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Carbon-Nitrogen Interactions in Plants: Regulation of Nitrogen Assimilation and Metabolic Homeostasis

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Abstract

Carbon (C) and nitrogen (N) are the two major elements that jointly determine plant growth, biomass production, developmental plasticity, and productivity. Carbon metabolism supplies the energy, reducing power, and carbon skeletons required for inorganic nitrogen assimilation, whereas nitrogen is an essential component of photosynthetic proteins, chlorophyll, nucleic acids, amino acids, and enzymes required for carbon fixation. Consequently, plants must continuously coordinate C and N acquisition, assimilation, transport, storage, and utilization according to developmental stage and environmental conditions. Nitrogen assimilation begins with nitrate reduction to nitrite and ammonium, followed primarily by incorporation of ammonium into glutamine and glutamate through the glutamine synthetase/glutamate synthase (GS/GOGAT) cycle. These reactions are strongly dependent on carbon-derived metabolites, particularly 2-oxoglutarate (2-OG), ATP, reductant, and sugars. Conversely, nitrogen availability influences photosynthetic capacity, carbohydrate partitioning, respiration, organic acid metabolism, and plant architecture. Increasing evidence demonstrates that sugars, nitrate, amino acids, and signaling metabolites such as sucrose and trehalose-6-phosphate (Tre6P) participate in C–N sensing. Regulatory hubs including TARGET OF RAPAMYCIN (TOR), SUCROSE NON-FERMENTING1-RELATED PROTEIN KINASE1 (SnRK1), nitrate-responsive transcription factors, and hormone signaling pathways integrate nutritional information with plant growth. Understanding these interactions is particularly important for improving nitrogen-use efficiency (NUE), reducing excessive fertilizer use, and developing climate-resilient and sustainable cropping systems. This review summarizes the biochemical basis of C–N interactions, regulation of nitrogen assimilation, metabolic and signaling networks involved in C–N homeostasis, responses to environmental stresses, and emerging strategies for improving crop productivity through coordinated manipulation of carbon and nitrogen metabolism.

Keywords: carbon metabolism; nitrogen assimilation; C–N balance; GS/GOGAT; nitrate signaling; nitrogen-use efficiency; sucrose; 2-oxoglutarate; TOR; SnRK1; sustainable agriculture.

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1. Introduction

Carbon and nitrogen metabolism represent two interconnected metabolic networks that underpin plant growth and development. Carbon is primarily acquired through atmospheric CO_2 and converted into carbohydrates through photosynthesis, whereas nitrogen is obtained mainly as nitrate and ammonium from the soil. Carbon compounds provide energy and carbon skeletons for nitrogen assimilation, while nitrogen is incorporated into proteins, chlorophyll, nucleic acids, enzymes, amino acids, and other cellular constituents. Thus, plant productivity depends not simply on the availability of either nutrient individually but on their coordinated acquisition and utilization.

The close relationship between C and N metabolism has been recognized for several decades. Early studies demonstrated that changes in nitrate availability can reprogram carbon metabolism, while changes in sugar availability affect nitrogen uptake and assimilation (Coruzzi & Bush, 2001; Stitt, 1999). More recent research has established that this relationship is mediated by complex metabolic and signaling networks rather than by simple substrate availability. Plants continuously monitor their nutritional status through sugars, nitrate, amino acids, organic acids, energy status, and hormones, thereby adjusting gene expression and enzyme activities to maintain metabolic homeostasis (Artins et al., 2024).

Nitrogen assimilation is particularly dependent on carbon metabolism. Nitrate assimilation requires reducing equivalents and energy, while ammonium assimilation requires carbon skeletons, principally 2-oxoglutarate. The GS/GOGAT cycle therefore represents an important biochemical intersection between C and N metabolism. The GS/GOGAT pathway incorporates ammonium into glutamine and glutamate, which subsequently serve as nitrogen donors for the synthesis of most nitrogen-containing compounds (Liu et al., 2022).

Conversely, nitrogen availability has profound effects on carbon fixation. Nitrogen is required for the synthesis of chlorophyll, Rubisco, photosynthetic electron transport proteins, and other components of the photosynthetic apparatus. Consequently, N deficiency frequently decreases photosynthetic capacity, whereas adequate N availability can support greater carbon assimilation and biomass production. Recent reviews emphasize that the coordination of photosynthesis, N uptake, and N assimilation is central to improving crop NUE and reducing the environmental costs associated with excessive fertilizer application (Liu et al., 2022; Li et al., 2018).

2. Biochemical Basis of Carbon–Nitrogen Interactions

2.1 Carbon metabolism as the foundation of nitrogen assimilation

Photosynthesis provides carbohydrates that serve several functions in nitrogen metabolism. Sugars can be transported from source leaves to roots and other sink tissues, where they provide respiratory substrates and contribute carbon skeletons for amino acid biosynthesis. In addition, photosynthetic electron transport generates reducing power that can support nitrate and nitrite reduction.

Nitrate assimilation is an energetically demanding process. Nitrate is first reduced to nitrite by nitrate reductase (NR) in the cytosol. Nitrite is subsequently reduced to ammonium by nitrite reductase (NiR), primarily within plastids. Ammonium is then assimilated through GS and GOGAT (Liu et al., 2022). The overall pathway can be represented as:

$NO_3^- \rightarrow NO_2^- \rightarrow NH_4^+ \rightarrow$ Gln $\rightarrow$ Glu $\rightarrow$ amino acids

Nitrate assimilation therefore depends on ATP, reducing equivalents, and carbon skeletons. In non-photosynthetic tissues, carbon skeletons and reductant are largely supplied through respiration and organic

acid metabolism. In photosynthetic tissues, chloroplast metabolism provides substantial reducing power for nitrogen assimilation (Foyer & Noctor, 2002).

2.2 The GS/GOGAT cycle as the central C–N metabolic junction

The GS/GOGAT cycle represents the principal route for ammonium assimilation in higher plants. GS catalyzes the ATP-dependent incorporation of ammonium into glutamate, generating glutamine. Subsequently, GOGAT transfers the amide nitrogen of glutamine to 2-OG, producing two molecules of glutamate.

The simplified reactions are:

Glutamate + NH_4^+ + ATP → Glutamine + ADP + Pi

Glutamine + 2-OG + reductant → 2 Glutamate

The importance of this pathway is that 2-OG is derived from carbon metabolism, particularly the tricarboxylic acid (TCA) cycle. Therefore, nitrogen assimilation requires an adequate supply of carbon metabolites. The glutamate produced by GOGAT functions both as an amino acid and as a substrate for further transamination reactions, linking inorganic N assimilation with the synthesis of numerous amino acids (Coruzzi, 2003; Liu et al., 2022).

Plants possess distinct GS and GOGAT isoforms that operate in different tissues and cellular compartments. Plastidic GS2 and ferredoxin-dependent GOGAT are particularly important in leaves, whereas cytosolic GS1 and NADH-dependent GOGAT contribute significantly to nitrogen metabolism in roots and vascular tissues. Such compartmentalization allows nitrogen assimilation to respond to local carbon availability and metabolic requirements (Liu et al., 2022).

3. Reciprocal Regulation Between Carbon and Nitrogen Metabolism

The C–N relationship is bidirectional. Carbon availability regulates N acquisition and assimilation, whereas N availability regulates carbon fixation, allocation, and respiration (Figure 1).

3.1 Regulation of nitrogen metabolism by sugars

Sugars are not merely products of photosynthesis; they also function as signaling molecules. Sucrose, glucose, fructose, and related metabolites can regulate genes involved in nitrate uptake, nitrate reduction, amino acid biosynthesis, and carbohydrate metabolism. Sugar signaling therefore enables plants to coordinate N acquisition with carbon availability.

When photosynthetic carbon supply is high, increased sugar availability can stimulate nitrate uptake and assimilation. Conversely, under carbon limitation, plants may restrict the energetically expensive conversion of inorganic N into organic compounds. Stitt and Krapp (1999) demonstrated that sugar availability can influence nitrate and ammonium uptake, organic acid synthesis, nitrogen assimilation, and the expression of genes associated with nitrogen metabolism.

This coordination is physiologically logical. Assimilating nitrate without adequate carbon skeletons can result in accumulation of nitrogenous intermediates and inefficient expenditure of cellular energy. Plants therefore use carbon status as an important determinant of whether additional nitrogen can be assimilated effectively.

3.2 Regulation of carbon metabolism by nitrogen

Nitrogen availability also modifies carbon metabolism. Nitrogen deficiency generally decreases chlorophyll concentration, photosynthetic enzyme abundance, leaf expansion, and photosynthetic capacity. At the same time, carbon allocation can shift toward storage compounds, including soluble sugars and starch.

Under adequate nitrogen supply, carbon can be invested in protein synthesis, leaf development, photosynthetic machinery, and reproductive growth. In contrast, when nitrogen becomes limiting, carbon assimilation may exceed the capacity for growth and nitrogen-containing compound synthesis, resulting in accumulation of carbohydrates. Such interactions explain why increasing atmospheric CO_2 does not necessarily result in proportional increases in biomass when nitrogen availability is insufficient (Stitt & Krapp, 1999).

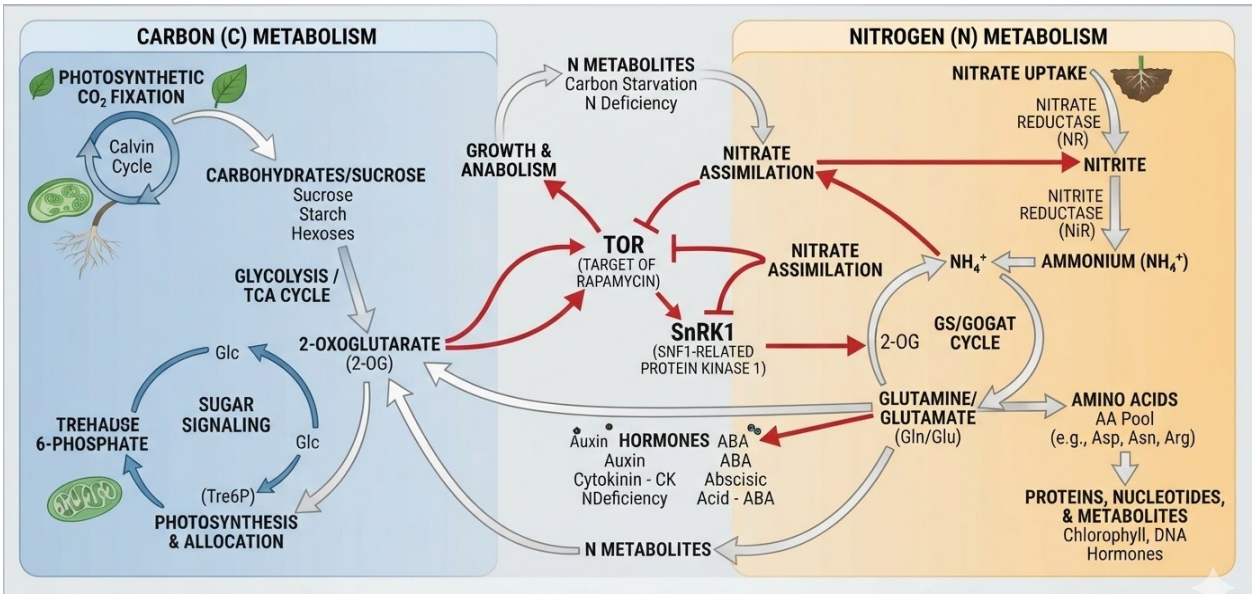


Figure 1: Metabolic coordination and signaling crosstalk between Carbon (C) Metabolism (blue) and Nitrogen (N) Metabolism (orange) in plants.

4. Carbon Skeletons and the Regulation of Nitrogen Assimilation

One of the most important metabolic links between C and N is the supply of 2-oxoglutarate. Nitrogen assimilation consumes carbon skeletons, particularly during the GS/GOGAT cycle and subsequent amino acid synthesis.

2-OG is produced primarily through TCA-cycle metabolism. Its availability is influenced by photosynthetic carbon fixation, sucrose metabolism, glycolysis, respiration, and anaplerotic reactions. Phosphoenolpyruvate carboxylase (PEPC), for example, contributes to the production of oxaloacetate, which can subsequently feed TCA-cycle metabolism and increase organic acid availability. The interaction between nitrate assimilation and organic acid metabolism is therefore highly coordinated. Increased N assimilation can stimulate the production of organic acids required as carbon acceptors, while increased carbon availability can facilitate N assimilation. This reciprocal relationship prevents excessive accumulation of either carbon or inorganic nitrogen.

In roots, where photosynthesis does not directly occur, sucrose transported from leaves provides an important carbon source. Root respiration generates ATP and reducing equivalents, while TCA-cycle activity supplies

carbon skeletons for ammonium assimilation. Studies of nitrate-to-glutamate assimilation in roots have emphasized the importance of photosynthate-derived carbon and reductant supply for supporting nitrate assimilation (Takahashi et al., 2019).

5. Nitrate as a Nutrient and Signaling Molecule

Nitrate has a dual function in plants: it is both a nitrogen nutrient and a signaling molecule. Following nitrate perception, plants rapidly modify the expression of genes involved in nitrate transport, reduction, assimilation, root development, and carbon metabolism.

Nitrate transporters, particularly members of the NRT1 and NRT2 families, participate in nitrate uptake and distribution. Some transport proteins can also function as nutrient sensors or "transceptors," linking nitrate availability to intracellular signaling (Krapp et al., 2014). The primary nitrate response involves rapid transcriptional changes following nitrate exposure. Regulatory components including NIN-like proteins (NLPs), LBD transcription factors, and nitrate transport/sensing systems participate in this response (Medici & Krouk, 2014).

Importantly, nitrate signaling is not independent of carbon status. Nitrate-induced gene expression is influenced by sugars and metabolic intermediates. Thus, the nitrate response can be viewed as a component of an integrated nutritional signaling network rather than an isolated pathway.

6. Glutamine, Glutamate, and 2-Oxoglutarate as Metabolic Signals

The products of nitrogen assimilation can themselves function as metabolic signals. Glutamine and glutamate occupy central positions in plant metabolism because they connect inorganic nitrogen with amino acid biosynthesis.

Glutamine is not only a product of GS activity but also serves as an N donor for the synthesis of nucleotides, amino sugars, amino acids, and several other metabolites. Glutamate participates in transamination reactions and contributes to both N redistribution and C metabolism. Recent research has also strengthened the concept that glutamine functions as a signaling molecule, although the mechanisms and physiological consequences of glutamine sensing remain incompletely resolved (Liao et al., 2023).

The ratio of carbon metabolites such as 2-OG to nitrogen metabolites such as glutamine may provide the plant with information about the relative availability of C and N. A high 2-OG status can indicate adequate carbon skeleton availability for N assimilation, whereas high glutamine levels may indicate that N assimilation is proceeding rapidly relative to carbon availability. Such metabolite-based information can feed back to transporter activity, gene expression, and enzyme regulation.

7. Sugar Signaling and Trehalose-6-Phosphate

Trehalose-6-phosphate (Tre6P) has emerged as an important metabolic signal linking sucrose status with growth and metabolism. The sucrose–Tre6P relationship provides a mechanism through which carbon availability can influence anabolic activity.

Tre6P has been associated with regulation of sucrose metabolism and plant growth, and experimental manipulation of Tre6P can influence nitrate reductase activity, organic acid metabolism, and amino acid accumulation. Figueroa et al. (2016) demonstrated that increased Tre6P stimulated nitrate assimilation and anaplerotic organic acid synthesis, thereby redirecting carbon toward amino acid production.

This finding is particularly significant for C–N integration because it indicates that a sugar-related signaling metabolite can coordinate carbon partitioning with nitrogen assimilation. Tre6P may therefore represent an important regulatory interface between photosynthetic carbon production and nitrogen-dependent growth.

8. TOR and SnRK1: Central Regulators of C–N Homeostasis

At the whole-cell level, plants employ major energy and nutrient signaling pathways to coordinate growth with resource availability. Two important regulators are TOR and SnRK1.

8.1 TOR signaling

TOR promotes anabolic growth when carbon and nutrient resources are sufficient. Increased sugar availability can activate TOR-associated growth processes, including protein synthesis, cell proliferation, and biosynthetic activity.

Because protein synthesis requires large quantities of nitrogen, TOR activity must be coordinated with nitrogen availability. Thus, TOR provides a mechanism for coupling carbon availability and nutrient status with growth.

8.2 SnRK1 signaling

SnRK1 acts as an energy and carbon-status sensor. Under energy limitation, carbon starvation, or environmental stress, SnRK1 promotes metabolic reprogramming toward energy conservation and survival. Recent evidence indicates that SnRK1 participates directly in the integration of C and N signals and interacts with nitrate-responsive regulatory mechanisms (Artins et al., 2024).

The antagonistic relationship between TOR and SnRK1 provides a conceptual framework for understanding how plants balance growth and survival. When carbon and nutrients are abundant, anabolic processes dominate; when carbon or energy availability becomes limiting, conservation and stress-adaptation pathways become more prominent.

9. Hormonal Regulation of C–N Interactions

C–N metabolism is further integrated with phytohormonal signaling. Auxin, cytokinin, abscisic acid (ABA), ethylene, and other hormones interact with nitrate and sugar signaling.

Nitrate availability can influence root architecture through interactions with auxin and cytokinin. Local nitrate availability can stimulate lateral root development under appropriate conditions, thereby modifying the plant's capacity to acquire additional nutrients. Cytokinin synthesis and transport are also closely linked to nitrogen status and can influence shoot growth.

ABA provides an important connection between nutritional status and environmental stress. Under drought or other stresses, ABA signaling modifies stomatal behavior, carbon fixation, and resource allocation. Recent work indicates that ABA also interacts with TOR and SnRK1, creating a regulatory network that integrates energy status with environmental adaptation (Li et al., 2025).

Therefore, C–N homeostasis should not be considered an isolated metabolic phenomenon. It is embedded within a broader network involving nutrient sensors, sugars, amino acids, hormones, calcium signaling, and stress-responsive pathways.

10. C–N Balance Under Abiotic Stress

Environmental stresses frequently disturb C–N homeostasis. Drought, salinity, temperature extremes, elevated CO_2, and nutrient deficiency can modify photosynthesis, respiration, nitrate uptake, nitrogen assimilation, and carbohydrate allocation.

10.1 Drought

Drought decreases stomatal conductance and CO_2 assimilation, thereby reducing carbon availability. Simultaneously, soil water limitation restricts nutrient mobility and root N uptake. Reduced carbon availability may consequently limit nitrate assimilation, while altered N metabolism can further influence photosynthetic performance.

10.2 Salinity

Salinity affects both carbon fixation and nitrogen nutrition through osmotic stress, ion toxicity, oxidative stress, and altered nutrient transport. Plants may redirect carbon toward compatible solutes and antioxidant metabolism, potentially reducing carbon availability for growth and N assimilation.

10.3 Temperature

Temperature strongly influences enzyme activities and respiratory carbon expenditure. Recent global-scale modeling work indicates that nitrogen assimilation carries substantial carbon costs and that warming can alter these costs by changing soil N availability and plant metabolic requirements (Hu et al., 2025).

These findings emphasize the importance of considering C and N metabolism together when predicting plant responses to climate change.

11. Carbon–Nitrogen Interactions and Nitrogen-Use Efficiency

Nitrogen-use efficiency is broadly determined by the capacity of plants to acquire, assimilate, utilize, and remobilize nitrogen. Improving NUE is an important objective because excessive nitrogen fertilizer use contributes to economic losses and environmental problems, including nitrate leaching and eutrophication (Liu et al., 2022).

Manipulation of nitrogen assimilation enzymes such as NR, NiR, GS, GOGAT, and ASN has been investigated as a strategy for improving NUE. However, modifying a single N-assimilation enzyme may not always produce the desired improvement because nitrogen assimilation is constrained by carbon availability.

For instance, increasing GS activity without sufficient 2-OG, ATP, or reducing equivalents could create a metabolic imbalance. Similarly, enhancing nitrate uptake without increasing assimilation capacity could increase internal nitrate pools without proportionally increasing biomass production.

Therefore, future NUE improvement should increasingly focus on coordinated manipulation of C–N networks**,** including:

- enhanced photosynthetic carbon fixation;
- improved carbon allocation to roots;
- optimized nitrate uptake;
- efficient nitrate reduction;
- improved GS/GOGAT activity;
- enhanced 2-OG production;
- improved amino acid transport and remobilization;

- optimization of sugar and nitrogen signaling;
- manipulation of TOR/SnRK1 pathways; and
- development of crops with improved C–N coordination under stress.

Recent reviews similarly emphasize integration of photosynthesis, C–N metabolism, signaling, and crop improvement rather than treating nitrogen metabolism as an independent pathway (Li et al., 2025).

12. Implications for Sustainable Agriculture

The integration of C and N metabolism provides an important physiological foundation for sustainable agriculture. Conventional crop production often relies heavily on nitrogen fertilizers to maximize yield. However, nitrogen application beyond crop demand can result in substantial economic and environmental costs. Improving the coordination between carbon assimilation and nitrogen use could allow crops to produce greater biomass and yield from a given amount of available nitrogen. This could be achieved through conventional breeding, marker-assisted selection, genomic selection, transgenic approaches, genome editing, and precision nutrient management.

An important target is the synchronization of nitrogen supply with photosynthetic carbon availability. For example, improving root carbon allocation during periods of active nitrate uptake may support more efficient nitrate assimilation. Similarly, increasing photosynthetic efficiency could provide additional carbon skeletons and energy for nitrogen assimilation.

At the molecular level, manipulation of nitrate-responsive transcription factors, sugar signaling components, GS/GOGAT enzymes, and C–N regulatory hubs may provide opportunities for developing crops with improved NUE. However, because these pathways also regulate growth and stress responses, modifications need to be evaluated carefully across developmental stages and environmental conditions.

13. Future Perspectives

Despite substantial progress, several aspects of C–N integration remain incompletely understood. First, the precise mechanisms through which plants quantify their C:N status remain unresolved. Although sugars, amino acids, nitrate, and organic acids are recognized as important signals, their relative contributions under different developmental and environmental conditions require further investigation.

Second, spatial and temporal aspects of C–N signaling deserve greater attention. C–N interactions differ between roots and shoots, source and sink tissues, and day and night periods. Single-cell transcriptomics, spatial metabolomics, isotope tracing, and high-resolution imaging can provide new insights into these processes.

Third, climate change creates a need to understand C–N interactions under combined stresses. Elevated CO_2, warming, drought, and altered nitrogen deposition can interact in complex ways. The carbon cost of nitrogen assimilation may change under future climates, making C–N integration increasingly important for crop productivity (Hu et al., 2025).

Finally, future crop improvement should move beyond the optimization of individual genes or enzymes toward systems-level engineering of C–N metabolism**.** Integrating metabolic modeling, phenomics, genomics, and precision agriculture could facilitate the development of crops that synchronize carbon fixation, nitrogen acquisition, assimilation, and allocation.

14. Conclusion

Carbon and nitrogen metabolism are fundamentally interconnected processes that determine plant growth, development, productivity, and environmental adaptation. Carbon provides the energy, reductant, and carbon skeletons required for nitrogen assimilation, while nitrogen supports the photosynthetic machinery required for carbon fixation. The GS/GOGAT pathway represents a central biochemical connection, with 2-OG providing an essential carbon skeleton for the assimilation of ammonium into organic nitrogen.

Beyond metabolic interactions, plants possess sophisticated C–N signaling networks involving sugars, nitrate, amino acids, Tre6P, hormones, TOR, SnRK1, and nitrate-responsive transcription factors. These networks enable plants to balance growth with resource availability and to modify metabolism under environmental stress. Current research increasingly demonstrates that efficient nitrogen use cannot be achieved by optimizing nitrogen uptake or assimilation alone; rather, nitrogen metabolism must be coordinated with photosynthetic carbon supply and whole-plant carbon allocation.A systems-level understanding of C–N interactions therefore offers an important pathway toward improving NUE, maintaining crop productivity under changing environmental conditions, reducing fertilizer requirements, and strengthening sustainable agricultural production.

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