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REVIEW

Crop nitrogen (N) utilization mechanism and strategies to improve N use efficiency

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Abstract

Nitrogen (N) is an essential plant macro-nutrient for crop sustainability and productivity. Substantial quantities of N fertilizers are being applied in soil, but only about 33% is utilized by the plants. Its availability in soil varies to a great extent in terms of time and space. Plant root systems should efficiently respond to fluctuating N by tailoring root growth and development. However, N fertilizer production consumes massive energy resource, and excessive application has negative consequences on the environment and human health. Therefore, innovative solutions are imperative to enhance crop yields and N use efficiency (NUE) simultaneously, while maintaining and/or reducing N application amount. Crop NUE is a complex attribute, because it is controlled by numerous genetic as well as environmental factors interact to govern the mechanisms involved in N sensing, uptake, translocation, assimilation, and remobilization in plants. Hence, a better understanding of these mechanisms is a key factor for improving NUE in cropping systems. In this review, we discussed the molecular, biochemical, and enzymatic mechanisms involved in NUE in crop plants, ways to increase NUE through the identification of plant factors with special consideration of their interaction, and different management strategies. In addition, adaptation of classical approaches, i.e., root architecture studies, quantitative trait loci (QTLs), and selection of genes for better NUE, are briefly discussed. Broadly, from root uptake to accumulation of N assimilates in various plant tissues, an array of physiological mechanisms is involved which is still not fully understood. Moreover, employing an integrated approach by combining expertise from fundamental and applied investigations in crop sciences may add further to available knowledge regarding crop N utilization.

Keywords Root foraging · Nitrogen transporters · Assimilation · Nitrogen use efficiency (NUE) · Translocation · Site-specific nitrogen management · Quantitative trait loci

Introduction

Nitrogen (N) is among the most essential elements for life on Earth. It is a major constituent of proteins, nucleic acids, and other important organic compounds (Castro-Rodriguez et al. 2016). Naturally, N occurs as two isotopes, viz., ^{14}N (99.632 atom %) and ^{15}N (0.368 atom %), including seven synthetic radioisotopes: ^{12}N, ^{13}N, ^{16}N, ^{17}N, ^{18}N, ^{19}N, and ^{20}N. The N is abundantly found up to 0.1% by weight in the earth's crust and about 78% in the atmosphere by volume (Ohyama 2010).

Plants require more N than any other nutrients, but only a small fraction of soil N is accessible to plants, because about 98% of organic forms cannot be absorbed by plant roots. In contrast, plants can readily acquire mineral forms of N which account for merely 2% of the total N (Carison and Philips 2021). Soil is the prime source of all essential nutrients; however, it is also supplied through fertilizers to overcome native soil N deficiency to sustain and/or enhance crop yields. Soil N supply depends on soil type, management practices, and weather conditions. About 3–4% N is found in above-ground plant tissues, a much higher concentration compared to other nutrients. On dry basis, almost 1–5% of total plant biomass contains N as an integral constituent of proteins, nucleic acids, phytohormones, co-enzymes, chlorophyll, and secondary metabolites (Marschner 2012). Instead of all, N is the first

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element to become deficient in crop production (Hawkesford 2014; O'Brien et al. 2016). Therefore, N availability to plant roots is a decisive factor for sustainable crop growth and productivity.

N in plant biology

Nitrogen is an essential macro-nutrient and important signal molecule which regulates multiple aspects of plant metabolism as it is a key component of nucleic acids, proteins, chlorophyll, enzymes, auxin, ATP, and cytokinins (Tegeder and Rentsch 2010; Xu et al. 2012). Plants accumulate more N within enzymes such as leaf Rubisco involved in carbon fixation (Castro-Rodriguez et al. 2016). Under N deficiency, plants have evolved different strategies to acquire N and its assimilation into various organic compounds (O'Brien et al. 2016). Several physiological functions in plants associated with biomass production are influenced by the N availability, uptake, and translocation (Tegeder and Masclaux-Daubresse 2018). Adequate N concentration enhances leaf area, establishes photosynthetic capacity, maintains photosynthetic activity, and enhances net assimilation rate, thereby contributing towards higher biomass production (Herrera et al. 2016). Moreover, N has a central role in the formation and continuance of sink and source capacity in terms of numbers and size of seeds and also affects the quality of crop products (Tegeder and Masclaux-Daubresse 2018). Furthermore, optimum N accelerates root growth, improves growth of leafy vegetables, improves fruit quality, and increases the protein content of fodder (Pasley et al. 2019). Nitrogen is also essential for canopy development and has significant impacts on growth, boll development, lint yield, and fiber quality in cotton (Luo et al. 2018). In addition, NO_3^- can serve as a signaling molecule to break seed dormancy (Fan et al. 2017), and alter flowering (O'Brien et al. 2016). Inadequate N supply results in limited leaf area, photosynthetic rate, and ultimately lower biomass production. On other hand, over application of N has negative impacts on plant growth, and causes succulence in plant and results in reduced fruit quantity with the least quality (Tegeder and Rentsch 2010). Hence, sufficient N needs to be taken up and allocated to support optimum plant growth and development.

N in soil–plant system

The N has a unique place in crop production systems at a global scale to meet the food demand for the burgeoning human population and play significant role in global food safety and security. Because of high N fertilizer practices, its heavy losses take place within the soil–plant systems (Maqsood et al. 2016). About 112.5 million tons of N fertilizers were used in 2015 and is expected to reach 118.7 million tons in 2020 to fulfill the N requirement (Table 1), while the global population is predicted as 7.9–10.5 billion till 2050 (Sharma and Bali 2018). A large proportion (~60%) of the total N fertilizer is being utilized for cereals production, worldwide (Pires et al. 2015) with wheat receiving the highest 18.1% N, followed by maize (16.8%), rice (15.4%), and other cereals accounting for 4.8% (Reddy and Ulaganathan 2015). However, only 30–50% of applied N is utilized by crops, thus resulting in significant losses to the environment. Finally, the lost N sources pollute soil resources and harm off-site ecosystems (Marschner 2012; Maqsood et al. 2016).

Nitrogen naturally present in the atmosphere is continuously being transformed from organic to inorganic form and vice versa. Fertilizer production helps to build up the natural source of N. Elemental N (N_2) is very unreactive and hard to extract from the environment (Ghaly and Ramakrishnan 2015). All living organisms, except few N fixing algae, fungi, and bacteria, cannot use N_2 as a source of N and require fixed N in different forms for protein synthesis. Plants mainly acquire N from the rhizosphere as inorganic N (Sharma and Bali 2018; Xinget al. 2019). Atmospheric N, nitrous oxide, and nitrite are also found in soil, but the main fraction of soil N (> 98%) exists in organic form which plants are unable to use directly. These forms of N are not naturally accessible to plants unless converted to NH_{4+} or NO_{3-} via bacterial fixation or lightning fixation (Fowleret al. 2013).

Synthetic fertilizers, legumes, and manures are the most important N sources in soil–plant systems and small amounts of N are also received from the rain. While some N is sequestered in living organisms which serves as another natural source of N (Ghaly and Ramakrishnan 2015; Sharma and Bali 2018). Nevertheless, microbial utilization of inorganic N depletes its availability to plants.

Table 1 Total world demand for N, P, and K fertilizers (million tons)

Year	2015	2016	2017	2018	2019	2020
Nitrogen (N)	110.02	111.57	113.60	115.37	117.11	118.76
Phosphate (P_2O_5)	41.151	41.945	43.195	44.12	45.013	45.858
Potash (K_2O)	32.838	33.149	34.048	34.894	35.978	37.042
Total ($N+P_2O_5+K_2O$)	184.017	186.668	190.85	194.39	198.107	201.663

Nitrogen availability to plants is usually determined by the balance among various N transformation processes in soil, such as mineralization, nitrification, and denitrification. The NH_{4+} and NO_{3-} concentrations in soil range from micro-molar (µM) to hundreds of millimolar (mM) (Marschner 2012). The predominant N fertilizer applied to crop plants is urea. Naturally, soils exhibit less amounts of urea (~ 3 µM) much less than fertilized soils containing 70 µM levels (Reddy and Ulaganathan 2015). Another source of urea to plants is arginine degradation under the ureide catabolism and urea cycle (Winter et al. 2015). Plant roots acquire N through transpiration-dependent mass flow. Mass flow alone cannot meet the N demand of the roots and diffusion complement for N uptake. The NO_3/NH_4concentration gradients and their diffusion coefficients determine their diffusion. The low diffusion coefficient of NH_4 results in low leaching and less availability for plant uptake (Marschner 2012; Olofsson et al. 2019).

N use efficiency (NUE)

The current agriculture practices focus on maximum production from the less land and inputs nutrients, especially N. This also concerns N fertilizer use efficiency. Pires et al. (2015) have suggested various management strategies to enhance the NUE of crops, perhaps minimizing fertilizer demands and greenhouse gas emission associated with N fertilization. The N fertilizers use is recommended at the optimal concentration according to the crop and soil type to reduce the excessive applications. Applied N fertilizers are lost through leaching, ammonification, volatilization, and denitrification, hence, result in low NUE 30–50% (Marschner 2012). On another hand, the recovery of N fertilizer (NRE) directly depends upon weather conditions (Ghaly and Ramakrishnan 2015; Herrera et al. 2016). Globally, NUE ranges from 35–65% for cereals, but it could reach 50–80% under best nutrient management at lower N doses (Chuan et al. 2016). Barley has the highest N recovery efficiency, while rice has the lowest ones at global scale (Herrer et al. 2016). The N recovery also depends on the harmony between plant need for N and the amount of N released from applied N fertilizer. With the increase in N input, annual direct fertilizer NRE decreased (Yan et al. 2014). This represents an incredible waste of resources and the overuse has detrimental environmental and economic consequences (Xu et al. 2012; Hawkesford 2014). High recovery efficiency of N results in higher crop production and reduces potential N losses to the environment (Yan et al. 2014). As N is deficient on almost all the arable soils worldwide which necessitates devising precise N applications using plant-based approaches to fulfill the crop demands.

The concept of NUE may help to maintain and increase soil fertility. Improving the nutrient uptake efficiency of crops is a significant means of improving land-use efficiency. Hawkesford (2014) has reported that NUE could be enhanced by matching spatial and temporal N supply to meet crop need. However, precise N fertilizer recommendations during the highest crop demand, near the roots, and split applications could minimize N losses, and increase the economical yield and quality of the crops. Many researchers have contributed to enhancing the understanding of N utilization in crops designed to improve NUE, even considering optimal yield under N deficiency (Reddy and Ulaganathan 2015; Taulemesse et al. 2015).

Nitrogen utilization in plants

N localization

Nitrogen is a highly mobile element that constantly transforms from complex to simpler forms concomitantly with high temporal and spatial variation in soil N reserves. Plants must continuously sense and respond to these variations in soil by modification in the root system architecture system (Giehl et al. 2017; Jia et al. 2019; Jia and Wiren 2020). Under heterogeneous N conditions, plants respond by variation in root system architecture and release of root exudates or the expression of transporters. The exact mechanism of root signaling is not yet completely understood. However, nutrient-driven signaling for the development of specific root structures in *Arabidopsis thaliana* has been reported. The plant roots preferentially colonize in N-enriched patches by targeted lateral root development to maximize soil exploration and obtain N by rapid root expansion under deficient conditions (Jia et al. 2019; Jia and Wiron 2020). Primarily, root expansions are multidirectional and assumed as a hit-and-try mechanism. As root hairs or its segment grows towards N-rich area, then plant roots respond by signaling. Experimental evidence shows that NO_3^- itself acts as a potent signaling molecule to stimulate lateral root growth in NO_3^- rich soil (Mounieret al. 2014), while NH_4^+ induces lateral root branching; nevertheless, both inorganic forms of N alter plant root system. In *Arabidopsis*, localized NO_3^- alters lateral root growth by regulating meristematic activity in the lateral root tip via the NO_3^- transporters NRT1.1/NPF6.3 and NRT2.1 (Remans et al. 2006; Mounier et al. 2014). Auxin appears to play an active role, as its biosynthesis gene TAR2 is up-regulated under N deficiency (Ma et al. 2014). Nonetheless, root architectural responses are reported in response to phytohormone balance or fluxes under variable N supplies.

Recently, the role of phytohormones in root signaling has been hypothesized in response to N availability. Some evidence expounds on the cellular and molecular footing of root signaling, and the role of phytohormones and peptides transmitting local and systemic N signals in the *Arabidopsis*. Jia et al. (2019) found a brassinosteroid (BR) called BSK3, in conjunction with the brassinosteroid co-receptor BAK1, to modify root growth in *Arabidopsis thaliana* under low N. It was assumed that an N-dependent messaging affects BR signaling in roots by upregulating BSK3. Further, genome-wide association analysis revealed that BR signaling-dependent upregulation of gene BSK3 modulates root system architecture such as primary root length under altered N availability in *Arabidopsis thaliana*. This localized NO_3^- mobilized towards the shoot via the signaling of small peptides and cytokinin. It has been suggested that trans-zeatin transmits a long-distance signal of acquired systemic N, altering root growth in zones of low and high NO3- concentrations (Poitout et al. 2018). TCP20 expression is regulated by irregular NO3- supply to roots and contributes to lateral root growth (Guan et al. 2014).

Likely, optimized concentrations of NH_4^+ favor gravitropism, while surplus NH_4^+ causes gravitropism by modifying the root growth angle (Zou et al. 2013). On the other hand, root branches only develop when they are in direct contact with soil moisture via an adaptive response called 'hydropatterning', controlled by a branching master gene called ARF7, and under soil hydrated conditions, ARF7 becomes activated to promote root branching like ARF8 which is linked to low N availability (Gifford et al. 2008). Moreover, plants may exude root secretions to increase the bioavailability of nutrients in the soil.

Physiology of N acquisition and transport

N uptake

Efficient N acquisition is the primary step to improve its utilization efficiency in crop plants. N is found in two major forms (organic and inorganic) in arable lands. Plants acquire inorganic N as NO_3^- and/or NH_4^+, but roots also uptake amino acids (AAs) and other organic compounds, i.e., peptides and proteins (Tegeder and Rentsch 2010; Hawkesford 2014; Bloom 2015). Root system architecture and upregulation of NH_4^+ and NO_3^- transporters in response to N form and concentration may influence N acquisition by the roots (Nacry et al. 2013). The transport proteins of the plasma membrane of epidermal and cortical root cells also affect the uptake of NO_3^- and NH_4^+, while chloride channels (CLCs) mediate vacuolar storage (Tegeder and Masclaux-Daubresse 2018).

The NO_3^- is the primary form of N available for plants in arable soils. Its concentration usually varies from 1 to 20 mol m^{-3} depending on the level of applied N fertilizer (Andrews 2013). For NO_3^- uptake, higher plants have evolved a high-affinity transporter system (HATS) as well as a low-affinity transporter system (LATS) in their roots. At low concentrations (< 1 mM), plants acquire NO_3^- through a high-affinity transport system (Taulemesse et al. 2015). Conversely, at higher external concentrations NO_3^- is absorbed via a low-affinity transport system (Pii et al. 2015). Both transport systems co-exist in plants and act in synchrony to acquire NO_3^- from soil solution for its allocation to the whole plant (Fan et al. 2017). The NO_3^- is transported into root hair cells by symporter along with two protons which must be actively pumped out of the cell using ATP for an influx of NO_3^- ions (Fig. 1). Thus, the inhibitors of respiration or uncouplers of ATP synthesis in roots can inhibit NO^{3-} uptake. The NO_3^- uptake rate by a localized root segment is dependent primarily on the uptake kinetics of NO_3^- (Fig. 2), which determines its influx as a function of the outside NO_3^- concentration. Therefore, the net uptake of NO_3^- ions is mostly determined by factors affecting influx (Fan et al. 2017).

There are two gene families *NRT1* and *NRT2* encode proteins that regulate NO_3^- acquisition in plants (Orsel et al. 2002; Pii et al. 2015; Fan et al. 2017; Fig. 1). The NO_3^- transporters belonging to the *NRT1* family were lately renamed the Nitrate Transporter1/Peptide Transporter Family *(NPF)* in a low-affinity system. While high-affinity NO_3^- transporters encoded by the *NRT2* family, representing seven genes in A. *thaliana* (Orselet al. 2002; Nacryet al.2013; Leran et al. 2015; Fan et al. 2017; Table 2). Among them, NRT2.1 is the main contributor, unfolding up to 75%, of the total HATS activity (Li et al. 2007; Nacryet al.2013). The *NPF/NRT1* and *NRT2* families members mediate proton-coupled import, excluding the bi-directional *NPF7;3/NRT1;5* transporters, and *NPF2;7*/Nitrate Excretion Transporter1 *(NAXT1)*, which are involved in NO_3^- efflux. Other NO_3^- transporters function as either anion proton exchangers or anion channels and are found within the Chloride Channel *(CLC)* family (Tegeder and Masclaux-Daubresse 2018). In *Arabidopsis*, at least six NRT2 family members need NART2.1 to transport NO_3^-, but there are three members of the OsNRT2 family (OsNRT2.1, 2.2, and 2.3a) that require OsNAR2.1 for NO_3^- uptake in rice (Feng et al. 2011; Yan et al. 2011; Table 2). The NPF family also contains *NPF6;3/NRT1;1*, commonly known as Chlorate Resistance Protein 1 *(CHL1)*; one of the family members, *NPF4;6/NRT1;2*, generally functions under eminent NO_3^- availability, while others (*NRT2;1*, *NRT2;2*, *NRT2;4,* and *NRT2;5*) activate under NO_3^- deficit (Kiba et al. 2012; Lezhneva et al. 2014). Thus, the NFPs are also involved in the transport of a vast range of substrates comprising nitrite, peptides, amino acids, and plant hormones (Sugiura et al. 2007; Tegeder and Rentsch 2010; Kanno et al., 2012). The *NRT2;1* and *NRT2;2* along with the other two members from the *NRT2* family act as main contributors and acquire about 95% of the entire NO_3^- under a restricted supply of nitrogen (Lezhneva et al. 2014). Primarily expression and localization investigations

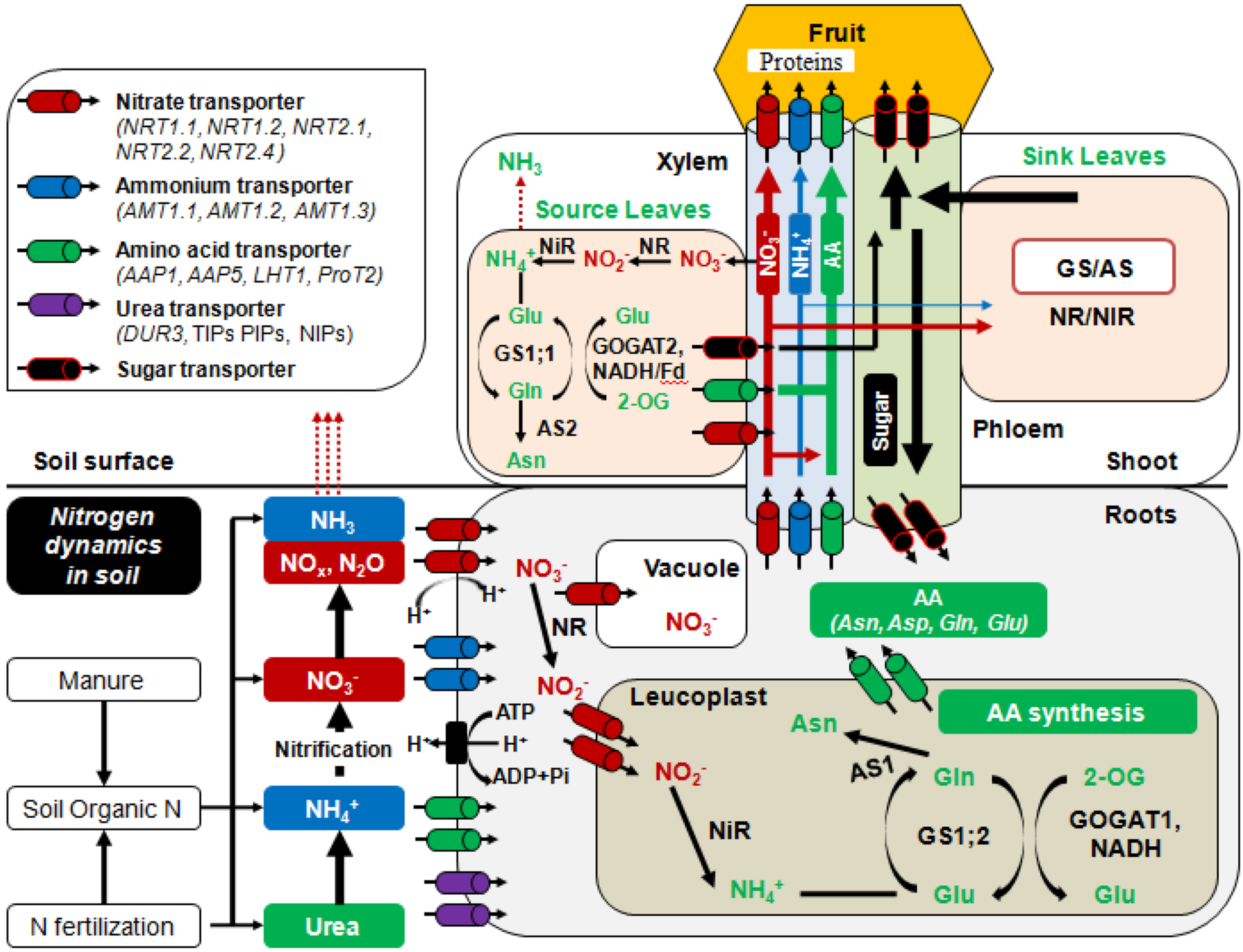


Fig. 1 Schematic representation of steps involved in N uptake and assimilation in plants. **a** N uptake from the rhizosphere mainly occurs in the form of inorganic N (NH_4^+ and NO_3^-), and small fraction in the form organic N (amino acids), **b** reduction of NO_3^- to NO_2^- by nitrate reductase (takes place in cytosol of root and leaf cells), **c** reduction of NO_2^- to NH_4^+ by nitrite reductase (takes place in plastids of root or leaf cells), **d** conversion of NH_4^+ to AA by GS and regeneration of glutamine by GOGAT for synthesis of other AA from glutamine and glutamate in root and leaf cells, **e** translocation of assimilated AA to shoot, and **f** remobilization of assimilated N and translocation of NH_4^+ and NO_3^- to some extent toward grains. *NR*, nitrate reductase; *NiR*, nitrite reductase; *AA*, amino acids; *GS*, glutamine synthetase; *GOGAT*, glutamine-2-oxoglutarate aminotransferase; *GDH*, glutamate dehydrogenase; *AS*, asparagine synthetase; *Asn*, asparagines; *Asp*, aspartate; *Gln*, glutamine; *Glu*, glutamate

revealed that the *NRT2;4* and *NRT2;5* are directly involved in the uptake of soil NO_3^- by the epidermis and cortical cells, mainly in the root hair zone; however, *NRT2;1* and *NRT2;2* mediate apoplastic import of NO_3^- into cortical and endodermal cells as well (Kiba et al. 2012; Lezhneva et al. 2014). The characterization of NO_3^- transporters function has also been done in maize, rice, and tomato (Fu et al. 2015; Fan et al. 2017).

Ammonium (NH_4^+), uptake is regulated by high-affinity transporters of the ATM family (Fig. 1) that is an important component of a bigger group of NH_4^+ permeases of the Ammonium Transporter/Methyl Ammonium Permease/Rhsus (AMT/MEP/RH) superfamily (Sonoda et al. 2003; Kiba and Karpp 2016). High external or increased cytosolic NH_4^+ concentrations decrease its root influx (Yuan et al. 2007). Thus, the Ammonium Transporters (AMTs) characterized by saturable high-affinity transport and non-saturable low-affinity uptake systems comprising of aquaporins or cation channels regulate NH_4^+ transportation and cell homeostasis. The two well-reputed gene families AMT1 and AMT2 encode presumptive NH_4^+ transporter proteins in plants. Six AMT genes, encoding high-affinity NH_4^+ transporters identified in *Arabidopsis*, 10 in rice, 14 in poplar, and 3 in pine (Masclaux-Daubresse et al. 2010; Castro-Rodriguez et al. 2016). Among the identified genes in *Arabidopsis*, four genes encode ATMs that mediate the acquisition

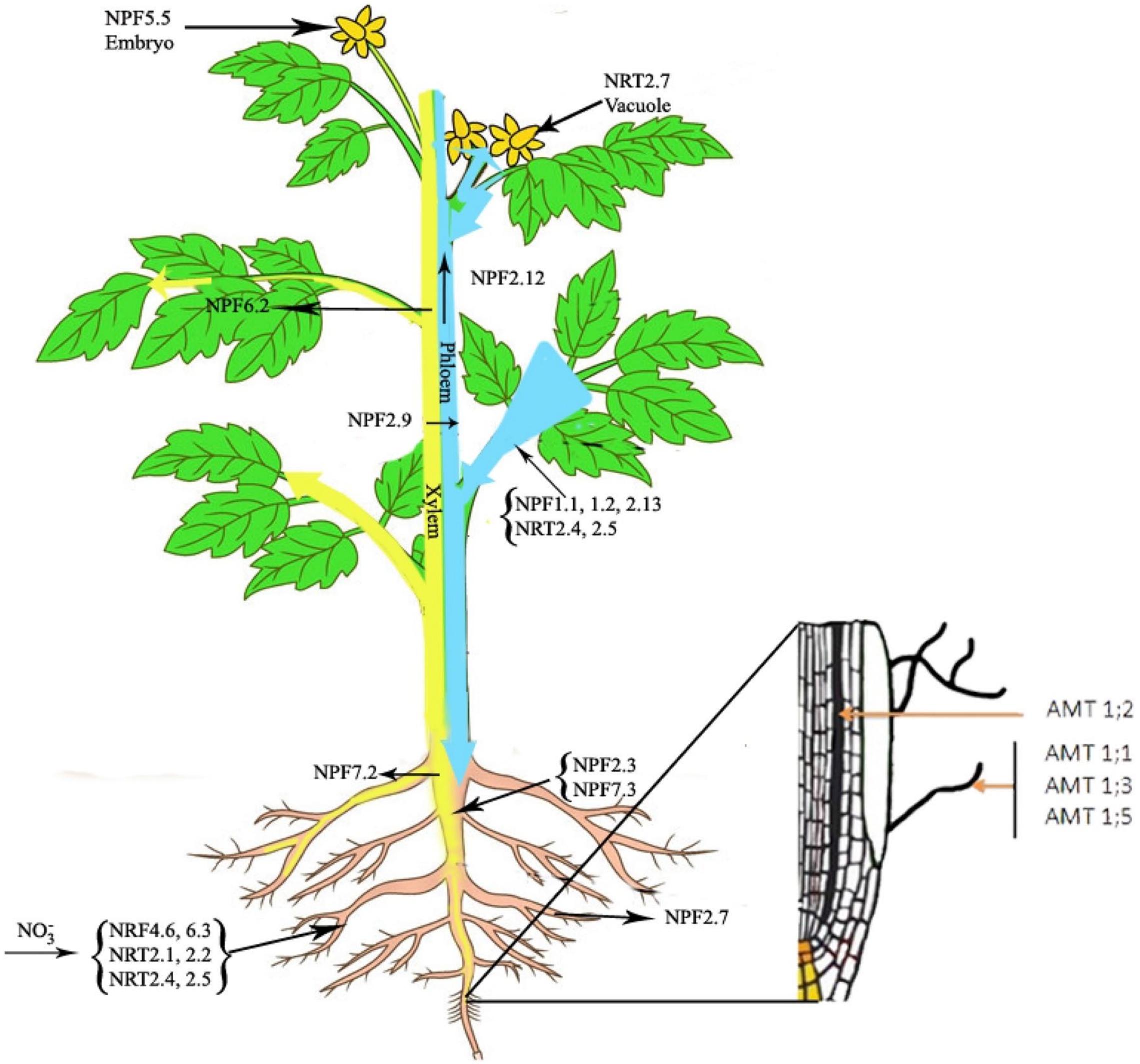


Fig. 2 Localization of NO_3^- transporters and their respective roles in NO_3^- acquisition by roots (NPF4.6, 6.3, NRT2.1, 2.2, 2.4, 2.5) from soil and in efflux (NPF2.7), loading (NPF2.3, 7.3), and unloading (NPF7.2) of NO_3^- from root to phloem via xylem (NPF2.9), from older leaves to phloem NO_3^- loading (NPF1.1, 1.2, 2.13, NRT2.4, 2.5) to younger leaves, translocation to seeds (NPF2.12), and within seeds to embryos (NPF5.5) and vacuoles (NRT2.7). NH_4^+ transporters (AMT1.1, AMT1.3, AMT1.5) localized in outer root cells including root hairs, for direct uptake from the soil solution and from the apoplastic absorption of NH_4^+ ions (AMT1.2)

of NH_4^+ by roots. Several studies exploring the function of AMT genes illustrated that each protein has a distinct function in NH_4^+ transport, AMT1.1 and AMT1.3 playing a similar role by exhibiting a capacity of 30–35%, whereas AMT1.2 contributed a much lower capacity of 18–25% to this process. These proteins cumulatively mediate about 95% of high-affinity uptake of NH_4^+ under N starvation, while the remaining capacity is achieved most probably by AMT1.5 transporter (Yuan et al. 2007; Masclaux-Daubresse et al. 2010). These studies further explore the complexity of spatial organization exhibited by AMT1 proteins (Fig. 2), indicating the cytological location of NH_4^+ transporters (AMT1.1, AMT1.3, and AMT1.5) in plasma membranes of outer root cells (epidermis) comprising root hairs, possess maximum NH_4^+ affinities function for direct uptake from the soil solution. While AMT1.2 with lower affinity located in endodermal cells mediates the apoplastic absorption of NH_4^+ ions or that is released from the cortex cells (Kiba and Krapp 2016). Likewise, ten putative OsAMT transporter genes identified in rice are categorized into four subgroups, ranging from OsAMT1 to OsAMT4. Until now, the three OsAMT1 genes, i.e., OsAMT1;1, OsAMT1;2, and OsAMT1;3, have been intensively investigated, and it was observed that OsAMT1;1, OsAMT1;2, and OsAMT1;3 were found to be predominantly expressed in the roots where it plays a critical function in NH_4^+ uptake (Sonoda et al. 2003; Li et al. 2016). Thus, under high concentration of NH_4^+, the expression of OsAMT1;1 and OsAMT1;2 genes

Table 2 Candidate NO_3^-transporter and regulation genes for crop application regarding NUE

Gene	Plant	Characteristics	References
NRT1.1	*Arabidopsis*	Regulating root growth by sensing outside NO_3^- levels, also increase shoot dry weight and its NO_3^- content	Mounier et al. (2014) Leran et al. (2015)
NRT1.5	*Arabidopsis*	Restraining of NO_3^- deprivation-induced senescence of leaf	Meng et al. (2016)
NPF7.3/NRT1.5	*Arabidopsis*	Limited NO_3^- directing K^+ translocation from root to shoot	Drechsler et al. (2015)
NPF2.3	*Arabidopsis*	NO_3^- excretion transporter and contribution to NO_3^- translocation to the shoot	Taochy et al. (2015)
NPF3.1	*Arabidopsis*	Stimulate pathogen-inducible NO_3^-/NO_2^- transporters encoding	Pike et al. (2014)
NPF5.5	*Arabidopsis*	Influencing N accumulation in *Arabidopsis* embryo	Leran et al. (2015)
NRT2.5	*Arabidopsis*	NO_3^- loading into N-starved plant's phloem	Lezhneva et al. (2014)
NRT2.7	*Arabidopsis*	Seed-specific NO_3^- transporter for accumulation/oxidation of proanthocyanidins	David et al. (2014)
NRT2.1	N. tabacum	Improve nitrate influx under low N conditions	Fraisier et al. (2000)
TaNRT2.1	Wheat	Induce NO_3^- uptake at post-flowering stage	Taulemesse et al. (2015)
LeNRT2.3	Tomato	Uptake of NO_3^- and its long-distance transport	Fu et al. (2015)
OsNRT1.1B	Rice	Improving NUE in indica rice	Hu et al. (2015)
OsNRT2.3a	Rice	Enhance NO_3^- transport from root-to-shoot	Tang et al. (2012)
OsNPF2.2	Rice	Unloading NO_3^- from the xylem and effects on root-to-shoot NO_3^- transport	Li et al. (2015a, b)
TaNAC2-5A	Wheat	Positive control of NO_3^- transporter expression and improving NO_3^- accumulation and plant growth	He et al. (2015)

is up-regulated, while OsAMT1;3 gene is expressed in response to low N availability which demonstrates its key role in adaption of rice to restricted NH_4^+ conditions (Ferreira et al. 2015). Based on above discussion, it is presumed that the ATM genes' systematic regulation patterns can be fairly complicated relying on plant genotypes and habitat.

Organic nitrogen is another important factor in soil to plant N nutrition; thus, the relative contribution of organic sources in soil to plant system is still need to fully understand. Although N-containing compounds, including peptides, amino acids, and proteins, are also acquired by plant roots, thus the investigations on root intake of organic N have primarily concentrated on AAs and urea (Nacry et al. 2013; Tegeder 2014). High-affinity urea transporter (DUR3) is reported in *Arabidopsis* plants which mediates uptake of urea from surrounding but may also involve in the transport of urea within a plant. Thus, the green ancestry including algae and higher plants possesses the orthologs of AtDUR3; generally, single-copy genes encode it. Expression of protein took place at the plasma membrane of epidermal cells of roots particularly in N-starving plant and urea is responded by the promoter in the lack of other N supply which confirms its function as a urea transporter (Nacry et al. 2013; Pinton et al. 2016). Hence aquaporins (TIPs PIPs and NIPs) facilitate the passive transport of urea. Until now, assumed plant AA transporters have been classified as members of five gene families. *Arabidopsis* contains about 100 putative amino acid transporters, members of the Amino Acid-Polyamine-Choline (APC) family, and the Usually Multiple Acids Move In and Out Transporter (UmamiT) family of transporters (Pratelli and Pilot 2014). Plasma membrane is active site of most of the AA transporters responsible for import of a variety of AAs at cellular level transported with protons. Amino acids' root uptake systems mainly depend on APC group, three transporters families, Lysine/Histidine-like Transporters (LHTs), Amino Acid Permeases (AAPs), and Proline and Glycine Betaine Transporters (ProTs) actively participate in uptake of AA. It is assumed that the AAPs are moderate-affinity systems having comprehensive substrate particularity. The AAP1 in *Arabidopsis* mediates the uptake of glutamate and neutral AAs (Perchlik et al. 2014), while the AAP5 is involved in root uptake of basic AAs such as L-lysine or L-arginine depending on the available concentration range. AAP1 protein also facilitates the transport of uncharged AA but only when their concentrations are high in the surrounding environment. LHTs are known as high-affinity transport systems. The LHT1 is key mediator for the root acquisition of acidic and neutral AAs (Nacry et al. 2013; Tegeder 2014), and also play an important role in transport of 1-aminocyclopropane-1-carboxylic acid which is ethylene precursor. Likewise, the LHT6 facilitates the import of acidic AAs, i.e., alanine and glutamine from the soil (Perchlik et al. 2014). In *Arabidopsis*, *ProT2* works to acquire organic osmolytes proline and glycine betaine, while expression of *ProT2* in roots of salt-stressed plants, indicating its role in enhanced acquisition of compatible solutes (mostly AA) under water scarcity (Lehmann et al. 2011).

Nitrogen transport

Plant xylem vessels mediate the transport of $NO^-{}_3$ and their assimilation, in addition to water and other nutrients from root to aerial parts. This root-to-shoot transport occurs by transpiration-derived hydrostatic pressure gradient developed in downward extending roots xylem (Tyree 2003). Endodermis, pericycle, or vascular parenchyma of roots exports N compounds into the apoplast probably through passive transport during xylem loading (Tegeder 2014). The N-containing compounds laden into the xylem are generally transported to photosynthetically active leaves along the long-distance pathway. However, N perhaps unloaded from the xylem and immediately moved to the phloem to prompt come up with fast-growing sinks (Van Bel 1984). Both the NPF7.2/NRT1.8 and AAP6 restrained to the xylem parenchyma down the transportation pathway and play a crucial role in the recovery of N from the xylem and in xylem-to-phloem trafficking, correspondingly (Li et al. 2010). The subtraction of NO^{-}_{3} from the xylem and its translocation into parenchyma cells are also mediated by a low-affinity transporter, and OsNPF2.2 has been reported in rice (Li et al. 2015a, b).

On other hand, scarce information available about the characterization of transporters facilitates the unloading of xylem N and import to mesophyll cells, although their role is anticipated to strongly impact N concentrations in leaf apoplast, which might influence the shoot synchronization of N acquired from soil (Hirner et al. 2006; Tegeder 2014). The transport of AAs also occurs within the xylem and AAP2 together with AAP6 plays a crucial role in AAs xylem-to-phloem transfer. However, the quantity of distinct AAs may vary relying on crop types and growing environment; often, aspartate, asparagine, glutamate, and glutamine are found abundantly (Lemaitre et al. 2008; Bloom 2015). Ureides are the principal N forms in the phloem and may contribute to > 90% of the xylem N in tropical legumes. During the N assimilation in leaves, the concentration of NO_3^- in the xylem may surpass other organic compounds (Tegeder and Masclaux-Daubresse 2018). Additionally, the xylem transports N along its transport path to create N storage pools in roots, stems, leaf veins, and pod walls, as well as facilitating a prompt supply of N to shoot tissues for various physio-biochemical functions. Transport proteins are most certainly responsible for the partitioning of this stored N in different plant parts.

The source-to-sink N allocation is influenced by its acquisition and metabolism in source tissues, the potential of source organs to export, and sinks to import N. It was observed in *Arabidopsis* and legumes that AA transports in shoot exert regulatory control for root N uptake, metabolism in sources, and partitioning to sinks (Zhang et al. 2015a, b; Perchlik and Tegeder 2017). Higher N accessibility in leaves improves photosynthesis, as well as accelerates phloem loading of carbon in engineered plants (Zhang et al. 2015a, b), illustrating the importance of N allocation for carbon assimilation and source-to-sink transport. Plant developmental stage significantly influenced the regulatory effect of N phloem loading on the C and N concentrations as reported in *aap8* plants of *Arabidopsis* (Santiago and Tegeder 2017). In the reproductive period, apart from the governing role in the uptake of N and its metabolism in the source, AAs transporters contribute to phloem loading intensely impacts the quantity of N allocated from source to sink subsequently influencing the vegetative sinks development and seed formation. For instance, reduced AAs' concentrations in the *aap8* phloem did not affect N concentrations in seeds, whereas the number of seeds was considerably reduced (Tan et al. 2010; Santiago and Tegeder 2017). Usually, seed-localized AAs and NO_3^- transporters regulate the amount of N being transported to the embryo and affect the storage protein accumulation by modulating the seed loading (Tan et al. 2010; Zhang et al. 2015a, b).

Mechanism of N assimilation

Nitrogen absorbed by plant roots can either undergo assimilation or transport to other plant parts via xylem/phloem or stored inside the vacuoles. Being toxic in nature, immediately after acquisition by the plant roots NH_4^+ is assimilated in organic form before transported to shoots. Contrary, NO_3^- and urea either assimilated in roots or translocated to shoot for assimilation. In both roots and shoots, NO_3^- reduction takes place; however, it is spatially dispersed amid the cytoplasm where this reduction occurs and plastids/chloroplasts which carried out nitrite reduction (Fig. 1). Hence, uncertainty persists regarding extend of NO_3^- assimilation by roots and its transport to shoots, but it might be due to different aspects explicitly crop species, growth stage, temperature, and light interception.

Nitrate assimilation

Acquired NO_3^- by plant roots should be reduced to NH_4^+ before assimilation. Therefore, NO_3^- is primary converted to NH_4^+ and AAs for transport within plant body. The initial reduction of NO_3^- to nitrite (NO_2^-) takes place in the cytoplasm in the presence of nitrate reductase (NR) (Fig. 1).

The primary conversion of NO_3^- to NH_4^+ and AAs within the plant body occurs at this level. In the presence of the nitrate reductase (NR) in the cytoplasm, the first step in converting NO_3^- to nitrite (NO_2^-) takes place in the cytoplasm.

After the NO_3^- reduction, NO_2^- is translocated to the plastid/chloroplast by Nitrite Transporter *NITR2;1* (Reddy and Ulaganathan 2015) where nitrite reductase (NiR) reduces it to NH_4^+. The NiR enzyme is encoded by *Nii* genes, cloned from different species; however, the gene copies differ from one to two copies. However, shoot or roots are the major sites of NO_3^- assimilation based on the genotype and soil NO_3^- concentration. The NADH located in the cytoplasm of root and shoot cells is used as a reductant during NO_3^- assimilation in most plant species (Masclaux-Daubresse et al. 2010; Krapp 2015).

Ammonium assimilation

The NH_4^+ originates from NO^-_3 reduction, and also from AAs recycling assimilated into AAs mainly in the plastid/chloroplast via glutamine synthetase (GS)/glutamate synthase (GOGAT) pathway (Suzuki and Knaff 2005; Krapp 2015; Fig. 1). The NH_4^+ is fixed on a glutamate molecule to generate glutamine. The ATP-driven transformation of glutamate and NH_3 to glutamine is catalyzed by the GS enzyme. The GS is comprised of two major isoforms, i.e., GS1 is present in the cytoplasm of phloem, root, and leaf cells, while GS2 is present in plastids/chloroplasts. During N assimilation in roots, a crucial role is played by cytosolic GS1 enzyme, exclusively under high NO_3^- concentration (Masclaux-Daubresse et al. 2010; Reddy and Ulaganathan 2015; Guan et al. 2016). The glutamine formed in the presence of GS combines with 2-oxoglutarate to produce two glutamate molecules. Enzyme glutamine 2-oxoglutarate aminotransferase (GOGAT) catalyzes the transition of glutamine and 2-oxoglutarate to glutamate in the presence of nicotinamide adenine dinucleotide (NADH) and ferredoxin (Fd). The Fd and NADH donate electrons to two dissimilar kinds of GOGAT (glutamate synthase) found in many plants (Vanoni et al. 2005). It is well documented that two disparate genes encode NADH-GOGAT in each of rice (Tamuraet al. 2011) and maize (Plett et al. 2016), have specific functions, and are expressed differentially. The GS1- and NADH-dependent GOGAT are found in leaf plastids and root companion cells of plants and take part in primary NH_4^+ assimilation in roots and leaves (Suzuki and Knaff 2005; Masclaux-Daubresse et al. 2010). The GS2 and Fd-GOGAT isoforms found in chloroplast vigorously take part in the re-assimilation of NH_3 produced in the leaves of C3 plants during photorespiration (Carvalhoet al. 2011). A recently reported new variant of PEP carboxylase enzyme located in chloroplast likewise plays an important function in the assimilation of NH_4^+ into AA in rice (Masumotoet al. 2010). Cytosol and chloroplasts are the main locations of de novo biosynthesis of many proteinogenic AAs, while membrane transporter proteins play vital role to transport through the plastids and move to phloem tissues. Only two chloroplast AAs transporters, the Petunia hybrida Cationic Amino Acid Transporter (PhpCAT) and the *Arabidopsis* glutamate/malate exchanger dicarboxylate transporter (DiT2), have been characterized which significantly mediate the efflux of aromatic AAs (Widhalm et al. 2015).

Three other enzymes, i.e., Carbamoyl phosphate synthase (CPSase), cytosolic asparagine synthetase (AS), and mitochondrial NADH-glutamate dehydrogenase (GDH), perhaps also play a role in NH_4^+ assimilation besides GS/GOGAT pathway. However, Masclaux-Daurese et al. (2006) reported that AS can also utilize NH_3^+ as a substrate. The AS catalyzes the glutamate and asparagine production mediated by ATP-dependent amido group transfer from glutamine to aspartate molecule (Xu et al. 2018). CPSase reacts with bicarbonate and NH_4^+ or the amide group of glutamine to produce a precursor of citrulline and arginine called carbamoyl phosphate. This reaction occurs within plastids which require energy from ATP molecules (Masclaux-Daurese et al. 2010). Finally, the GDH can, on the other hand, integrate NH_4^+ into glutamate under excessive NH_4^+ stress. Thus, the GDH major catalytic activity reported in plant cells is to mediate glutamate deamination (Masclaux-Daurese et al. 2006; Xiaochuang et al. 2020).

Urea assimilation

Urea assimilation takes place both in roots and shoots; nevertheless, the possible mechanism behind the assimilation is still unclear. Urea assimilation to NH_3 is catalyzed by urease enzyme, and this NH_3 is further assimilated by GS/GOGAT pathway enzymes to synthesize AAs (Fig. 1). Being a nickel-metallo enzyme, urease requires three additional proteins, UreD, UreF, and UreG, to be activated (Winter et al. 2015; Myrach et al. 2017). Among the sources of urea in plants are urea transported by DUR3 and NIP proteins, arginine degradation in the urea cycle, and purine catabolic ureides. Urease hydrolyzes urea produced by urea cycle in mitochondria into NH4 + in the cytoplasm (Pinton et al. 2016).

N translocation and storage

N translocation

Plant vegetative tissues acquire N either direct from the soil or via the fixation of atmospheric N by symbiosis. The N translocated within the plant originates from soils, mainly absorbed as NO_3^-, NH_4^+, AA, and organic molecules. To understand the N translocation inside the plant, the exploration of the N dynamics in the soil is indispensable. In dryland, nitrate–N is the main source of N for growing crops, while in paddy fields, ammonium-N is the major form. Soil NO_3^- contents and the potential of roots determine the capability of the plant to acquire N, because plant roots can absorb NO_3^- via transporters (Xu et al. 2012). The absorption of NO_3^- by a distinct root section depends on NO_3^- uptake kinetics that regulates the NO_3^- incursion as a function of the NO_3^- concentration outside the plant. The NO_3^- transporters also mediate the NO_3^- translocation inside the whole plant (Fig. 2). In addition to NO_3^- uptake, the NRT1 transporters predominantly play a key role in the translocation of NO_3^- within the plant; even the NRT2 gene expression is also noticed in plants above-ground tissues (Allen et al. 2016). The NO_3^- loading into xylem vessels is the first and central step in root-to-shoot NO_3^- translocation. This process is facilitated by NRT1.5, a low-affinity NO_3^- transporter found in the plasma membrane and expressed in pericycle cells of the root, as reported in *Arabidopsis* (Wang et al. 2012). Moreover, NPF7.2/NRT1.8 and NPF2.9/NRT1.9 mediate the translocation of NO_3^- from root to shoot by bringing back xylem-NO_3^- into root cells (Li et al. 2010). The central cylinder in mature parts of roots showed the expression of NPF6.3/NRT1.1, a dual-affinity NO_3^- transceptor (Remans et al. 2006), and transport activity of an encoded protein in ^{15}N-nitrate translocation within plant confirms the involvement of NPF6.3/NRT1.1 in root-to-shoot translocation of NO_3^- ions (Leran et al. 2015). In the recent past, several efforts have been made to improve NO_3^- translocation in different plants. Allen et al. (2016) observed overexpression of ZmNRT1.1 and ZmNRT1.3 in transgenic maize plants mediated by a root-specific promoter, e.g., ZmRM2 and NAS2 under low and normal N in the field. Overexpression of these transporters was non-significant under low nitrogen conditions, whereas improved N translocation was observed under normal N levels. In another study under high NH_4^+ availability, the transcript levels of AMT2;1 were signified, and its promoter action reallocated ideally to the pericycle, which indicates the involvement of AMT2;1 in xylem loading for elevated root-to-shoot translocation of NH_4^+ (Giehl et al. 2017). Additionally, in a quadruple mutant (amt1;1 amt1;2 amt1;3 amt2;1), AMT2;1 co-expression accompanied by either AMT1;2 or AMT1;3 considerably increased translocation of ^{15}N to shoots, representing a synergetic effect by AMT1 and AMT2;1 transporter.

It is well known that plant roots and leaves act as major storage organs for inorganic N assimilation to AA and protein synthesis during vegetative growth. Before the onset of grain filling, the plant root system uptakes N directly from the rooting medium and then transports it to the vegetative tissues through the xylem (Orsel et al. 2002). During translocation, vegetative tissues begin to translocate the stored N toward the reproductive organs for grain filling (Xing et al. 2019). After uptake, NH_4^+ is mostly assimilated in the roots and mainly converted to AA, preferably translocated to shoots via the xylem in the form of glutamine. It is also evident from cereals, tomatoes, and tobacco that the preferential export of N compounds is glutamine. It is noted that glutamine synthetase and methionine sulfoximine primarily impact the rate of N translocation. Thus, the AA produced as a result of protein degradation might be transiently stored in the central vacuole of mesophyll cells before phloem loading (Masclaux-Daubresse et al. 2010). During the grain-filling period in cereals, the senescence of vegetative parts is crucial as it is closely associated with N translocation to developing grains. The senescence of vegetative organs results in a decrease in protein and chlorophyll content and consequently causes leaf yellowing. However, the N translocating from vegetative tissues regulates the N buildup in developing grains throughout the grain-filling period. It indicates the significance of this crucial process important for defining the economical yield, seed quality, and protein content in different crops (Canas et al. 2010: Hu et al. 2015; Tegeder and Masclaux-Daubresse 2018; Xing et al. 2019).

The vigorous root system plant develops in the early growth stage is a critical aspect for N uptake which is then translocated to the reproductive organ during the grain-filling stage. The development of the root system depends on the type of soil (Xu et al. 2012; Tian et al. 2016). The different soil types considerably induced changes in the morphological characteristics of roots that are linked with N acquisition and translocation (Pii et al. 2015). Diverse tillage practices could influence soil properties and root growth which leads to efficient N translocation to shoot. Xu et al. (2006) reported that N translocation from leaf and stem to grains was significantly improved under moderate water stress. Hence, the grain N reserve pool generally seems to be controlled by the N source as Bertheloot et al. (2011) reported that grain N accumulation and kinetics of rubisco content propose that N translocation from the vegetative organs during grain filling is primarily restricted by substrate availability in the source organs. In addition to optimizing N fertilizer, improving crop genetics is one of the important factors to achieve greater NUE and yield potential. Significant variations exist among various crop genotypes for NO_3^-absorption and storage ability (Chardon et al. 2010). Genetic variations in crops considerably influence N uptakes and NUE which are usually associated with N translocation from the stems over leaves (Xuet al. 2012). High biomass production is connected with a higher concentration of N translocated to grain resulting in better yield and improved NUE as reported by Pal et al. (2017) in direct-seeded RIL-367 rice. Similarly, N translocation efficiency and the amount of N translocated in winter wheat in the Yangtze River Basin of China improved with varietal development since 1950 (Tian et al. 2016). Two growth stages showed NUE-increasing potential, i.e., seedling to the pre-flowering stage by improving N uptake and post-flowering stage by increasing N translocation (Xing et al. 2019). Ureide transporters AAP and UPS1 in legume are located in the xylem parenchyma or transport phloem (Tegeder et al. 2014; Tegeder and Masclaux-Daubresse 2018), signifying their role in transient N storage beside the path, in addition to transporting xylem-derived or transiently deposited organic N into the transport phloem. Therefore, current high-yielding crop breeding programs may help to ameliorate the equilibrium between NO_3^-, NH_4^+, and AA uptake. The genetic differences in the activity of various transporters must be explored to improve N uptake and translocation using transporters.

N storage

Nitrogen acquired by plants from soil is utilized for various metabolic processes within the plant. Following absorption and assimilation of N, it is mainly transported to the rest of the plant parts as glutamine, glutamate, aspartate, and asparagine for subsequent usage and/or storage in different tissues (Okumoto and Pilot 2011). Primarily N is stored in leaves in the forms of nitrate ions, amino acids, and proteins. It is also reported that the amide group of asparagines is comprising nearly half of the stored N in some plants (Lehmann and Ratajczak 2008). Asparagine has a greater nitrogen-to-carbon ratio compared to glutamine which makes it a potential compound for long-range transport and subsequent storage, particularly in legume crops (Lam et al. 2003). Proline, arginine, and glutamine are also used as N storage sources, though the use of stored N differed among plant species. Nitrogen can also be stored in huge quantities in photosynthetic proteins, i.e., PEPc and Rubisco (Nunes-Nesi et al. 2010), indicating that a restricted N uptake, impaired assimilation, and storage can lead towards a lesser overall carbon fixation in plants.

Plants can store NO_3^- within their tissues, and this N storage can play a critical role during later growth and grain filling. Under high cytosolic concentration, NO_3^- is subjected to store in the vacuoles, and subsequently relinquished to the cytosol in low N conditions. Many times, higher NO_3^- contents are found in the vacuole than the cytosol in leaves and roots. About 58–99% of total leaf NO_3^- is usually stored in vacuoles (Tegeder and Masclaux-Daubresse 2018). Storage N in herbaceous plants is found to be more than 50% of leaf N (Xuet al. 2012), while winter oilseed rape (*Brassica napus* L.) showed an average of 43.8% of stored N in their leaves (Liu et al. 2018). Cellular NO_3^- pools are essential for both tissue expansion and N storage during vegetative growth (Fan et al. 2007). The N stored in plant acts as a buffer pool for sustainable leaf growth by facilitating the production of photosynthetic proteins in early growth stage. The concentration of stored N reduces gradually along with leaf expansion (Liu et al. 2018). Multiple physiological traits including the N storage and the N remobilization from senescent tissues can influence NUE in crops. The potential of a plant to remobilize stored N during grain filling is one of the key factors for NUE in cereals. The efficient remobilization facilitates the plant to grow even under N-limited conditions. Expression of NO_3^- transporter NRT1.7 reported in phloem of minor veins of old leaves is liable for transporting excess NO_3^- accumulated in source leaves towards phloem and helps NO_3^- transport to sink leaves (Chen et al. 2020). In cells, NO_3^- stored in vacuoles regulates cellular transformations of inorganic N and thus regulates N utilization at cellular level. While NO_3^- stored in stems facilitate vegetative growth after remobilization. Therefore, an ability to accumulate sufficient NO_3^- in stem tissues may indicate lower concentrations in xylem vessels NO_3^- that may regulate N supply to leaves for improved NUE (Fan et al. 2007). Contrary to N translocation, a little knowledge is available on genotypic variations for N storage and its effect on NUE. Literature suggested that both genotypic and fertilizer-induced variations exist among plant species regarding the accumulation of protein and amino-N in storage organs (Tegeder and Masclaux-Daubresse 2018). Accumulation of protein in storage organs enhances with the application of N fertilizers, thereby increasing the rate of later shoot growth. Vegetative storage proteins, particularly allocated to N storage in vegetative tissues, also build up under stress environment when the plant slows down its growth (Lee et al. 2014). It is also assumed that the N rate and cultivar significantly influenced the N storage pool of a crop as Li et al. (2020) have noticed that the N addition has a major impact on N storage in maize, where the total N pool enhanced with a rise in N application. It is also assumed that the N-efficient maize cultivar had greater N acquisition and storage potential compared to the N-inefficient maize cultivar, particularly at the middle and late growth stages.

NUE indices

The NUE is an intricate attribute that depends on soil ability to supply N and the N acquisition capacity of plant, root–shoot transportation, and remobilization. Various concepts of NUE have been illustrated depending on targeted produce, i.e., biomass or grain yield etc. Thus, the ability of a system to convert inputs N (total N, soil N, or N fertilizer applied) into outputs (total plant N, grain N, biomass yield, or grain yield). Thus, the NUE of a cultivar is broadly dissected into uptake efficiency and utilization efficiency. N-uptake efficiency (NUpE) is the ability of a plant to absorb/recover N from the soil, while N-utilization efficiency (NUtE) refers to the capacity of a plant to assimilate and remobilize N to ultimately produce biomass and/or grain yield (Moll et al. 1982). However, some other common NUE terms include agronomic efficiency, physiological efficiency, apparent recovery efficiency, and harvest index are summarized in Table 3. These definitions may include absolute yield and amount of N absorbed under N deficiency, N acquisition, and utilization efficiency, N stress factor, rate of N absorbed per unit of root length or root weight and relative shoot dry weight, etc.

Table 3 Nitrogen use efficiency and some important NUE-related indices

Indices	Abbreviation	Definition	Formula
Nitrogen use efficiency	NUE	Efficiency to uptake and utilize biologically reactive nitrogen from the growth medium	$NUE = NUpE \times NUtE$
N uptake efficiency	NUpE	The quantity of N absorbed by the plant relative to the available N in soil	$NUpE = PlantN(Nt)/Ns$
N utilization efficiency	NUtE	The efficiency of assimilation and remobilization of plant N to produce grain	$NUtE = Gw/Nt$
Agronomic efficiency	AE	The ratio of net increased grain yield to total amount N (soil + applied through fertilizer)	$AE = GY_f - GY_o/N_t$
Physiological efficiency	PE	The grain yield obtained per unit of N uptake. It indicates plant ability to transform acquired N into economical yield	$PE = (GY_f - GY_o)/(U_f - U_o)$
Apparent recovery efficiency	ARE	The ratio of the difference in N uptake by plants with or without N fertilization to the total amount of fertilizer N	$ARE = N_f - N_u/N_a$
N harvesting index	NHI	Percentage of the total N allocated to the grain	$NHI = GN/SN \times 100$

GY_f, grain yield of crop with nitrogen applied; GY_0, grain yield of crop with no nitrogen applied; U, nitrogen uptake in above-ground crop biomass with nitrogen applied; U_0, nitrogen uptake in above-ground crop biomass with no nitrogen applied; N_t, total nitrogen; N_s, nitrogen in soil; *GW*, grain weight; *GY*, grain yield; N_f, N, uptake by plants with N fertilization; N_u, N uptake by plants with N un-fertilization; N_a, nitrogen applied; *GN*, grain nitrogen; SN, shoot nitrogen

Strategies for NUE improvement

For sustainable agriculture, improving NUE is a crucial and great challenge worldwide to fulfill crop need by 100–110% up to 2050. Therefore, balanced use of natural resources including water and fertilizers for in crop production systems is critical for sustainable agriculture.

Soil and crop management

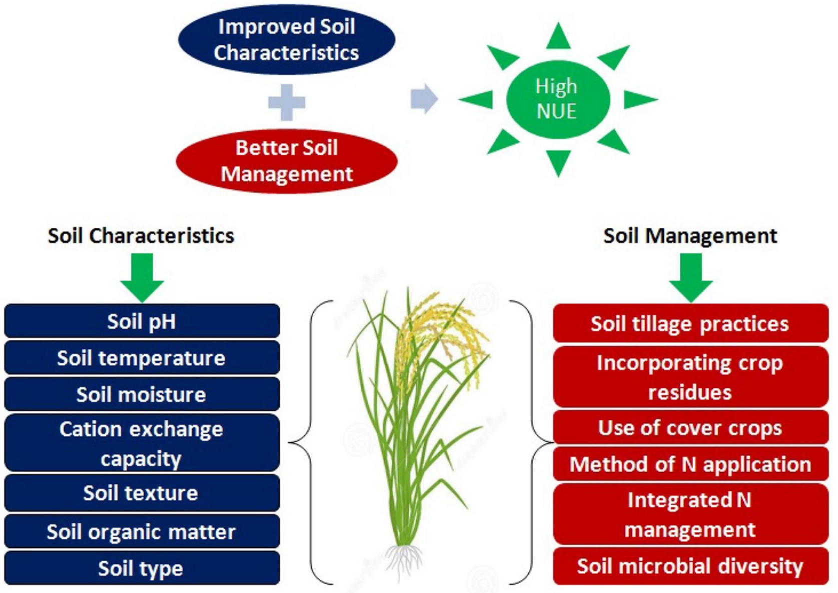
Soil characteristics and management

Improving N utilization is of vital importance worldwide as more than 50% of applied N in agriculture is liberated to the environment, causing serious threats to atmosphere, soil, water, and biodiversity. Globally, NUE for major crops seldom exceeds 40% and has been estimated 35–45% for wheat, 30–40% for rice, and 37% for maize (Cassman et al. 2002; Rimski-Korsakov et al. 2012). It is estimated that about 22–53% of applied N is lost to the environment as ammonia volatilization in arid and semi-arid regions due to alkaline soil pH and high temperature. Another main source of N losses from agro-ecosystem is denitrification. The NH^{4+}-fertilizers are rapidly nitrified under hot climate, while NO^{3-} is susceptible to denitrification under reduced conditions (Maqsood et al. 2016). Various soil characteristics play a crucial role in regulating N transformations and N losses and thus influence NUE (Fig. 3; Ye et al. 2007).

Ammonia (NH3) volatilization is affected by different soil characteristics like temperature, soil texture, soil pH, cation exchange capacity (CEC), moisture, organic matter, and management factors including tillage practices, incorporating crop residues and methods of N application (Maqsood et al. 2016). Soil pH usually determines the relative concentration of NH3, which increases with high pH as well as with the addition of N fertilizers. Similarly, the NH3 volatilization is accelerated with the increase in temperature (Ghaly and Ramakrishnan 2015). Conversely, high moisture contents can significantly reduce NH3 volatilization. In addition, soil with high CEC can have less NH3 volatilization and vice versa (Maqsood et al. 2016). Nitrification occurs in well-aerated soils with an optimum pH range of 6.7–8.5. However, when soil pH goes below the critical value, it inhibits plant growth and reduces NUE. Thus, N accumulation and NUE reach maximum at pH 5.0 in the sandy Ultisol and then change slightly with a further increase in pH of soil (Pan et al. 2020). The addition of K, Ca, and Mg salts may reduce the rate of N release from urea. Hence, soil acidification can reduce NH3 volatilization by lowering pH and inhibiting urease activity, regardless of N rates or sources (Potter et al. 2001). Acidifying N fertilizers causes lower risks and recent studies have demonstrated that these N sources can often produce superior yields on alkaline soils (Nie et al. 2018). Thus, the soil varied conditions may also affect the NUE of crops. In rice, physiological use efficiency and N harvest index may be higher in sandy texture than in clay, emphasizing that the N supply ability of clay was higher than that of sandy soil (Ye et al. 2007).

Improved soil structure can be achieved by appropriate cultivation techniques. Soil organic matter (SOM) is generally predicted as a vital feature for soil quality and hence can improve several soil characteristics to influence crop performance. SOM can contribute in a variety of ways to improving some of the factors influencing soil biological, physical, and chemical properties (Oelofse et al. 2015). Increasing organic matter levels improves soil structure and pH which

Fig. 3 Key soil characteristics and soil management factors influencing NUE in cereals



NUE (%) in cereal crops	
Wheat	35-45 %
Rice	30-40 %
Maize	32-37 %

enhance activities of N mineralizing and N_2 fixing bacteria in the soil. In the nutshell, sufficient amount of organic matter content in soil is crucial to ascertain soil quality, and ensure crop yield sustainability and to minimize N losses to environment (Fageria 2012). Similar characteristics also improved by SOM in black soils may contribute to better NUE (Zha et al. 2014). The organic mixed farming system is characterized by a relatively high N input and N output, accumulation of soil organic N, highest NUE, and lowest N surplus. While shifting from organic arable farming to organic agroforestry can reduce N input, increase biomass yield, and result in the N surplus within an optimal range (Lin et al. 2016).

Soil management factors, including soil tillage practices (Laine et al. 2018), incorporating crop residues (Chen et al. 2017), use of cover crops (Schipanski et al. 2014), N application methods (Jiang et al. 2018), integrated N management (Zha et al. 2014), and sustaining soil microbial diversity (Niena 2019), are the key factors influencing N dynamics in cropping systems (Fig. 3). The tillage practices can promote mineralization by exposing naturally protected SOM to microbial community improving N mineralization in soil. Under no-till (NT) system, gross N mineralization is higher which is indicative of increased soil N supply than the conventional tillage system in barely (Laine et al. 2018). The average rate of change of NO_3^- content in soil cannot be affected by the tillage system but is only influenced by fertilization. However, combined NT and retained residues could help to decrease the negative impact of NT over N losses in rice field due to the higher microbial activities, and soil characteristics (Huang et al. 2012). Studies also revealed that wheat and maize crop residue improve soil organic N when crop residue was incorporated continuously for 6 years. However, organic soil N along with corn residues in combination treatments plus fertilizer application was found significantly higher than in wheat straw plus fertilizer combinations (Chen et al. 2017). In certain farming systems, during fellow periods, catch crops are sown instead of main crop as a key management strategy to decrease NO_3^- leaching and N_2O emission (Schipanski et al. 2014). In a 2-year field trial, the effect of two catch crops (rye and ryegrass) on yield, NO_3^- leaching, and N_2O emissions were investigated in a maize cropping system. It was observed that the catch crop was significantly decreased NO_3^- leaching, and N_2O emissions without compromising yield (Komainda et al. 2018) inferring that a suitable catch croop may reduce N losses and protect environment.

In typical lime concretion black soil, Jiang et al. (2018) compared N application methods, i.e., single root-zone fertilizer application (RZF) and split surface broadcasting (SSB) in maize crop. Rootzone fertilization of urea has a 7.0% higher yield compared to SSB using recommended dose (N @180 kg ha^{-1}). Thus, RZF was significantly enhanced the fertilizer derived N and ^{15}N uptake in maize plants by 28.5% and 28.7%, respectively, while considerably declined the N losses by 30%. In a long-term experiment compared to the values in 1990, farmyard manure plus inorganic N fertilizer application significantly enhanced total N concentration by 10–21% in 2008 (Zha et al. 2014), which indicates that high soil N play a crucial role in improving soil productivity of maize crop in black soils. In addition, the alkaline black soil is characterized by fine texture, poor physical properties, and low fertility status. Therefore, such soil exhibits lower NUE of wheat compared to Chao soil, and poor N retention, but showed a higher release of urea than that in fluvo-aquic soil (Cao et al. 2016). Application of *Trichoderma* sp. with N fertilization enhances the colonize seedling roots and establishment of the wheat plant and improved NUE under varied N doses in alluvial, red, and black soils. Maximum N uptake, and agronomic and physiological NUE were significantly higher with alluvial soil as compared to black and red soils (Meena et al. 2016). The improved NUE might be due to the integrated effect of *T. harzianum* and N fertilizer to enhance N availability and uptake, and thus promote plant growth.

Conservation agriculture

Conservation agriculture (CA) involves three major principles, including reduced soil tillage, protection of soil through organic residues, and diversification in crop rotation. Resource conserving practices conserve resources and ensure their optimal use and increase resource use efficiency. Such practices have the potential to increases utilization efficiency of N and other nutrients. The CA amend soil's physical, chemical, and biological quality components in comparison with conventional practices involving tillage and thus impacts N cycling in the soil (Karki and Shrestha 2015; Acharya 2018). Long-term adoption of CA practices improves soil health and can enhance the soil potential to supply nutrients to plants by harmonizing N mineralization from the decomposition of crop residue and applied N fertilizer to enhance NUE.

In a conservation cropping system, mulching alters the soil temperature and modifies the micro-environment for optimal plant growth. It favors mineralization of soil organic N and its availability to plants by increasing soil water content due to reduced evaporation. Cover crops provide mulching to the soil permanently and may contribute to increased total biomass production (Jat et al. 2011; Acharya 2018). They further contribute via N fixation in the case of legumes, mulch mineralization, or animal manure returns. Thus, crop residue retention as mulching can prolong N availability, better synchronized with crop demand, and thus reduce the losses and increase NUE (Singh et al. 2018). Dendooven et al. (2012) observed that retaining crop residue can significantly decrease the NH_4^+ concentration in zero tillage than conventional tillage. This decrease might be due to plant uptake, denitrification, microbial N immobilization, and NO_3^- leaching. Legumes residue is an effective source of N and can mineralize at a faster rate even half of the amount of N can be available to the plants within 2 months after incorporation (Singh et al. 2018). Residue retention and cover cropping also improve soil organic matter, ultimately enhance NUE. Carvalho and Lourenço (2014) revealed that enhancing soil organic matter from 1 to 2% will improve NUE from 19.1 to 36.6 kg of wheat per kg of applied N. In addition, the adoption of suitable crop sequences is critical for enhancing N recovery in crops. However, inconsistent results for NUE were reported for crop rotation in CA systems, crop monoculture had negative impacts on yield and NUE, and therefore, legumes should be included in the rotation to improve soil health and crop yield. Lynch et al. (2016) inferred that the lower C:N ratios of legume-based crop residues may improve the physico-chemical and biological properties of soil by improving total carbon contents and higher N supply and improved NUE.

N application methods

Conventional method

The rate, time, and method of N fertilizer application are strongly related to the growth, development, and yield of the crop. In the developing world, the broadcasting method is usually practiced before planting and/or mid-season to the soil surface without incorporation. Broadcasting of N fertilizers results in low recovery and huge N losses via surface runoff, volatilization, denitrification, and leaching from the soil–plant system (Yadav et al. 2017). Urea is the most common source of N and, if not incorporated in the soil, can lead to N losses through ammonia volatilization, lower crop yields, and NUE. Thus, using modified N fertilizers (urea super-granules, USG) and considering the N application methods, maximum recovery of applied N fertilizer can be achieved by deep placement and foliar spray, because N is vulnerable to various soil transformations, thus can influence NUE. Therefore, N fertilizer must be applied in such ways that maintain high N availability to plants. Fertilization of N below the soil surface could be more effective. Deep placement of urea-based fertilizers results in higher NUE. It has been demonstrated from large-scale rice experiments that recovery efficiency for SSB was not more than 37%, while it was found at about 49% for deep placement of USG (Balasubramanian et al. 2002). The impact of N application and planting methods on maize grain yield was studied using the conventional methods and Oklahoma State University engineered hand seed planter (OSU-HP). It was established that OSU-HP ultimately increased yield and reduce N losses by placing N below the soil surface in root zone closer to the growing plants (Oyebiyi et al. 2019). In comparison to traditional broadcast, greater increases in grain yield per kg of N fertilizer and improved NUE were found for fertilizer applied in rows, with or without top dressing (Szulcet al. 2016). Side dressing of fertilizer is among the easiest method to improve NUE. Nitrogen fertilizers are best to be placed at 3–5 cm below the seed and about 5–10 cm away from roots in case of side dressing but not more than 20 cm. However, Yong et al. (2018) showed that under low N treatments with topdressing, performed better at a distance of 15 cm and 30 cm than 45 cm in a maize–soybean intercropping. Suitable fertilizer placements may further aggravate root growth; increase the potential to uptake soil N, and improve N fixation and NUE without compromising yield.

Foliar application of N could enhance NUE as it decreases various N losses (such as volatilization, denitrification, immobilization, and runoff) before being absorbed by the plant (Yadav et al. 2017). Foliar applied N in wheat produces higher NUE and net economic return in comparison with soil-applied method (Khatak et al. 2017). The increased NUE might be due to the readily availability of foliar-applied N to crop through leaf stomata than the soil-applied method. In general, balanced N management practices need to be established and followed to improve NUE leading to desirable grain yield. More studies may be carried out to find out the better utilization of foliar N in different field crops.

Site-Specific N management (SSNM)

Crop yield is a complex outcome of several factors like soil, climate, and the environment (Xu et al. 2012). Soil characteristics are perhaps one of the major factors responsible for better agricultural production. However, these traits are highly variable not only in different types of soil but also within the same field. Several physicals, biological, and chemical processes taking place in the soil make it very different and variable from one place to another (Tripathi et al. 2015). In such varying soil conditions, the application of a fixed quantity of fertilizer in the field is not an efficient way, because it may cause a shortage in some areas while present in excess in other places (Sharma and Bali 2018).

Under such a scenario, site-specific N application is favorable for farmer's economy and environmental protection. In Australia, it has been investigated that about 50 kg N ha^{-1} excessive application to cotton, while about 15–25% of the applied fertilizer can be decreased without compromising yield (Rochester 2011). Under such conditions, site-specific N management (SSNM) predetermines appropriate N level in terms of space and time within individual fields to increase NUE and diminish adverse environmental effects (Papadopoulos 2015). SSNM analyzes the amount of N and its application time, before sowing, based on N supplying capacity of the soil, expected N requirement of the crop to achieve require yield, and estimate N efficiency of applied fertilizer (Yadav et al. 2017). Moreover, SSNM also focuses on the N status of standing crops by applying spatial analysis using geographical information systems (GIS), a key factor in improving agriculture production, particularly concerning soil fertilizer application (Papadopoulos 2015). The SSNM is used to decrease N fertilizer application without yield reduction yet a significant in grain yield and its qualitative attributes in different crops (Papadopoulos 2015; Liu et al. 2017; Shankar et al. 2020). SSNM significantly reduced the average N rate by 33.8%, increased N uptake after the heading period by 11.8–55.1%, and improved average yield by 9.8% in rice (Xian-long et al. 2007). Likewise in cotton, 30–40% less total N use was recorded with high NUE under SSNM (Shankar et al. 2020). Liu et al. (2017) revealed that N recovery efficiency with SSN fertilizer was greater than farmer field practice, regardless of annual variations in N fertilizer recommendations, also increased seeds yield by 11.9% in rapeseed. However, a lack of knowledge about spatial variability in the soil available N or soil N supply during different growing seasons reduces the success of SSNM.

Integrated N management (INM)

A most viable option to revamp the cropping system is the use of management tools (intercropping, crop rotations, and perennial crops) and optimal use of native N components (organic manure, crops residues, biological N fixation, synthetic fertilizer, and their corresponding interactions to enhance N recovery) which are the principal components of INM (Yadav et al. 2017). Integrated management revealed that NUE can be improved by reducing N rates, increasing planting densities and tillage depths, better irrigation management, and consolidated use of mineral and organic N sources (Liu et al. 2017). Such measures are related to adjusting the physical, chemical, and biological properties of crop rhizosphere soil or due to improved growth of roots and increased availability of other essential nutrients. Similarly, adequate available P is required to enhance the NUE; it is obvious that balanced availability of all needed nutrients is crucial (Reis et al. 2016). Therefore, balanced and judicious use of N and P from all available means will lead to higher productivity. These positive interactions among the plant nutrients play a significant role to give maximum returns to the farmers in terms of soil quality, yield, and NUE of applied N (Singh et al. 2018). Hence, this complimentary effect as a result of judicious N fertilization led to high crop productivity and net income (Table 4). The N nutrition status of crop can also be assessed by remote-sensing approach using visible-light reflection of canopy and through satellite hyperspectral photographs to study temporal and spatial variations of N concentration in leaves (Tripathi et al. 2015; Sharma and Bali 2018).

Table 4 Improved performance of integrated nitrogen management compared to farmers' practice for different crops in China from 2003 to 2010 (Zhang et al. 2012)

Crops	On-farm trials	Δ Yield (%)	Δ *N* rate (%)	Δ Net income (\$ ha^{-1})
Wheat	558	10	29	92
Maize	2100	16	25	111
Rice	1861	8	21	99
Cotton	310	6	39	397
Vegetable	57	13	28	775
Fruit	239	12	8	196
Rape	22	7	36	164
Average	5147	12	24	132

n, number of on-farm demonstration trials; Δ*Yield*, increased yield; Δ*N rate*, decreased N fertilizer rate; Δ *Net income*, increased net income between INM and farmer's practice

N fertilizer modification

The N is a major element responsible for plant growth and development. Being highly mobile, this nutrient tends to leach down or vaporize to the atmosphere reducing the efficiency of fertilizer (Maqsood et al. 2016; Reis et al. 2016; Sharma and Bali 2018). Moreover, the interaction of environmental factors with plants also has a great influence over N uptake and use efficiency. NUE can be boosted via management practices; however, these are crop-specific. Modification of fertilizer physically or chemically is perhaps one of the best general-purpose strategies for boosting NUE. The different strategies are discussed below.

Slow-release fertilizers

Slow-release fertilizers have modified nutrient transformation mechanisms for their reduced loss. Slow-release fertilizers control different N losses thus, influencing its availability and recovery. These fertilizers slowly release the nutrient in the soil which is usually achieved either via coating or chemical formulations. NO_3^- containing fertilizers are susceptible to leaching while NH_4^+ fertilizers to volatilization. A variety of controlled fertilizers are now available which can decrease N losses and improve NUE (Pires et al. 2015). The use of polymer-coated fertilizer is becoming very popular due to its durability and predictability in releasing nutrients under average temperature and moisture conditions. The sulfur coating has been used to slow-release urea; however, sulfur and polymer-coated fertilizers are less common due to their unpredictable behavior. In recent years, a mixture of polymers is used which makes a semi-permeable layer around fertilizer. This also boosts yields and fertilizer use efficiency using such coated fertilizers in crop plants (Mehmood et al. 2019). Although, the release of urea from such coating is predictable; however, it depends upon several factors like the chemistry of polymers used, the thickness of the coating, soil moisture, and temperature. Several slow-release fertilizers have urea-aldehyde additive which delays N release in the soil via slow decomposition.

Urea-based fertilizers are widely used for crop production due to their high N percentage but are subjected to ammonia volatilization when applied to the soil surface (Maqsood et al. 2016; Sharma and Bali 2018). Nitrosomonas bacteria present in the soil oxidize the ammonia present in urea into nitrite (NO_2^{-1}) then NO_3^-. Additives are used to reduce the N volatilization thus minimizing fertilizer losses (Killorn et al. 2011). Nitrification inhibitors control the transformation of NH_4-N into NO_3-N and ensure the highest concentration of ammonical-N in the soil medium, to improve NUE and crop yield (Singh et al. 2018). Nitrification inhibitors regulate the activities of Nitrosomonas bacteria in the soil for a certain period. Nitrapyrin is one of the most widely used nitrification inhibitors to improve N recovery and higher yield using nitrapyrin, Dicyandiamide, and 3,4-dimethyl pyrazole phosphate has been used in winter wheat, corn, rice, grain, sorghum, sugar beet, and cotton (Jat et al. 2011). In conclusion, modified fertilizer as controlled release enhances NUE, the yield of crops, and minimizes environmental pollution due to high efficiency of N fertilizers.

Urease inhibitors

Urea being the most extensively applied N fertilizer, undergoes hydrolysis via the urease enzyme, increases pH of soil around the granules, and results in NH_3 volatilization losses of about 16% of applied N worldwide (Cantarella et al. 2018). Improved inorganic fertilizers' efficiency is achieved using N inhibitors which play a crucial role to enhance productivity and reduce environmental damage (Maqsood et al. 2016; Singh et al. 2018). Several compounds have been applied as urease inhibitors, but only *N*-(*n*-butyl) thiophosphoric triamide (NBPT) is used worldwide. In comparison to urea, NBPT-treated urea reduced the damage to seed germination and increased root growth including reduced NH_3

loss by 53% and enhanced grain yield from 0.8 to 10.2% depending on crop species (Cantarella et al. 2018).

Azadirachta indica's (Neem) extract has been used as a urease inhibitor in India. Neem is considered to have great potential as a nitrification inhibitor, and all urea manufactured and applied in India since 2015 is essentially coated with neem-based products (Kashiri et al. 2017). Moreover, compounds cable to inhibit ureases activity has long-term benefits in soils. Boric acid is another compound that can decrease urea hydrolysis in soil (Benini et al. 2014) and dicyandiamide (DCD) is also used as nitrification inhibitor easily degraded in the soil, influence plant growth. Numerous investigations have demonstrated that DCD significantly decreased leaching losses and N_2O emissions from field crops and pasture systems (Cuiet al. 2011). Therefore, urease inhibitors significantly decrease volatilization losses, but their complete elimination could not be achieved. Therefore, there is a good scope to further improve current inhibitors strategies to develop novel molecules to improve coating formulations, and their integration with production technologies to decrease N losses and improve NUE of field crops and pasture systems.

Plant modification

NUE is a complex trait that resulting from multiple genetic and environmental interactions. The transgenic efforts have focused on different targets including genes related to N uptake, metabolism, and assimilation. However, regulatory elements and signaling targets have recently materialized as potential candidates for biotechnological intercession. For improving NUE, investigators have utilized different promoters (chiefly CaMV 35S) to change the expression of numerous candidate genes regarding N utilization. During the past decade, several transgenic approaches have been carried out involving overexpressing or knockout mutations in candidate genes to enhance NUE (Table 5).

Root architecture and NUE

The root system of many species mainly relies on the N availability and internal status of N within plant body. Root exploration primarily describes the capability of plants to extract N from growing medium. Therefore, genetic variability and the complicated regulatory mechanisms of plant's root system are of immense significance for enhancing crop NUE (Li et al. 2015a, b). Several studies have reported a positive correlation between QTLs for N uptake and root traits. Numerous QTLs for root system architecture about N starvation have been characterized in *Arabidopsis* (Mounier et al. 2014), rice (Arai-Sanoh et al. 2014), and maize (Li et al. 2015a, b). Soil nitrate is a key N resource for plants and is mainly taken up by roots through various NO_3^- transporters. Few members of the NRT1 and NAR2/NRT2 family (such as NRT1.1, NRT2.1, and NAR2.1) have been observed in NO_3^--induced development of roots. Fan et al. (2017) expressed the role of NO_3^- transporters for their potential use as targets for root architecture and nutrient acquisition, thereby improving crop NUE. In *Arabidopsis*, the NO_3^- transporter NRT1.1 play role in an auxin-mediated NO_3^- signaling pathway linked with alterations in root architecture, whereas the high-affinity NO_3^- uptake transporter, NRT2.1, has been observed having dual functions concerning to NO_3^- uptake and synchronizing lateral root growth with NO_3^- availability (Remans et al. 2006; Mounier et al. 2014).

Only a few genes like the plasma membrane proton pump, AHA2, CLE peptides, and a CLV1 leucine-rich repeat receptor-like kinase in *Arabidopsis* have been characterized, which take part in the regulation of root growth concerning N availability (Araya et al. 2014; Mlodzinska et al. 2015). While TAR2 (an auxin biosynthetic gene) is crucial for low N-mediated reprogramming of root architecture in *Arabidopsis* (Ma et al. 2014), further corroborating the key roles auxin plays in controlling root architecture in response to N availability. Moreover, DRO1 (DEEPER ROOTING) and DRO1-related genes are present across diverse plant phyla. Overexpression of DRO1 influences the orientation of the root system and led to deeper-rooting phenotypes in rice (Table 5; Arai-Sanoh et al. 2014), *Arabidopsis*, and plum (Guseman et al. 2017). These data are specifically applied for expression of DRO1-related genes to alter root architecture for drought stress escape mechanisms and higher NUE. In addition, micro-RNAs emerge to accomplish a substantial role to manage the responses of N deficiency in plants. Two micro-RNAs, miR167 and miR393, were discovered in *Arabidopsis* to control their target genes ARF8 and AFB3, respectively, to amend root structure modulations under changing N supply (Gifford et al. 2008; Vidal et al. 2010).

Manipulating nitrate and ammonium transporters

Nitrate uptake and allocation in plants can be altered by changes in the expression pattern of NO_3^- transporters. Some evidence for NO_3^- transporter in different crops to improve their performance is available. Overexpression of an NAC2 gene, the cereal-specific ATAF, CUC, and NAM transcription factor, augmented the expression of key N assimilatory enzyme glutamine synthetase TaGS2. The TaNRT2.1 has a putative role in the post-flowering uptake of NO_3^- in wheat (Taulemesse et al. 2015). Moreover, an important transcription factor (TaNAC2-5A) optimistically manages NO_3^- transporters expression and appears as an important handler in the N regulation system in wheat plants (He et al. 2015). In tomatoes, LeNRT2.3 regulates low-affinity NO_3^- transport whose expression increased

Table 5 A list of genes with transgenic approaches to improve plant nitrogen use efficiency (NUE)

Name	Gene family	Host	Promoter	Effect on characteristics related to NUE	References
AMT1-1	Ammonium transporter	Rice	*Ubiquitin*	Enhance NH^+_4 uptake and reduced dry weight under high NH^+_4	Yuan et al. (2007)
STP13	Hexose transporter	*Arabidopsis*	CaMV 35S	Increase plant growth, biomass and NUE in response to exogenously applied sugar	Schofield et al. (2009)
DEP1	G-protein g subunit	Rice	Ubiquitin	At modest input levels of N, improved N uptake, assimilation and grain yield	Sun et al. (2018)
DRO1	IGT	Rice	*CaMV 35S*	Increase in downward growth of root, N uptake and leaf N content and grain yield by 10% regardless of fertilizer treatment	Arai-Sanoh et al. (2014)
SnRK	SNF1-related kinase	Tomato	*CaMV 35S*	NUpE augmented in overexpressing plant	Wang et al. (2012)
ENOD	Early nodulin like protein	Rice	Ubiquitin	Increased N accumulation, total amino acids, dry biomass and grain yield as well	Bi et al. (2009)
NpNia2	Nitrate reductase	Wheat	*CaMV 35S*	Foliar NR activity enhanced and improved seed protein content and grain weight under optimal soil N level	Zhao et al. (2013)
SoNiR	Nitrite reductase	*Arabidopsis*	*CaMV 35S*	Higher NO_2 assimilation	Takahashi et al. (2001)
NpNR	Nitrate reductase	Tobacco	*CaMV 35S*	Greater NO emission and NO^-_2 excretion from leaf and root tissues	Lea (2004)
AtASN1	Asparagine synthetase	Arabidopsis	CaMV 35S	Enhanced N status in seeds and grain yield under low N input	Lam et al. (2003)
GS1	Glutamine synthetase	Rice	Ubiquitin	NUE increased under high N condition	Brauer et al. (2011)
GS1	Cytosolic glutamine synthetase	Wheat	Rubisco small unit	Increased N accumulation capacity and improved NUE	Zhang et al. (2017)
GS2	Plastidic glutamine synthetase	Wheat	Ubiquitin	Enhanced plant NUE and grain yield	Hu et al. (2018)
OsGS1;2	Glutamine synthetase	Rice	Ubiquitin	Spikelet yield as well as NUE increased by 29–35% and 30–33% under high N	Brauer et al. (2011)
OsGS1;2	Glutamine synthetase	Rice	CaMV 35S	Grain yield decreased by 7–25% while total N content increased under both LN and HN	Cai et al. (2010)
ZmGS1	Glutamine synthetase	Maize	Ubiquitin T-DNA Insertion	No change in shoot DW, grain yield enhanced by 45% under LN, TN and leaf TAA augmented while grain yield decreased by 85% under LN	Martin et al. (2006)
GOGAT	Glutamate synthase	Rice	CaMV 35S	Improved grain filling, TN and DW Modulated N assimilation and C-N balance	Tamura et al. (2011) Yang et al. (2016)
Fd- GOGAT	Fd dependent glutamate synthase	Tobacco	CaMV 35S	Diurnal changes in NH_3^+ assimilation	Ferrario-Mery et al. (2002)

Table 5 (continued)

Name	Gene family	Host	Promoter	Effect on characteristics related to NUE	References
AlaAT	Alanine aminotransferase	Brassica	btg26	Produced better yields even with 50% less amount of N fertilizer	Good et al. (2007)
AtCAT6	Amino acid transporter	*Arabidopsis*	T-DNA insertion	Supply AA to sink tissues of plant	Hammes et al. (2006)
AtASN1	Asparagine synthetase	*Arabidopsis*	*CaMV 35S*	Total N and AA content increased in seeds	Krall et al. (2016) Gaufichon, et al. (2017)
ZmDof	Dof TF	*Arabidopsis*	*35SC4PPDK*	Increased plant growth rate under LN	Yanagisawa et al. (2004)
ZmDof1	Dof TF	*Rice*	*Ubiquitin*	Altered C and N metabolites and enhanced N assimilation and growth under LN	Kurai et al. (2011)
AtPPDK	Pyruvate orthophosphate Dikinase	*Tomato*	*pSAG12*	N remobilization accelerated from leaves	Taylor et al. (2010)
SAT1	bHLH transcription factor	Soybean	GmAMF3	Enhanced nodulization to improve N fixation and NH_4^+ transport activity	Chiasson et al. (2014)

CaMV 35S, cauliflower mosaic virus 35S promoter; *ubiquitin*, maize ubiquitin promoter; *pSAG12*, senescence associated gene 12 promoter; *35SC4PPDK*, CaMV 35S promoter with TATA box and the transcription site of the maize *C4PPDK* gene; *LN*, low nitrogen concentration; *T-DNA*, transfer DNA; *AA*, amino acid; *TN*; total nitrogen content; *TAA*; total amino acid; *btg26*, canola root-specific promoter; *NR*, nitrate reductase activity; *DW*, dry weight; *FW*, fresh weight

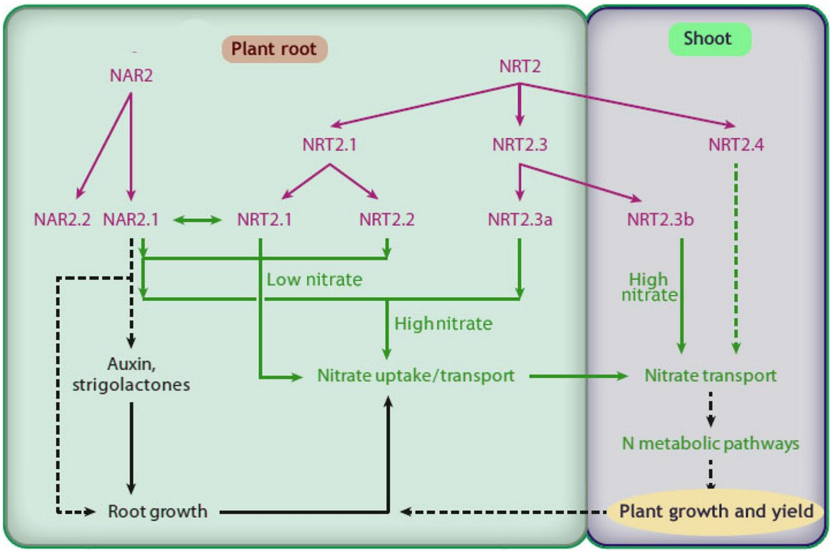


Fig. 4 Schematic representation of proposed evolution, characterized, and predicted functions for the rice NAR2/NRT2 nitrate transporters. In roots, mainly OsNAR2.1, OsNAR2.2, OsNRT2.1, OsNRT2.2, and OsNRT2.3a expressed; OsNRT2.3b and OsNRT2.4 are expressed primarily in shoots. OsNRT2.1 and OsNRT2.2 in association with OsNAR2.1 transport NO_3^- in the high-affinity concentration range. For NO_3^- transport, OsNRT2.3a requires OsNAR2.1; hence, the protein has a tenfold lower affinity for NO_3^- than OsNRT2.1 and OsNRT2.2. A switch can be provided by OsNAR2.1 depending on the partner transporter, to enable a rapid response in uptake over the dynamic ranges of external NO_3^- concentrations (Feng et al. 2011; Yan et al. 2011). The solid red arrows represent defined direct functions of the transporters in NO_3^- uptake and translocation; the dashed arrows represent presumed relationships based on the tissue localization of the genes in rice and functional expression in oocytes. The blue arrows indicate the proposed evolution of individual members of the NAR2 and NRT2 nitrate transporter families. Black arrows indicate the possible relationships between NAR2.1 and root growth and between the functions of NRT2 members and plant growth and development

NO_3^- acquisition in roots, its transport to areal parts, improved biomass, and weight of fruits (Fu et al. 2015). Higher expression of OsNRT2.1 fairly increased seedling growth in rice; however, it did not influence its uptake (Feng et al. 2011; Yan et al. 2011). Contrary, overexpression of OsNRT2.3b might considerably boost grain yield and overall N uptake (Fig. 4; Xu et al. 2012). In the recent past, a low-affinity NO_3^- transporter gene (OsNRT1.1B) contributes to elevated N use efficiency in rice has been identified (Hu et al. 2015). The upregulation of OsNRT1.1B may participate to improve NUE by improving the detection of various levels of NO_3^- and increasing the potential for N buildup into the rice grain. Fan et al. (2017) reported that *OsNRT2.3b* overexpression in rice significantly increased NUE and grain yield both under glasshouse and field conditions. For other crops, variation in NO_3^- transporters' activity to enhance NO_3^- uptake and utilization is regarded as a significant goal for increasing yield and NUE.

The NH_4^+ uptake capacity is enhanced by overexpression of *AMT1* genes, and hence, it reduces root and shoot biomass at comparatively greater NH_4^+ levels, maybe due to toxicity and the failure of NH_4^+ assimilation to manage (Yuan et al. 2007). Therefore, higher expression of AMT1 members could be useful to ameliorate N uptake in NH_4^+-deficient soils. NH_4^+ transporter *OsAMT1.1* has been engineered in rice. Ranathungeet al. (2014) revealed that overexpression of *OsAMT1.1* in rice increases the NH_4^+ acquisition rate, NH_4^+ content in roots and shoots, and grain yield under low N supply. It is also noted that a few AMT1 family members (like LjAMT1;3) might function as an intracellular NH_4^+ sensors in legumes as did not directly contribute to NH_4^+ uptake (Rogato et al. 2010). Thus, the N transporters' family is a promising gene resource that can be manipulated through transgenic approaches to improve NUE in crops.

Quantitative trait loci (QTL) mapping for high NUE

The manifestation of methods to spot molecular markers helped the consequent appraisal of NUE inheritance. A perspective to exploit the classical genetics to increase plant NUE is associated with the conventional breeding approaches and quantitative trait loci (QTL) mapping in alliance with marker-assisted selection (MAS) to trail important regions of the chromosome that segregate for NUE. One of the initial steps to accomplish this aim is to differentiate the NUE-associated genes followed by the use of specific genes to merge plant physiology and genetics to ameliorate plant performance. QTLs for NUE have been characterized in *Arabidopsis,* wheat, rice, maize, and barley. In cereals, the QTL mapping revealed that NUE traits are governed by several conserved vital gene clusters (Quraishi et al. 2011; Liu et al. 2012). The existence of conserved structure and function for key genes permits us to evaluate the suggested relationship between GS, GOGAT, and NUE in barley. Genome-wide association mapping techniques are used to look for insight QTLs required in NUE-related traits in barley (Pasam et al. 2012). In tropical maize, QTLs have been identified for NUE, grain yield, and its contributing traits that comprise of many genes encoding key enzymes playing a crucial role in N and C metabolism. Thus, for tolerance to low N, the QTLs have also been identified in *Arabidopsis*, rice, and barley (Hirel et al. 2011). QTLs transgenic approaches provide an exciting opening to find out the factors that can influence growth, yield, and its components in a straight line or indirectly, consequently improving NUE. In general, an extensive root system has been proposed to increase N acquisition in the deep soil layer. Arai-Sanoh et al. (2014) inferred that QTL (*DRO1*) developed through cloning regulates the growth patterns of roots and growth angles in rice which ensure roots grow more in the downward direction to acquire more nutrients and water uptake. The *OsTOND1* along with a major QTL is responsible for tolerance to N deficiency in *indica* rice encodes the expression of a thaumatin protein and translates a low N-induced root growth and higher NUE. This increase in NUE might be associated with the overexpression of *OsTOND1* which influences many genes that encode N assimilation enzymes (Zhanget al. 2015a, b). The huge difference in growth performance and NUE exists among the genotypes of the same species that can be utilized as parent lines for a population of recombinant inbred lines to conduct QTL mapping of attributes associated with the constituent of yield potential and NUE (Chardon et al. 2010). Eleven genes have been mapped in wheat by keeping confidence intervals of 10, and it was observed that NUE meta-QTLs colocalized with vital developmental genes such as *Rht* (reduced height), *Ppd* (photoperiod sensitivity), and *Vrn* (vernalization requirement) (Quraishi et al. 2011).

Conclusion and future prospects

Conclusion

The main challenges in agriculture are to sustain global crop productivity and the quality of the product without compromising human well-being and environmental quality. The NUE for major crops including rice, maize, and wheat seldom exceeds 40%. Therefore, ameliorating NUE in crop plants is a great challenge. Significant improvements in NUE can be achieved by increasing either NUpE, NUtE, or both. The plant root architecture and factors influencing the roots' capacity to acquire available N from the soil can affect NUpE. Consequently, soil N recovery and its utilization efficiency perhaps enhanced by optimum N management approaches to counter N losses from the soil–plant system, besides the greater potential of crop cultivar to acquire and utilize existing N. Improved crop management and agronomy integrated with advanced crop genetics approaches have been the key factors behind enhanced NUE and crop productivity. A significant genetic variation and phenotypic plasticity exist among the plants for NUE. Recent advances in crop plant genomics have discovered the composition of nitrome as well as the genes regulated by the existence or absence of various forms of N. Introgression and enhancing expression of NO_3^-transporter, N assimilation genes or their altered expression with greater ability to sense, uptake or assimilate N in diverse cultivars can improve NUE or other related traits. A major uplift in biological research is being caused by novel gene-editing technology CRISPR/Cas9 in association with the Cas9 nuclease, which offers new opportunities to produce field crops with greater potential for NUE. Overall improvements in NUE will help to achieve agronomic, economic, and environmental goals.

Outline unknowns

We lack knowledge about different mechanisms involved in the efficient utilization of N in crop plants, which explains why farmers and breeders want a cultivar with a high yield even under identical fertilizer applications. In response to low N, underlying mechanisms of plant root architecture modification are still elusive. As NO_3^- absorption is inhibited by NH_4^+ immediately, the reason for the inhibitory action and the amount of NO_3^- assimilated in roots and NO_3^- transported to shoots remains unclear, though they may be affected by different aspects, such as plant species, growth stages, temperature, and light intensity. Both inorganic and organic N transporters play crucial roles in the N flux from root to leaf and sink, and its metabolism in source and sink. How the various transporters and downstream N assimilatory processes are harmonized is presently uncertain. A large quantity of N is applied to arable lands in the form of urea, but no detailed characterization of the plant's response to urea and associated transports has yet been performed. Urea also assimilates in roots and shoots like NO_3^- and NH_4^+, and thus, the pathway for this assimilation is needed to explore. Several signaling modules are also present in crop plants which coordinate with NO_3^- availability during primary and lateral root growth. However, plants are not well known for their ability to coordinate these modules effectively, so that they can respond in an integrated manner. Furthermore, several positive or negative regulators controlled plant growth and development to accomplish potential environmental challenges. To breed crops with high NUE, it is important to know how altering negative growth regulators via CRISPR/Cas9 technology can be more effective than overexpressing positive growth regulators.

Future prospects

Considerable development has been made to the mechanism involved in N utilization. Extensive research is required to assess the physiological demand for N of various crop cultivars influenced by the rate of N fertilizer and time, or more notably, developing the most effective method of N fertilizer application for diverse crop cultivars. Redesigning crop management practices to exploit the biological, physical, and chemical attributes of soil to enhance N uptake, transport to shoot, and translocation need consideration. Because positive correlations between root architecture traits and QTLs for N uptake exist; therefore, efforts to increase plant NUpE by changing phytohormones balance to direct the root architecture and transporters activity are a challenge. The NO_3^- allocation to the plant is also a future challenge. Using different genetic engineering approaches to stimulate the expression of NO_3^- and NH_4^+ transporters directed by low N-induced promoters could be a viable option to increase N uptake at suboptimal soil N levels. Next-generation sequencing can also provide a better understanding to explore the diversity of NO_3^- transporters in plants to be exploited either by genetic engineering or marker-assisted breeding. Moreover, there is a drastic need to characterize urea transporters and how their overexpression can modulate the plant responses to varying N supply. Urea assimilates in plant roots and shoots; therefore, the use of novel genomic techniques can help to generate genotypes with high urea assimilation and N utilization. The possible mechanism controlling N utilization in crop plants to explore its necessity to determine how the existing knowledge can be practically translated for enhancing crop productivity.

Author contribution statement WM and GY gave concept. WM prepared initial content for manuscript drafting that was edited and approved by GY, WM wrote the manuscript, and Irfan has been reviewing and editing the manuscript and also contributed in 'N uptake and transport, and soil characteristics'. GY supervised and critically reviewed the whole manuscript drafting and approved the final version of the manuscript. WM, GY, and MI do not have competing interests and take responsibility for the integrity of the work.

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Data availability No datasets were generated or analyzed during the current study.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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