Review

Amino Acids on the Move: Boosting Permeases for High-Quality Crops Under Reduced Nitrogen Supply

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Amino Acids on the Move: Boosting Permeases for High-Quality Crops Under Reduced Nitrogen Supply

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Abstract

Nitrogen (N) availability is a major determinant of crop productivity; however, nitrogen use efficiency (NUE) remains relatively low in most agricultural systems. After uptake from the soil, inorganic N is assimilated into organic forms, primarily amino acids, which represent the principal long-distance transport form in most plants. The distribution of amino acids from source tissues to developing sink organs therefore plays a central role in plant growth, yield formation, and the nutritional quality of harvested organs. Amino acid transporters (AATs), also known as permeases, regulate the cellular and long-distance movement of amino acids and play a central role in nitrogen partitioning within the plant. These membrane proteins belong to the AAAP, APC, and UMAMIT transporter families and participate in multiple physiological processes, including amino acid uptake in roots, xylem and phloem transport, intracellular compartmentalization, and partitioning to reproductive tissues. Recent functional studies in both model plants and crop species demonstrate that manipulation of amino acid transporters can significantly influence biomass production, seed yield, grain protein content, and nitrogen use efficiency. In this review, we synthesize current knowledge on the structure, transport mechanisms, and physiological roles of plant amino acid transporters, with particular emphasis on their contribution to nitrogen partitioning and crop productivity. We also discuss emerging opportunities for exploiting amino acid transporters in crop breeding and biotechnology to enhance nitrogen utilization and improve the sustainability of agricultural systems.

Keywords: amino acid transporters; crop quality; crop yield; nitrogen partitioning; nitrogen use efficiency

1. Introduction

Nitrogen (N) is the most quantitatively important essential nutrient for plants and frequently represents a major limiting factor for crop growth and yield (Lawlor et al., 2001). Nitrogen is a key component of biomolecules essential for cellular structure and function, including amino acids, proteins, nucleic acids, hormones, chlorophylls, and specialized metabolites (Rengel et al., 2023). In addition to its structural role, N availability strongly modulates plant growth and development by regulating physiological processes such as root architecture, seed dormancy, or leaf development (Liu and von Wirén, 2017; Vega et al., 2019).

In modern agricultural systems, large amounts of nitrogen fertilizers are applied to maximize crop yields. However, plants typically utilize only a fraction of the applied nitrogen, resulting in low nitrogen use efficiency (NUE) and significant environmental consequences, including nitrate

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leaching, greenhouse gas emissions, and eutrophication of aquatic ecosystems (Tilman et al., 2002; Masclaux-Daubresse et al., 2010; Xu et al., 2012). Improving NUE has therefore become a major objective in crop research and breeding programs aimed at increasing productivity while reducing the environmental footprint of agriculture (Good et al., 2004; Xu et al., 2012).

Plants acquire nitrogen mainly as nitrate (NO_3^-) or ammonium (NH_4^+) from the soil through specialized transport systems located in root cell membranes (Crawford and Glass, 1998; Wang et al., 2012). Following uptake, inorganic nitrogen is assimilated into organic compounds, primarily amino acids, through the coordinated activity of the nitrate reduction and ammonium assimilation pathways (Campbell, 1999; Lea and Miflin, 2011). Amino acids constitute the principal transportable forms of reduced nitrogen in plants and are distributed from source tissues, where nitrogen assimilation occurs, to sink tissues that require nitrogen for growth and storage, including developing leaves, roots, flowers, and seeds (Tegeder and Rentsch, 2010; Tegeder and Masclaux-Daubresse, 2018).

The cellular and long-distance distribution of amino acids depends on a diverse group of membrane transport proteins known as amino acid transporters (AATs) (Rentsch et al., 2007; Tegeder, 2012). These transporters regulate nitrogen partitioning by mediating amino acid uptake, export, and intracellular compartmentalization, thereby influencing plant growth, reproductive development, and crop productivity. Increasing evidence indicates that amino acid transporters play important roles in determining agronomic traits such as biomass production, seed yield, grain protein content, and NUE (Tegeder, 2014; Tegeder and Masclaux-Daubresse, 2018). Manipulation of specific permeases can alter nitrogen partitioning among tissues and organs, highlighting their potential as targets for crop improvement strategies. Despite increasing knowledge, how amino acid transport is coordinated with whole-plant nitrogen allocation and crop productivity remains poorly understood.

This review summarizes the roles of amino acid permeases in plant physiology, focusing on their impact on crop yield, nutritional quality, and NUE, and highlights their potential for improving sustainable agriculture through breeding and biotechnology.

2. Nitrogen Uptake and Assimilation

Plants primarily acquire N from the soil as nitrate, although in certain soils, conditions, or management practices, ammonium, urea, or amino acids may constitute alternative sources (Loqué and von Wirén, 2004; Maathuis, 2009; Masclaux-Daubresse et al., 2010; Witte, 2011).

N assimilation can occur in roots or shoots depending on the species and plant conditions (Andrews, 1986). In herbaceous species, absorbed nitrate is usually assimilated in leaves (Foyer et al., 2003; Hachiya et al., 2016). There, nitrate is transported into the cytosol of mesophyll cells and reduced to nitrite, a reaction catalyzed by nitrate reductase (Meyer and Stitt, 2001). Nitrite is subsequently translocated to the chloroplast, where it is reduced by the second enzyme in the pathway, nitrite reductase (NiR), to ammonium. The ammonium derived from nitrate reduction, as well as from photorespiration or amino acid metabolism, is primarily assimilated by the glutamine synthetase (GS)/glutamate synthase (GOGAT) cycle in the chloroplast (Lea and Miflin, 1974). Chloroplastic glutamine synthetase (GS2) fixes ammonium to a glutamate (Glu) molecule to generate glutamine (Gln). Gln then reacts with 2-oxoglutarate to produce two Glu molecules, in a reaction catalyzed by GOGAT (Suzuki and Knaff, 2005). In leaves and other organs, various cytosolic glutamine synthetase forms (GS1) may be involved in ammonium recycling under specific conditions, such as senescence, or in glutamine synthesis for phloem partitioning (Bernard and Habash, 2009). In addition to the GS/GOGAT cycle, asparagine synthetase (AS), carbamoyl phosphate synthetase (CPSase), and mitochondrial glutamate dehydrogenase (GDH) also contribute to ammonium assimilation (Masclaux-Daubresse et al., 2010). Moreover, in leguminous species, amino acids assimilated in the root nodules are also partitioned in the plant (Garneau et al., 2018).

Ammonium taken up from the soil is preferentially assimilated in roots via cytosolic GS1 forms, especially under high nitrate availability conditions (Hachiya and Sakakibara, 2017). At

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concentrations exceeding GS capacity, part of the ammonium may be transported to the shoot for assimilation (Schjoerring et al., 2002).

Nitrogen assimilation into amino acids requires energy in the form of ATP and reducing power, as well as carbon (C) skeletons for ammonium condensation. These products derive from photosynthesis, respiration, and photorespiration, underscoring the close relationship and regulation of C/N metabolism (Foyer et al., 2003). Synthetized amino acids in the leaves are used for metabolism, transiently stored or transported in the phloem to developing vegetative or reproductive sink tissues. Besides, amino acids assimilated in the root cells or taken directly from the soil were translocated to the shoot via xylem (Tegeder, 2014; Tegeder and Masclaux-Daubresse, 2018). In addition, N remobilization from storage pools or protein hydrolysis also contributes to the available amino acid pool in the plant (Tegeder and Hammes, 2018).

3. Amino Acid Transport in the Plant

Long-distance transport of amino acids involves multiple interconnected steps of inward and outward transport across the plasma membranes, including uptake from the soil, as well as xylem and phloem loading and unloading, and delivery to developing edible organs such as tubers and fruits (Pratelli and Pilot, 2014) (**Figure 1**). Furthermore, since amino acid metabolism and storage are compartmentalized within the cell (Galili et al., 2016), the movement between organelles, including chloroplasts, vacuoles, mitochondria and peroxisomes, and the cytosol is controlled by amino acid permeases (Snowden et al., 2015; The et al., 2024; Kuhnert et al., 2025).

In roots, amino acid uptake from the soil is mediated by plasma membrane transporters in epidermal and cortical cells (**Figure 1A**). Members of the AAP, LHT, and ProT families contribute to this process, with partially overlapping substrate specificities but distinct expression patterns that enable flexible responses to environmental conditions (Lee et al., 2007; Svennerstam et al., 2008; Hirner et al., 2006; Grallath et al., 2005).

Following uptake or local synthesis, amino acids are exported to the apoplast and subsequently loaded into the xylem for root-to-shoot transport, a process in which UMAMIT transporters play key roles (**Figure 1A**). In the shoot, amino acids are taken up by leaf cells and, together with those assimilated in the leaves, are redirected into the phloem for distribution to sink organs. Phloem loading typically involves an apoplastic pathway, with UMAMIT proteins mediating amino acid export from mesophyll cells and AAAP transporters (**Figure 1**), including AAPs, facilitating uptake into the sieve element–companion cell complex (Müller et al., 2015; Tegeder and Masclaux-Daubresse, 2018). Also permeases of these families regulate apoplastic unloading at the sinks, mainly fruits and seeds during the reproductive stage of the plant.

Together, these transport steps constitute a coordinated system that links nitrogen assimilation with whole-plant distribution, ultimately shaping growth, development, and reproductive success.

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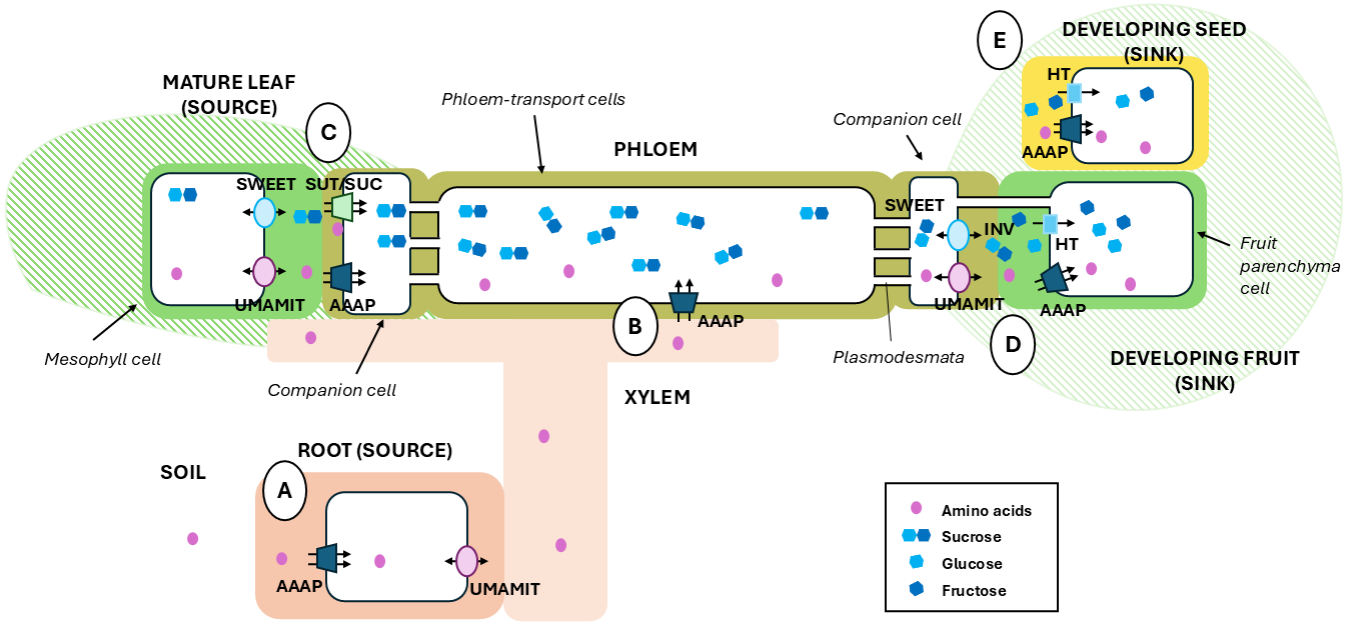
Figure 1. Schematic model of amino acid transporter function in long-distance nitrogen transport between source and sink organs in plants. A) Amino acid uptake in roots and loading into the xylem for transport to the shoot. B) Xylem-to-phloem transfer of amino acids during the root-to-shoot transport. C) Phloem apoplastic loading of amino acids in source leaves. D) Apoplastic unloading of amino acids at the reproductive sinks. E) Apoplastic unloading of amino acids in the developing seeds. Sugar (sucrose) loading and unloading processes were included in the model highlighting C/N interplay and co-regulation. AAAP and UMAMIT: amino acid permeases; SWEET and SUT/SUC: sucrose transporters; HT: hexose transporters; INV: invertase.



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4. Plant Amino Acid Transporters

Amino Acid Transporter Families

Plants display a multiplicity of amino acid transporters or permeases that differ in tissue or subcellular distribution, substrate specificity, affinity or regulation (Williams and Miller, 2001; Tegeder et al., 2011; Pratelli and Pilot, 2014). Based on sequence homology and transport properties, plant amino acid transporters fall into three major families: *Amino Acid/Auxin Permeases* (*AAAP*), *Amino acid/Polyamine/Choline transporters* (*APC*), both included in the *APC* superfamily (Zhao et al., 2021), and *Usually Multiple Acids Move In and Out Transporters* (*UMAMIT*), as summarized in **Table 1**.

The *AAAP* family represents the largest group and includes several subfamilies such as *Amino Acid Permeases* (*AAP*), *Lysine and Histidine Transporters* (*LHT*), *Proline Transporters* (*ProT*), *γ-Aminobutyric Acid Transporters* (*GAT*), *Aromatic and Neutral Amino Acid Transporters* (*ANT*), *Auxin Transporters* (*AUX*), *Amino Acid Transporter-like* (*ATL*) and *Vesicular Aminergic-Associated Transporters* (*VAAT*). The *APC* family consists of three subfamilies: *Cationic Amino Acid Transporters* (*CAT*), *Amino Acid/Choline Transporters* (*ACT*), and *Polyamine H^+ Symporters* (*PHS*). Genome-wide surveys reported that the *AAP*, *LHT*, *ATL* and *VAAT* subfamilies comprise the largest number of genes in the *AAAP* family, and the *CAT* were the most represented in the *APC* family (Zhao et al., 2012; Wu et al., 2015; Cheng et al., 2016; Ma et al., 2016; Tian et al., 2020; Omari Alzahrani, 2021). *UMAMIT* belongs to the nodulin-like family and might be divided into four subfamilies (Cao et al., 2025).

Some further amino acid transporter genes have been reported (Okumoto and Pilot, 2011; Haferkamp and Schmitz-Esser, 2012; Pratelli and Pilot, 2014), but most attention has been focused on *AAAP* and *UMAMIT* families.

Structure and Transport Characteristics of Amino Acid Permeases

Amino acid transporters of the *AAAP* and *APC* families share common structural and functional features as members of the *APC* superfamily. These proteins are integral membrane transporters typically containing 10-14 transmembrane α-helices with both C- and N-termini oriented toward the cytosol (Frommer et al., 1993; Bush et al., 1996; Vangelatos et al., 2009; Fan et al., 2023) (**Figure 2A,B**).

In general, it is considered that AAAP and APC transporters operate as proton-coupled symporters (**Figure 2D**). This secondary active transport mechanism underlies their role in amino acid import into the cell or the organelle (Bush, 1993; Frommer et al., 1993; Boorer et al., 1996; Boorer and Fischer, 1997; Meyer et al., 2006; Meier et al., 2024). Most of the AAAPs and APCs are suggested to be in the plasma membrane and therefore involved in amino acid import into the cell, playing central roles in processes such as root uptake, phloem loading and seed filling (Tegeder, 2012; Tegeder and Masclaux-Daubresse, 2018). Nevertheless, specific members of the superfamily, like CAT permeases, are predicted to be targeted to chloroplasts, mitochondria or vacuoles (Su et al., 2004; Snowden et al., 2015).

AAAP and APC transporters display broad but variable substrate specificity, mediating the transport of a broad spectrum of amino acids (Frommer et al., 1993; Boorer and Fischer, 1997; Fischer et al., 2002; Yang et al., 2020). Nevertheless, differences in the specificity and affinity for amino acids have been observed among subfamilies and between members of the same family (Fischer et al., 2002; Grallath et al., 2005; Svennerstam et al., 2008). By contrast, the permeases of other families show stronger specificity for amino acids. Among them, the ProT family mainly transports preferably proline and glycine betaine whereas GAT permeases show preference for GABA (Meyer et al., 2006). In addition, some members of the AAAP family transport other related metabolites, such as non-proteinogenic-amino acids 1-aminocyclopropane-1-carboxylic acid (ACC) and theanine or auxins (Shin et al., 2015; Choi et al., 2019; Dong et al., 2020; Hammes and Pedersen, 2024), highlighting their integration into broader metabolic and signaling networks.

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Table 1. Major amino acid transporter families in plants.

Family	Subfamilies	Transport	Functions	Examples
AAAP	AAP LHT ProT GAT ANT ATL VAAT	Import (H^+/amino acid symporters)	Root uptake Xylem loading Xylem unloading Xylem-to-phloem transport Phloem loading Seed loading	*AtAAP1*, *AtLHT1*, *AtProT2* *CsAAP2* *AtLHT1* *AtAAP2*, *AtAAP6*, *OsAAP3* *AtAAP8*, *PsAAP1* *AtAAP1*, *AtAAP8*, *AtCAT6*
APC	CAT ACT	Import (H^+/amino acid symporters)	Organelle transport	*AtCAT2*, *AtCAT4*, *SlCAT9*
UMAMIT	Multiple clades	Import/export (Bidirectional facilitators)	Xylem loading Phloem loading Phloem unloading Organelle transport Seed loading	*AtUMAMIT18* *AtUMAMIT11*, *AtUMAMIT14*, *AtUMAMIT18* *AtUMAMIT11*, *AtUMAMIT14* *AtUMAMIT24*, *AtUMAMIT44* *AtUMAMIT28*, *AtUMAMIT29*

References of the genes are indicated in the text.

Figure 2. Structural and functional features of amino acid transporters. (A-C) Predicted structures of representative amino acid transporters from the AAAP, APC and UMAMIT families generated using AlphaFold. A) AtAAP1 (Amino acid permease 1; 11 transmembrane domains). B) AtCAT9 (Cationic amino acid transporter 9; 14 transmembrane domains). C) AtUMAMIT14 (WAT-related protein; 10 transmembrane domains). D) Schematic model of transporter localization and transport mechanisms in plant cells. AAAP and APC transporters function as proton-coupled symporters mediating amino acid uptake, whereas UMAMIT transporters act primarily as facilitators enabling bidirectional amino acid transport. Some AAAP/APC members are localized to intracellular membranes and may function in amino acid exchange between organelles. AAP: Amino acid permease; APC: Amino acid/Polyamine/Choline transporters; UMAMIT: Usually Multiple Acids Move In and Out Transporters.

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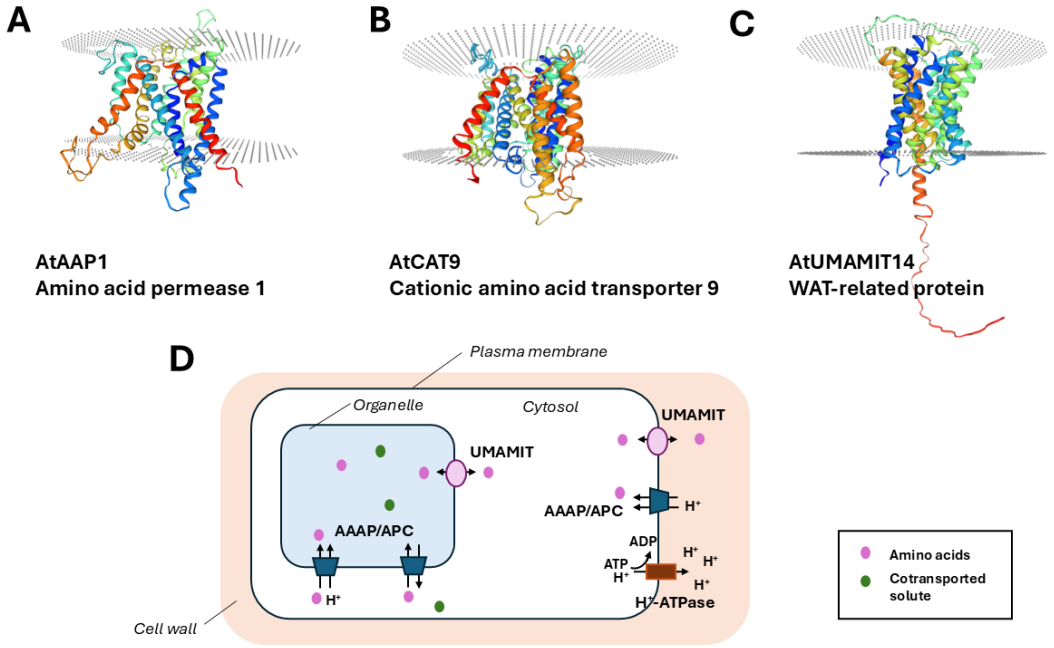

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In contrast, UMAMIT transporters represent a distinct, plant-specific family with unique structural and functional properties. These proteins typically contain 10 transmembrane helices arranged in two inverted repeats (Müller et al., 2015; Cao et al., 2025) (**Figure 2C**). Unlike AAAP and APC permeases, UMAMITs act primarily as facilitators, enabling bidirectional amino acid transport driven by concentration gradients rather than proton coupling (Müller et al., 2015). Those UMAMITs characterized to date promote the transport of a broad range of amino acids, although with specific features among genes (Müller et al., 2015; Besnard et al., 2018).

Regarding subcellular localization, UMAMITs were predominantly localized in the plasma membrane, tonoplast and chloroplasts, although some might be located at the endoplasmic reticulum, nucleus or mitochondria (**Figure 2D**). Notably, UMAMIT members located at the plasma membrane display mainly amino acid export activity, and are hypothesized to play, together with the H^+/amino acid symporters (**Figure 1C**), analogous role in the amino acid transport as the SUC-SUT/SWEET pair to transport sucrose (Kim et al., 2021). Interestingly, some UMAMIT proteins have been proposed to also facilitate the efflux of glucosinolates to the apoplast (Xu et al., 2023). The UMAMIT proteins located in the chloroplast and tonoplast membranes mediate subcellular transport of amino acids associated to amino acid metabolism or storage between organelles (Kuhnert et al., 2025).

5. Physiological Functions of Amino Acid Permeases

Amino acid permeases function across multiple organizational levels, from cellular uptake and intracellular compartmentalization to long-distance transport, thereby coordinating nitrogen allocation and partitioning throughout the plant. They are expressed in diverse organs and tissues, reflecting their wide range of physiological functions (Fischer et al., 1995; Zhao et al., 2012; Ma et al., 2016; Tian et al., 2020; Zhao et al., 2021; Chen et al., 2025; Ling et al., 2026). Expression analyses frequently reveal the presence of multiple transporters within the same tissue, indicating both functional redundancy and specialization among family members.

Amino Acid Transport in the Roots

Amino acid uptake from the soil solution requires specific transporters located in the plasma membrane of epidermal or cortical root cells (Tegeder, 2014). Once inside the cytosol, amino acids move symplastically through plasmodesmata toward the vascular cylinder. This flux might also include amino acids assimilated or stored in root cells. There, they are mostly loaded into the xylem, a process that requires another plasma membrane transporter to enter the apoplast, for long-distance distribution to the aerial parts of the plant following the transpiration stream (**Figure 1A**).

Members of the AAP, LHT and ProT families control amino acid uptake in the roots (**Table 1**). For example, AAP1, AAP5, LHT1, LHT6 and ProT2 mediate the inward transport of amino acids to root cells in Arabidopsis (Chen and Busch, 1997; Grallath et al., 2005; Hirner et al., 2006; Lee et al., 2007; Svennerstam et al., 2008, 2011; Lehmann et al., 2011; Perchlik et al., 2014), with similar functions reported for homologs in crop species such as cucumber and rice (Guo et al., 2020; Yao et al., 2023).

Although the mechanisms of xylem loading remain incompletely understood, UMAMIT transporters have been implicated in amino acid export to the apoplast (**Figure 1A**). For instance, SIAR1/UMAMIT18 facilitates amino acid efflux from pericycle cells, contributing to xylem loading, while BAT1 has also been proposed to participate in amino acid export into the xylem sap (Ladwig et al., 2012; Dündar and Bush, 2009). Similarly, cucumber *CsAAP2* is highly expressed in the root pericycle, and *aap2* loss-of-function mutants showed increased free amino acid contents in roots, suggesting a role in xylem loading (Yao et al., 2023).

Xylem Transport to the Shoot

Following transport to the shoot, amino acids are imported into the mesophyll cells for metabolism or storage (Tegeder and Masclaux-Daubresse, 2018). It has been hypothesized that

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vegetative organs like stems could act as transitory storage organs for N in tree species, but also in herbaceous (Millard, 1988; Kotowska et al., 2020). Transporters like AtLHT1 mediate amino acid uptake into mesophyll cells from the xylem (Hirner et al., 2006).

Amino acids can also be directly transferred from the xylem to the phloem along the long-distance pathway from roots to leaves, allowing direct transport to developing sinks with low transpiration rates such as fruits and flowers (Lalonde et al., 2003; Tegeder and Rentsch, 2010) (**Figure 1B**). This process involves several steps of membrane transport and the coordinated activity of diverse permeases (Tegeder, 2014). For example, AtAAP2 and AtAAP6 function in xylem-to-phloem transport (**Table 1**) at distinct sites in Arabidopsis (Hirner et al. 1998; Okumoto et al., 2002; Zhang et al., 2010) and have a marked impact on plant growth and seed yield (Perchlik and Tegeder, 2018). Similar functions have been proposed for OsAAP3, OsAAP5 and OsAAP5 in rice (Peng et al., 2014; Lu et al., 2018; Wang et al., 2019) and GmAAP6a in cucumber (Liu et al., 2020).

Phloem Partitioning to Sinks

The growth and development of the major sinks in the plant, like seeds, fruits and tubers, mainly relies on the photoassimilates transported in the phloem primarily from the leaves. Most species are apoplastic loaders and therefore, one transporter is required to export amino acids from the mesophyll cell to the cell wall and another to enter the phloem sap (**Figure 1C**). Bidirectional UMAMIT permeases are considered to mediate the first step. UAMAMIT11, UMAMIT14 and UMAMIT18 (SAR1) were localized in the leaf vascular bundle and proposed to be involved in phloem loading (Müller et al., 2015; Zhao et al., 2021). In coordination with the UMAMIT exporters (**Table 1**), the import of amino acids in the sieve elements is regulated by AAAP and APC permeases. Among them, functional evidence points to relevant roles to members of the *AAP*, *CAT* and ProT families (Zhang et al., 2010; Lehmann et al., 2011; Tegeder and Ward, 2012; Tegeder and Masclaux-Daubresse, 2018). As example, AAP8 regulates the import into the phloem of the amino acids exported by UMAMIT18 in Arabidopsis (Santiago and Tegeder, 2017). Interestingly, phloem loading not only determines sink growth and development, but also the physiology and primary metabolism of the sources (Pratelli and Pilot, 2014; The et al., 2021).

In many species, photoassimilates are unloaded via the symplastic pathway during the early stages of fruit development, which later shifts to an apoplastic pathway (Werner et al., 2011). This change is related to the closure of cell-to-cell connections and the new expression of plasma membrane transporters (**Figure 1D**). There is limited information about the unloading process in the tissues that will give rise to the fruit, whereas most studies have focused on the control of amino acid import into seeds. In the developing seeds, endosperm and embryo are symplastically isolated from the maternal seed coat (Patrick and Offler, 2001). In Arabidopsis, UMAMIT11, UMAMIT14, UMAMIT18, UMAMIT28 and UMAMIT29 facilitate amino acid unloading to the apoplast at the funiculus vasculature to fuel seed N demand (Müller et al., 2015). Once in the seed apoplast, AAP and CAT permeases, like AAP1, AAP8 and CAT6, facilitate amino acid loading into the embryo (Hirner et al., 1998; Hammes et al., 2006; Schmidt et al., 2007; Sanders et al., 2009; Tegeder and Masclaux-Daubresse, 2017 and references therein) (**Figure 1E**).

Subcellular Transport

In addition to their roles in long-distance transport between organs, amino acid transporters also regulate the distribution of amino acids among intracellular compartments (**Figure 1D**; **Table 1**). This intracellular trafficking is essential for maintaining amino acid homeostasis, supporting metabolic processes in different organelles, and coordinating nitrogen metabolism with cellular energy and carbon status (Tegeder and Rentsch, 2010; Pratelli and Pilot, 2014). Amino acid biosynthetic pathways involve cytosol, mitochondria, peroxisomes and chloroplasts, and transport across organelle membranes is required to link amino acid biosynthesis and catabolism (Heinig et al., 2013; Galili et al., 2016; Pan et al., 2020; Medeiros et al., 2021; Moller et al., 2021).

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The outer envelope membrane of plastids allows non-specific movement of amino acids through the OEP16 channel (Pohlmeyer et al., 1997), but the inner membrane acts as the barrier for controlled exchange of amino acids. The *DIT2.1* gene was reported to encode for a plastidic malate/glutamate translocator essential for the photorespiratory pathways (Renné et al., 2003). Furthermore, the UMAMIT44 permease of *A. thaliana* also regulates glutamate export and glutamate homeostasis within and outside the chloroplast (The et al., 2024). In addition, Arabidopsis RETICULATA1 (RE1) and PhpCAT from *Petunia hybrida* regulate the flux of basic and cationic amino acids, respectively (Widhalm et al., 2015; Kuhnert et al., 2025).

In the mitochondria, low selectivity VDAC porins facilitate the exchange of amino acids across the outer membrane (Pudelski et al., 2010). Among the mitochondrial MCF genes, two basic amino acid carriers, BAC1 and BAC2 are involved in the transport of amino acids across the inner membrane (Hoyos et al., 2003).

Vacuoles can store a large content of amino acid pool in plant cells (Winter et al., 1993; Tan et al., 2019). In Arabidopsis, AtCAT2 and AtCAT4 were primarily localized in the tonoplast membrane and might have a relevant role in the regulation of tissue amino acid contents (Yang et al., 2014). In tomato, the GABA/Glu/Asp exchanger SlCAT9 of the tonoplast is involved in the accumulation of all three amino acids in the vacuole of mature fruits (Snowden et al., 2015).

6. Role of Amino Acid Permeases in the Determination of Yield, Nutrient Use Efficiency and Quality of Crops

Efforts on improving crop yield and NUE have been traditionally focused on processes controlling the uptake of inorganic N from the soil, the assimilation of nitrate and ammonium, and the recycling of organic nitrogen (Yanagisawa et al., 2004; Masclaux-Daubresse et al., 2010; The et al., 2021; Melino et al., 2022). In several crop species, a positive correlation of the expression of key genes involved in N uptake, assimilation and remobilization with plant biomass, yield production and NUE have been reported (Martin et al., 2006; Egami et al., 2012; Fan et al., 2016; Fang et al., 2017; Gao et al., 2019; Yu et al., 2019). However, these approaches have often produced variable results due to metabolic and post-transcriptional regulation, as well as differences in nitrogen availability, since the factors limiting NUE differ under low and high nitrogen supply.

Beyond nitrogen acquisition and assimilation, the internal distribution of assimilated nitrogen within the plant is a key determinant of crop productivity. In particular, the transport of amino acids regulates nitrogen partitioning from source to growing organs and reproductive structures, thereby influencing biomass accumulation, yield formation, and the nitrogen content of harvested organs (Perchlik and Tegeder, 2017).

Role of Amino Acid Permeases in the Determination of Crop Yield

The adequate supply of sugars and amino acids to the developing sinks determines plant growth and yield (Lawlor, 2001). Amino acids are constituents of proteins and precursors of many components of the primary and specialized metabolites of the cells. The permeases regulate the long-distance transport of amino acids from organ sources to the sinks and therefore control the amount of imported amino acids by the harvested organs in crops (e.g., fruits, tubers, inflorescences, …). Besides growth and development of sinks, storage compounds like proteins, lipids and carbohydrates were also accumulated, being crucial for yield and nutritional value (Yadav et al., 2015; ElShamey et al., 2025; Winichayakul and Roberts, 2025).

Most functional analyses on the role of amino acid permeases in the determination of crop production have been addressed in legumes and cereals, where grain/seed are the harvested organs (**Table 2**). In rice, permeases OsAAP1, OsAAP4, OsAAP8, OsAAP15, OsAAP18, OsANT1 and OsLHT1 were reported to regulate growth and grain yield (Ji et al., 2020; Fang et al., 2021; Yang et al., 2023; He et al., 2025; Nie et al., 2025; He et al., 2026; Li et al., 2026). Overexpression of these genes enhances tillering and promotes amino acid transport to the developing grains, whereas loss-of-

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function mutants display the opposite effects. These effects have been linked, at least in part, to cytokinin-mediated regulation.

In contrast, other permeases such as OsAAP3, OsAAP5, OsAAP7 and OsAAP12 act as negative regulators of tillering and grain yield (Lu et al., 2018; Wang et al., 2019; Jin et al., 2024). Accordingly, a survey among 521 cultivated rice varieties showed a negative correlation in the expression of *OsAAP7* with grain yield (Jin et al., 2024). Similarly, variation in OsAAP5 expression has been associated with differences in tillering between indica and japonica varieties (Wang et al., 2019). Reduced expression of *OsAAP5* leads to the accumulation of specific neutral and basic amino acids (Lys, Arg, Val and Ala), which was proposed to promote tiller growth (Zhang et al., 2010; Wang et al., 2019).

Manipulation of amino acid transporters has also been shown to influence sink strength in other crops. In wheat, the endosperm-specific overexpression of *TaAAP13* increased grain size, N content and weight by enhancing amino acid import, although the total number of grains was reduced due to source limitations (Wan et al., 2021). Similarly, enhanced amino acid transport to developing seeds has been reported in maize and millet through overexpression of *AtAAP1* and *SiAAP9*, respectively (Chen et al., 2021; Meng et al., 2024).

In legumes, several AAP transporters have been implicated in the regulation of amino acid transport to seeds (Rolletschek et al., 2005; Zhang et al., 2015; Liu et al., 2020; Lu et al., 2020; Zhang et al., 2025a). Overexpression of the *PsAAP1* gene in pea source and sink tissues increased photosynthesis, vegetative biomass and amino acid content in the phloem, resulting in higher total N content in seeds and seed yield (Zhang et al., 2015). The enhanced yield was associated with an increased number of seeds but not seed size. Notably, also higher amino acid contents were reported in the xylem, as well as N uptake and assimilation.

A related 'push-and-pull' strategy combining carbon and nitrogen transport was demonstrated by overexpressing the sucrose transporter *SUT1* in pea source and sink tissues (Lu et al., 2020). Besides the expected increase in sucrose levels in leaves, phloem and seeds, enhanced amino acid assimilation and transport to developing seeds was observed. Expression of several amino acid transporters, including *PsAAP2*, *PsAAPP3* and *PsCAT9*, was up-regulated in developing cotyledons, leading to increased yield and protein and starch accumulation in mature seeds. These findings highlight the close and complex coordination between C and N metabolism, allocation and partitioning in the plant. Consistently, simultaneous overexpression of *PsSUT1* and *PsAAP1(3a)* increased seed number and protein content in pea, without affecting seed weight (Grant et al., 2021).

A positive impact of *AAP* genes in amino acid transport to sinks was also found in soybean (Liu et al., 2020; Zhang et al., 2025a). For example, the overexpression of the *GmAAP6-like* gene increased seed weight when expressed in Arabidopsis (Zhang et al., 2025a). Likewise, overexpressing the broad bean *VfAAP1* gene enhanced seed weight and yield in both pea and *Vicia narbonensis* (Rolletschek et al., 2005), supporting the general role of AAP transporters in regulating amino acid partitioning to the seed within the *Fabaceae* family.

Furthermore, amino acid permeases are also involved in the export of fixed amino acids in the nodules of legumes (Garneau et al., 2018). In pea, down-regulation of *PsAAP6* through miRNA interference reduced N supply to shoots and roots and resulted in amino acid accumulation in the nodules, suggesting a regulatory role of this transporter in the coordination of nodule activity with plant N demand (Garneau et al., 2018).

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Table 2. Representative examples of amino acid permeases influencing crop yield, nitrogen use efficiency (NUE) and nutritional quality.

	Species	Gene	Function/mechanism	Phenotype	Reference
Crop yield	Rice	*OsAAP1*	Amino acid transport to grain	Tillering. Grain number and yield	Ji et al. 2020
	Rice	*OsAAP5*	Amino acid transport to grain	Tillering. Grain number and yield	Wang et al. 2019
	Wheat	*TaAAP13*	Grain sink strength	Grain size	Wan et al. 2021
	Pea	*PsAAP1*	Amino acid partitioning	Seed number and yield	Zhang et al. 2015
NUE	Pea	*PsAAP1*	N uptake, assimilation and transport	NUpE and NUtE	Perchlik and Tegeder 2017
	Soybean	*GmAAP6a*	Source to sink N transport	NUtE	Liu et al. 2020
	Rice	*OsAAP15*	Panicle development	NUpE	Yang et al. 2023
	Rice	*OsLHT1*	Amino acid uptake and transport	NUpE and NUtE	Guo et al. 2020
Nutritional quality	Rice	*OsAAP6*	Amino acid unloading in grain	Grain protein content	Peng et al. 2014
	Wheat	*TaAAP13*	Amino acid unloading in endosperm	Grain amino acid content	Wan et al. 2021
	Maize	*ZmAAP6*	Amino acid unloading in grain	Grain protein content	Wang et al. 2022
	Tomato	*SlCAT9*	Amino acid storage in vacuole	Fruit amino acid content	Snowden et al. 2015

NUE: Nitrogen Use Efficiency; NUpE: Nitrogen Uptake Efficiency; NUtE: Nitrogen utilization Efficiency

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Compared with grain crops, relatively few studies have examined the role of amino acid permeases in edible fruit- and tuber-producing species. Nevertheless, evidence from cucumber, potato, and tomato suggests that these transporters also influence yield-related traits. In cucumber, disruption of CsAAP2 reduced leaf size and fruit weight, indicating a role in source–sink amino acid transport (Yao et al., 2023). In potato, altered expression of *StAAP1* influenced tuber morphology but did not significantly affect overall yield (Koch et al., 2003; Zhang et al., 2025b). In tomato, combinatorial manipulation of genes involved in carbon and nitrogen transport, including amino acid permeases, has demonstrated potential for improving fruit yield (Vallarino et al., 2020).

Taken together, these results demonstrate that amino acid permeases are key regulators of N partitioning from sources to sinks. By controlling amino acid fluxes at multiple stages of transport, these transporters influence biomass accumulation and crop yield (**Table 2**). Their effects are context-dependent, varying with developmental stage, nitrogen availability, and source–sink balance, but overall, they represent powerful targets for improving crop productivity through breeding and biotechnological approaches.

Impact of Amino Acid Transporters on Nutritional Value and Crop Quality

Amino acids are key components of the nutritional and organoleptic traits of cereal and leguminous crops, as free amino acid content or as components of storage proteins of seeds (Bright et al., 1983). Consequently, amino acid transporters may play important roles in regulating the flux of assimilated nitrogen to harvested organs and thus influence crop quality.

In cereals, grain protein content (GPC) is a key quality trait affecting both nutritional value and processing characteristics. Several amino acid transporters have been linked to the regulation of amino acid import into developing grains. The permeases *TaAAP2* and *TaAAP13* are highly expressed in grain transfer cells of wheat and are associated with protein accumulation in the endosperm (Wan et al., 2021). Manipulation of *TaAAP13* expression alters amino acid distribution within the grain and influences gluten protein accumulation.

In rice, the qPC1 QTL, encoding *OsAAP6*, controls grain protein content by regulating the synthesis and accumulation of several storage proteins like glutelins, globulins and prolamine (Peng et al., 2014). Additional AAPs, including OsAAP4, OsAAP5, OsAAP6, OsAAP10 and OsAAP11, have been also implicated in determining free amino acid content and grain protein levels (Wang et al., 2019; Guo et al., 2020; Wang et al., 2020; Yang et al., 2023; Li et al., 2026). Interestingly, several studies also reported trade-offs between nitrogen and carbon accumulation in grains when the expression of permeases like *OsLHT1* and *OsAAP8*, reflected in inverse relationships between protein and starch or amylose content in grains (Guo et al., 2020; Wang et al., 2020; Peng et al., 2024).

Similar regulatory roles have been reported in maize and legumes. For instance, ZmAAP6 influences protein accumulation during maize seed development (Wang et al., 2022), while overexpression of *VfAAP1* or *PsAAP1* in legumes increases seed nitrogen, amino acid content, and storage protein accumulation (Rolletschek et al., 2005). When sugars and amino acid partitioning was boosted by concurrent overexpressing the *SUT1* and AAP1(3a) genes in pea (Lu et al., 2020), an increase in sucrose and protein contents was induced in the developing seed (Grant et al., 2021).

In fruit and tuber organ crops, amino acid permeases also influence the nutritional composition of the edible organ. In cucumber, loss-of-function mutants of *CsAAP2* displayed reduced amino acid levels shoot and fruits (Yao et al., 2023). Similarly, the antisense suppression of *StAAP1* in potato reduced levels of free amino acids in the tubers, although starch contents were not affected (Koch et al., 2003). Similarly, potato *StAAP8* overexpression lines exhibit increased levels of amino acid and proteins (Zhang et al., 2025b). In tomato, overexpression of the tonoplast transporter *SlCAT9* altered fruit amino acid composition by increasing glutamate, aspartate, and γ-aminobutyric acid levels (Snowden et al., 2015). Genome-wide association studies in pepper have also identified amino acid transporter genes associated with fruit nutritional traits (von Steimker et al., 2025).

Summarizing, these findings demonstrate that AAAP permeases influence the accumulation of key metabolites affecting the nutritional and organoleptic quality of crop products (**Table 2**). Notably,

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alterations in assimilated N flux also impact C compound partitioning, thereby influencing carbohydrate content.

Members of the *UMAMIT* family also contribute to crop nutritional quality through their roles in the distribution of nitrogen-containing specialized metabolites. In *Brassicaceae* crops, glucosinolates are key compounds influencing flavour, anti-nutritional properties, and agronomic quality (Cartea and Velasco, 2008). Their long-distance transport involves both glucosinolate transporters (GTRs) and UMAMIT permeases, which mediate export from biosynthetic cells into the apoplast (Agyenim-Botaeng et al., 2025). In Arabidopsis, *umamit29 umamit30 umamit31* triple mutant lines resulted in marked reductions in glucosinolates in the seeds (Xu et al., 2023). Manipulating these transport processes may offer strategies to optimize glucosinolate distribution, reducing anti-nutritional compounds in edible tissues while maintaining their protective functions in source organs.

Role of Amino Acid Permeases in the Determination of Nitrogen Use Efficiency (NUE) in Crops

NUE is defined as the seed (or harvested organ) yield per unit of N available in the soil and fertilizer (Moll et al., 1982). Improving NUE is a major objective of sustainable agriculture, as it allows high crop productivity while reducing fertilizer inputs, and therefore costs and contamination to the environment (van Bueren and Struik, 2017). NUE is a complex parameter including several physiological processes involving N, like uptake, assimilation, remobilization, metabolism, storage and transport (Xu et al., 2012). Among these processes, permeases represent key determinants for NUE since they control the partitioning of assimilated nitrogen to the harvested organs (The et al., 2021).

Evidences from several crop species supports this view. In pea, overexpression of the *PsAAP1* transporter enhanced both nitrogen uptake efficiency and nitrogen utilization efficiency, resulting in increased yield under different nitrogen supply levels (Perchlik and Tegeder, 2017). Similarly, overexpression of *GmAAP6a* in soybean promoted amino acid transport to seeds and improved seed nitrogen content and NUE (Liu et al., 2020).

Additional studies in rice have further revealed complex regulatory roles for amino acid permeases in NUE. For example, OsAAP3 enhances amino acid partitioning to the grain (Lu et al., 2018), whereas OsAAP7 negatively regulates NUE in rice through its effect on N uptake efficiency (Jin et al., 2024). Other transporters such as OsAAP15 and OsLHT1 also influence NUE by regulating panicle development and amino acid transport between roots and shoots (Guo et al., 2020; Yang et al., 2023). More recently, OsLHT5 has been shown to enhance NUE through improved amino acid utilization, with natural variation in this gene affecting transport capacity (Wang et al., 2026).

Although functional evidence in non-grain crops remains limited, transcriptomic and association studies in *Brassicaceae* and tomato have identified amino acid permeases as candidate genes associated with NUE-related traits (Awasthi et al., 2025; Gil-Villar et al., 2025).

These results highlight the central role of amino acid permeases in controlling nitrogen partitioning within plants and emphasize their potential as targets for improving nitrogen use efficiency in crop production systems (**Table 2**).

7. Conclusions and Future Perspectives

Amino acid permeases play central roles in plant nitrogen economy by regulating the distribution of assimilated nitrogen among tissues and cellular compartments. Increasing evidence from both model species and crops demonstrates that the activity of these transporters influences key agronomic traits, including biomass accumulation, seed yield, nitrogen use efficiency, and the nutritional quality of harvested organs. Members of the AAAP and UMAMIT transporter families have emerged as major regulators of source–sink nitrogen partitioning and long-distance nitrogen transport.

Despite significant progress in the identification and characterization of amino acid transporters, many aspects of their physiological regulation remain poorly understood. A major challenge is the extensive functional redundancy observed among transporter family members, which complicates

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the interpretation of mutant phenotypes and often masks subtle transport functions. Future studies combining multiplex genome editing approaches (e.g., CRISPR/Cas-based multi-gene knockouts), advanced phenotyping platforms, and cell-type-specific expression systems will be essential to disentangle the contributions of individual permeases to plant nitrogen distribution.

Another important research direction concerns the coordination between amino acid transport and carbon metabolism and transport. Nitrogen and carbon fluxes are tightly interconnected, and several studies have shown that perturbations in amino acid transport can influence photosynthetic performance, carbohydrate partitioning, and overall metabolic homeostasis. A systems-level understanding of how amino acid permeases integrate into the regulatory networks governing carbon–nitrogen balance will therefore be critical for predicting the metabolic consequences of transporter manipulation.

In addition, the regulatory mechanisms controlling transporter activity remain largely unexplored. Beyond transcriptional regulation, post-translational mechanisms such as phosphorylation, ubiquitination, and membrane trafficking are likely to play key roles in modulating transporter localization and activity in response to developmental and environmental signals. Small RNA- and peptide-mediated regulation as well as epigenetic mechanisms may also contribute to the fine-tuning of transporter expression under fluctuating nutrient conditions. Elucidating these regulatory layers will provide new insights into how plants dynamically adjust nitrogen allocation and partitioning.

A major technological frontier for the field is the development of approaches capable of monitoring amino acid dynamics in vivo and at single-cell resolution. Conventional metabolomic analyses rely on bulk tissue extraction and provide only static snapshots of metabolite pools, masking cell-specific transport processes. Emerging tools such as genetically encoded fluorescent amino acid biosensors, including FRET-based metabolite reporters, together with stable isotope tracing and high-resolution mass spectrometry, offer promising opportunities to visualize and quantify amino acid fluxes directly in living tissues. In particular, real-time imaging of amino acid concentrations at the cellular and subcellular levels could provide unprecedented insight into transporter activity, source–sink gradients, and intercellular nitrogen movement. Integrating these approaches with cell-type-resolved transcriptomics and metabolic flux analyses will enable a more comprehensive understanding of amino acid transport networks.

From an applied perspective, amino acid transporters represent promising targets for crop improvement. Engineering strategies that enhance the partitioning of assimilated nitrogen to the harvested organs have already demonstrated potential to increase seed yield and protein content in several species. However, achieving optimal improvements will likely require coordinated manipulation of multiple transporters together with metabolic and regulatory components to maintain the balance between nitrogen uptake, assimilation, and partitioning.

Future research should therefore focus on integrating molecular genetics, in vivo metabolite imaging, and systems biology approaches to build a predictive framework for amino acid transport in plants. Such knowledge will facilitate the development of crop varieties with improved nitrogen use efficiency, reduced fertilizer requirements, and enhanced nutritional quality, contributing to more sustainable agricultural systems.

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