistance in rice; (4) the extent and regulation of the ureide pathway in non-legume monocots under combined drought and N starvation stress; (5) functional characterization of the NLP-NIGT1 feedforward loop in rice and the relationship between P starvation (PHR1 pathway) and N transport gene expression under combined N and P limitation; and (6) how the TOR-SnRK1 axis in cereals responds to combined biotic and abiotic stress to regulate N remobilization and senescence timing.

Translating these insights into crop improvement requires parallel advancement in genomic tools (CRISPR precision editing of N regulatory circuits), multi-omics pipelines for combined-stress NUE phenotyping, high-throughput field phenomics, and rigorous field validation under target environment stress conditions. The synthesis of mechanistic N biology from both *Arabidopsis* and monocot models each informing the other positions the field to deliver the next generation of N-efficient, stress-resilient cereal varieties essential for global food security under a rapidly changing climate.

DECLARATIONS

Acknowledgements

The authors are grateful for Tamil Nadu Agricultural University and for providing the library sources for the collection of literature.

Conflict of Interests

The authors declare no competing interests.

Funding

The authors declare that no funds, grants, or other support were received during the preparation of this manuscript.

Author Contribution

R.P. - wrote main manuscript text, L.M.R. - Conceptualization and Supervision, M.D. & G.M. - Edited manuscript text, K.P, S.K, I.R, S.V- reviewed manuscript.

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