



Review

Research Progress in Crop Root Biology and Nitrogen Uptake and Use, with Emphasis on Cereal Crops

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Abstract: The biological characteristics of crop roots are closely related to the efficient utilization of nitrogen and have become a research hotspot in agricultural cultivation and breeding in recent years. The root system and root microbiota play a crucial role in both the basic and the plastic growth and development of plants in response to external environmental changes. Nitrogen is an indispensable nutrient element for crop growth, and the efficient utilization of nitrogen is the key to achieving the high yield and quality of crops and establishing environmentally friendly agricultural production. The nitrogen absorbed and utilized by rice mainly enters the aboveground part of the plant through the root system from within the soil. This process is explored from the perspective of root biology (root morphology, physiological and biochemical characteristics, root growth and development process and regulation, rhizosphere microorganisms, and their symbiotic systems), which is in line with the directions of “less investment, increased production, environmental protection, and sustainable development” in China. Based on the research status in this field at present, this article explored the interaction mechanism between crop root biology and nitrogen absorption and utilization, and looks forward to the future research directions for root biology. This study provides a theoretical basis for reducing nitrogen fertilizer application, optimizing nitrogen-efficient cultivation management techniques, and selecting nitrogen-efficient varieties.

Keywords: root morphology; root physiology; nitrogen efficiency; microorganism



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1. Introduction

Roots are important vegetative plant organs that have physiological functions, such as absorbing and transporting water and nutrients, fixing plants, and synthesizing and storing nutrients. Healthy roots can guarantee high-yielding crops that resist adverse environmental conditions.

Root biology is a cutting-edge discipline specializing in the study of root systems. Its purpose is to take the root system, the underground part of the crop, as the research object, then explore its functions, characteristics, and microecosystem, and finally provide a theoretical basis for plant growth regulation and genetic improvement [1,2]. Root biology is an important agronomic and ecological indicator. The research contents of this discipline include root morphological configuration; physiological and biochemical characteristics; root growth, development processes and regulation; rhizosphere microorganisms and their symbiotic systems; genetic characteristics, etc. Root biology encompasses the fields of microbiology, soil science, plant physiology, botany, molecular biology, genetics, morphology, and other disciplines [3].

Nitrogen efficiency refers to the ability to produce dry matter or grain yield using a unit of nitrogen [4]. From the perspective of the crop absorption and the utilization of nitrogen fertilizer, it can be divided into nitrogen absorption and utilization rates, physiological utilization rate, agronomic utilization rate, nitrogen partial productivity, nitrogen harvest index, nitrogen dry-matter production efficiency, and nitrogen grain production efficiency [5]. Among these, nitrogen absorption and utilization rates refer to the ratio of the difference in nitrogen accumulation between the nitrogen application and blank areas to the total nitrogen application amount [6]. The comprehensive optimization of crop management (key technologies, such as increasing density, reducing nitrogen fertilizer application, delaying nitrogen application, moderate wet/dry farming, and applying rapeseed cake fertilizer) can achieve the dual goals of grain yield increase and resource utilization by improving agronomic and physiological performances related to higher grain yield, nitrogen utilization efficiency (NUE), and irrigation water yield (IWP) to improve efficiency [7]. The optimization of nitrogen-efficient cultivation and management techniques is of great significance for achieving the sustainable development of green agriculture.

The high application and low utilization rates of nitrogen fertilizer have always been a problem for rice production in China. The excessive application of nitrogen fertilizer often leads to soil acidification, greenhouse gas emissions, groundwater nitrate pollution, environmental pollution, and decreased rice quality, which have become serious threats to the sustainable development of global intensive agriculture [8]. Improving the nitrogen utilization efficiency of rice is an important issue that urgently needs to be addressed for high-quality, efficient, ecological, and safe crop production [9]. In recent years, the *OsCERK1^{DY}* gene, the first key gene that effectively enhances rice yield by regulating efficient symbiosis between rice and arbuscular mycorrhizal fungi, has been successfully cloned and a new rice variety, “Ganzhuangdao 1”, carrying the *OsCERK1^{DY}* gene has been cultivated [8]. Its ecological benefits include reducing nitrogen fertilizer application and reducing negative effects on soil, which are of great significance.

All nitrogen in the soil is called soil total nitrogen, which is divided into organic and inorganic nitrogen. Although almost all of the nitrogen absorbed by plants is in the inorganic form, the vast majority of soil nitrogen is organic nitrogen. Organic nitrogen in the soil nitrogen pool must be continuously transformed into nitrogen that is available to plants through microbial mineralization, namely, nitrate nitrogen and ammonium nitrogen, which are nitrogen forms in the soil that can be directly utilized by plants [10]. Ammonium nitrogen in the soil exists in the form of ammonium salts. After ammonium salt is dissolved in the soil solution, it is not only absorbed by crops or used by microorganisms, but is also transformed into nitrate nitrogen through nitrification [11]. Due to the anionic nature of nitrate nitrogen, it mainly exists in soil solutions. With the migration of water, nitrate nitrogen can be transported to various places and supplied to crops at any time and place to meet the absorption demands of different root systems. Therefore, nitrate nitrogen is the most important and primary form of nitrogen that crops can directly utilize, and it also causes the disadvantage of nitrate nitrogen being easily lost with water [12]. Thus, if inorganic nitrogen is mostly present in the form of ammonium nitrogen in the soil, it may be more conducive to retaining nitrogen. The excessive use of nitrogen fertilizer reduces soil pH, leading to a decrease in soil bacteria [13]. The combination of nitrogen and organic fertilizers can effectively improve the physical and chemical properties of soil and reduce soil bulk density [14]. As the “second genome” of plants, rhizosphere microorganisms can improve the development of primary roots, lateral roots, and root hairs, as well as promote plant growth and rhizosphere nutrient absorption. In recent years, the application of genomics metabonomics, genomics transcriptomics, and other related technologies has revealed the growth-promoting mechanism of microorganisms, providing new ideas for the development of microbial agents [15]. In recent years [16], the research has shown that the combination of plant growth-promoting rhizosphere bacteria (PGPR) and arbuscular mycorrhizal fungi (AMF), especially AMF+PGPR5, significantly improves rice growth, and yield, and the absorption of essential elements in rice plants. Microbial fertilizers will

become a new direction leading the future development of the fertilizer industry and an inevitable choice for the sustainable development of agriculture in China.

This article reviews the research progress of root biology and nitrogen absorption, and their utilization in China and other countries are summarized from the aspects of root configuration, physiological and biochemical characteristics, root growth and development process and regulation, rhizosphere microorganisms, and their symbiotic system (Figure 1). This study provides a reference for the future research on root biology and nitrogen absorption and utilization.

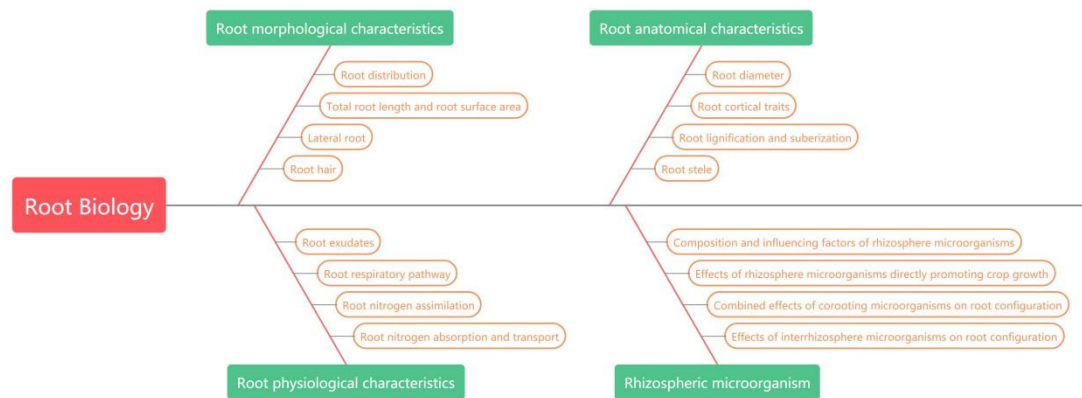


Figure 1. Key research contents of root biology in this paper.

2. Root Morphology and Nitrogen Absorption and Utilization

Root system architecture (RSA) refers to the spatial distribution structure and extension form of plant roots in soil [17], including two-dimensional plane geometry and three-dimensional geometry. RSA includes root distribution, and the planar geometric configuration refers to the distribution of various roots of the same root system along the root axis in a two-dimensional plane. It is generally described by parameters such as the number, length, surface area of roots, and the number and length of root hairs. The three-dimensional solid geometry configuration of roots refers to the three-dimensional spatial distribution of different types of roots in the medium. Usually, parameters such as root branching status, lateral root distribution, and root geotropism are used to indirectly describe the root configuration characteristics of crops. The main content of this study includes the root distribution, total root length, root surface area, root volume, lateral roots, and root hairs (Table 1).

2.1. Root Distribution

Because of the spatial heterogeneity of nitrogen resources distribution in the soil, root configuration affects crop nitrogen absorption. Compared with shallow roots, deep roots more easily obtain water and nitrogen under drought- and nitrogen-deficiency conditions [31]. Rice roots are mainly distributed in the 0–20 cm soil tillage layer, and the quality of the lower root (10–20 cm) is positively correlated with the yield, while the quality of the upper root (0–10 cm) is not significantly correlated with the yield. Therefore, properly increasing the proportion of roots in deep soil and reducing the proportion of roots in surface soil can increase crop yield [18]. Under low-nitrogen conditions, near-allelic lines containing the deep-root control site *DRO1*, compared with the shallow-root rice IR64, significantly increased the distribution of the deep-root system, which increased the nitrogen utilization efficiency and yield of rice [19]. At the same time, the deep-root system with a higher energy metabolism gene content can produce ATP faster, and has a higher cytokinin flux (CTKs) [32], which is conducive to nitrogen absorption and aboveground growth. The roots with deep and more longitudinal distributions have smaller leaf angles, which are beneficial for improving the ventilation and light transmission conditions of the population, increasing the photosynthetic efficiency and yield [33]. Therefore, deep-root

penetration is one of the important characteristics of high nitrogen absorption and utilization efficiency. The research has shown that, compared to monoculture, intercropping increases the shallow soil root biomass of broad beans and wheat and improves the root distribution of different crops in the deep soil of adjacent crops [34]. This indicates that different planting patterns also affect the root distribution of crops.

Table 1. The relationship of nitrogen uptake and utilization efficiency with root morphological characteristics.

Root Trait	Correlations with Nitrogen Uptake and Utilization Efficiency	Reference
Root distribution	The quality of roots shorter than 10 cm is positively correlated with crop yield and nitrogen absorption and utilization efficiency.	[18,19]
Total root length and root surface area	① Crop root length and root surface area are generally positively correlated with nitrogen absorption and utilization efficiency. ② Varieties with high root sap flow and vigor under low-nitrogen conditions still have high nitrogen absorption and utilization efficiency under short root length and low surface area conditions. ③ The root length and root surface area are negatively correlated with nitrogen use efficiency when the roots are grown in redundancy.	[20–24]
Lateral root	Lateral root growth and nitrogen absorption interact and are positively correlated within a certain range.	[25–27]
Root hair	Root hair growth is positively correlated with nitrogen uptake efficiency.	[28–30]

2.2. Root Length and Root Surface Area

The root length and root surface area of crops are closely related to efficient nitrogen absorption. Nitrogen-efficient varieties often have a greater root biomass, root length, and surface area [20–22]. However, even varieties with a reduced root biomass, root length, and root surface area still have high nitrogen application rates and yields under low-nitrogen stress due to their high root sap flow and root activity [23]. When the root system undergoes redundant growth, the nitrogen absorption efficiency and yield of crops are negatively correlated with their root length and surface area [31]. Within a certain range, the crop yield increases with the increasing root length and root surface area. When the root length and root surface area reach a certain value, the yield decreases [24]. Some rice varieties with a lower root dry weight, total root length, and root surface area also have higher nitrogen utilization efficiency under low-nitrogen stress, which may be related to their greater root vitality, root injury flow, and active absorption surface area in the later stages of growth [35]. Therefore, the effects of root length and root surface area on crop yield and nitrogen absorption and utilization efficiency depend on the variety, cultivation conditions, and cultivation period of the crop.

2.3. Lateral Root and Root Hair

The lateral root density of crops is significantly correlated with plant height, effective tiller number, and yield per plant [36]. On the one hand, the number of lateral roots affects the nitrogen uptake of plants, and on the other hand, the occurrence of lateral roots is affected by the nitrogen supply level [25]. Local nitrogen supply or short-term nitrogen-deficit treatment can induce the occurrence of lateral roots, thus promoting nitrogen uptake [26,27]. However, too high or too low a lateral root number is not conducive to aboveground growth. In a study on the lateral root and nitrogen absorption and utilization efficiency of maize, it was found that, within a certain range, the lateral root density of maize was significantly positively correlated with nitrogen application amount; however, when there were too many lateral roots, the nitrogen absorption and utilization rate would decrease and root redundancy growth would occur, increasing metabolic cost and thus reducing biological yield [27]. At present, there are few studies on the mechanism between lateral roots and nitrogen uptake and utilization in rice, which is worth further exploration.

Root hairs are the main part of the root system that absorbs nutrients, such as nitrogen [17], phosphorus [37–39], and potassium [40]. Long and dense root hairs increase the absorption surface area. Root hairs can enable roots to obtain more phosphorus under low carbon respiration, which is a root trait with low metabolic costs and efficient nutrient absorption [28]. Therefore, increasing the length and density of root hairs may be an important way to increase nitrogen utilization efficiency in rice [29,30]. At present, some scholars have discovered and located QTL (quantitative trait locus) loci related to root length, root surface area, lateral roots, root hairs, and root vitality, and cloned their development-related genes, such as the *OsCSLD1* and *OsRHL1* genes involved in the development of rice root hairs and the *TaMOR* genes involved in increasing root number [41]. These results provide important genetic resources for further research on the relationship between root traits and nitrogen uptake and use efficiency.

3. Root Anatomy and Nitrogen Uptake and Utilization

The main function of roots is to absorb water and nutrients for plant growth; they are an important medium for and reservoir of nitrogen in the soil–plant system. The process of roots absorbing nitrogen from the soil and transporting it to the aboveground plant is closely related to root anatomy. In this paper, the relationship between root anatomy and nitrogen uptake and utilization was revised from the aspects of root diameter, middle column, root cortex properties, keratinization, and bolting (Table 2).

Table 2. The relationship of nitrogen uptake and utilization efficiency with root anatomical characteristics.

Root Trait	Correlations with Nitrogen Uptake and Utilization Efficiency	Reference
Root diameter	Properly increase the proportion of coarse branched roots, increase the root length and root surface area to shape a good root configuration, and improve the nitrogen absorption and utilization efficiency of crops.	[41]
Root cortical traits	The formation of root aerenchyma enhances the nitrogen absorption and utilization efficiency of plants, improves the adaptability to stress, and is conducive to dry-matter accumulation.	[42–44]
Root lignification and suberization	Improve the resistance of crops to adverse environments, while lower root lignification and corkification levels have higher nitrogen absorption efficiency and are negatively correlated with external NH_4^+ levels.	[45–48]
Root stele	The transport capacity of root system is positively correlated with the diameter of root stele.	[49–51]

3.1. Root Diameter

Rice roots can be divided into fine-branching roots (diameter $D \leq 0.1$ mm), coarse-branching roots ($0.1 \text{ mm} < D \leq 0.3$ mm), and advents ($D > 0.3$ mm), and the development of coarse-branching roots directly affects nitrogen uptake efficiency. Under the condition of low nitrogen, the root length and surface area of coarse-branching roots had the greatest influence on nitrogen uptake and accumulation [52]. Appropriately increasing the proportion of coarse-branching roots and increasing the root length and root surface area can build a good root configuration system and improve nitrogen uptake and utilization efficiency in crops.

3.2. Root Cortex

The function of the root cortex (repair epithelial cells, RCC) is to support water and nutrient transport. Studies have shown that maize varieties with large cortical cells and few cortical cell layers have low root metabolic costs. The metabolic input process that maintains cortical cells is called the “cortical burden” [53]; root length increases significantly under drought stress. Additional substances and energy are used for deep-root lagging to obtain more water and nitrogen and improve crop growth and yield [54,55].

The aerenchyma is a collection of air chambers or cavities in the parenchyma of the root cortex. Its functions are to mainly supply nutrients, respiration, and transportation, as well as regulate the exchange of air inside and outside cells. Different rice varieties have different aerenchyma sizes and the size of aerenchyma increases with the development of the growth process of the same rice variety [56]. Studies have shown that rice aerenchyma formation is also affected by adverse stress, and stress factors, such as nitrogen deficiency, hypoxia, and drought, can induce the formation of rice root aerenchyma [57,58]. On the one hand, aerenchyma can improve the oxygen capacity of roots and the anti-hypoxia ability of crops [42], as well as the nitrification intensity of rhizosphere soil and the nitrogen mineralization ability of soil, to enhance the nitrogen absorption and utilization efficiency [43]. On the other hand, studies indicate that drought, high salt, low temperature, and other stresses have adverse effects on plant root metabolism, and at the same time, plants cope with stress by reducing root energy consumption, which is an adaptive response of plants via aerenchyma to various extreme environmental conditions [44]. Through simulation model studies [59], it was found that root cortex aerenchyma can improve root exploration and nitrogen acquisition in deep soil by reducing root metabolism costs, improving nitrogen use efficiency, and improving plant growth and development under nitrogen-deficit conditions [60,61]. Under low-nitrogen stress, crop promotes root growth, expands the root foraging range, nitrogen acquisition, and biomass by forming larger root cortical aerenchyma and cortical cells [62]. Programmed cell death can lead to the growth of aerenchyma, increase root vitality, delay root senescence [63], and promote the absorption of nutrients and water in rice under flooding stress, indicating that the formation of aerenchyma is beneficial for dry-matter accumulation.

3.3. Lignification and Embolization of Roots

The lignification and thromboplastization of root cortical cells form the extracellular barrier of the root endodermis and exoderm to resist various external stimuli. Lignification and corkification improve the resistance of crops to adverse environments and stabilize the normal growth and development of rice plants, such as enhancing the resistance of rice to salt alkali stress and improving its resistance to hypoxia stress by inhibiting oxygen emissions [45]. At the same time, salt stress and hypoxia stress exacerbate the lignification and corkification of rice roots [46,47]. Therefore, this barrier prevents nutrients and water from entering and exiting cells through the extracellular vesicles, leading to a decrease in root hydraulic conductivity and ion absorption permeability, affecting the normal growth and development of rice plants.

Studies have found that, at low nitrogen levels, lower root lignification and embolization levels have a higher nitrogen absorption efficiency [48] because lower root lignification and embolization levels are more conducive to increasing the permeability of roots to nitrogen, phosphorus, potassium, and other solutes, thus improving the absorption capacity of roots to solutes. At the same time, the lignification and corkification levels of rice roots are regulated by the nitrogen application level, and these levels gradually decrease with decreasing external NH_4^+ levels. At this point, the rate of root cell division and elongation accelerates, which is more conducive to the formation of large and deep-rooted roots and promotes nitrogen uptake by roots [64]. Under low-nitrogen conditions, root material and energy consumption can be reduced by reducing the lignification and bolting levels of the root cortex, thereby improving nitrogen use efficiency and enhancing their ability to resist low-nitrogen stress [65].

3.4. Root Column

Root column characteristics are closely related to root water and nutrient transport. The transport capacity of the root system is positively correlated with the diameter of the middle column [49], the high ratio of the middle column diameter to the root diameter [50], the number of xylem vessels, and the size of the cross-sectional area [51]. The diameter of the root column is affected by cultivation and fertilization methods [48]. Integrated and

layering fertilization in deep seeding can increase the diameter of the root column [66]. Furthermore, maize varieties with high nitrogen absorption and utilization have more developed root column diameters. Therefore, developed transport tissue is an important feature of efficient nitrogen utilization in crops [67].

4. Physiological and Biochemical Characteristics of the Root System

The two main forms of inorganic nitrogen absorbed by crops are ammonium nitrogen (NH_4^+) and nitrate nitrogen (NO_3^-).

4.1. Nitrogen Uptake and Transport in Roots

The coexistence of NO_3^- and NH_4^+ not only eliminates ammonia toxicity and promotes plant growth and development, but also regulates plant lateral root growth through the nitrate transporter NPF6.3 and ammonium transporter AMT1 [68]. Rice can significantly inhibit nitrification in soil by secreting biological nitrification inhibitors (BNIs) in the rhizosphere, improving the NH_4^+ utilization efficiency and increasing the reliance of the nitrogen cycle on fungal and prokaryotic populations [68]. In addition, a high expression of nitrogen transporters often leads to greater nitrogen uptake and utilization efficiency in rice under low-nitrogen conditions [69]. Strategies for the expression of high root nitrogen transport genes include the enhancement of plant light, an improvement in nitrogen use efficiency capacity, or an increase in the plant nitrogen absorption capacity; these strategies allow plants to absorb as much nitrogen as possible at the early growth stage for the same root size [70]. In wheat, SNP loci that are significantly associated with traits related to nitrogen efficiency are all related to *TaNRT2.1-6B*. The overexpression of *TaNRT2.1-6B* in wheat under both low and high nitrogen conditions improves its nitrogen absorption rate and promotes its root growth. Thus, wheat yield, total aboveground nitrogen uptake, grain nitrogen use efficiency, or aboveground nitrogen use efficiency can be improved [71]. The discovery of *TaNRT2.1-6B*, a key NRT gene and its related SNP locus, provides a useful target for the cultivation of nitrogen-efficient rice varieties (Figure 2).

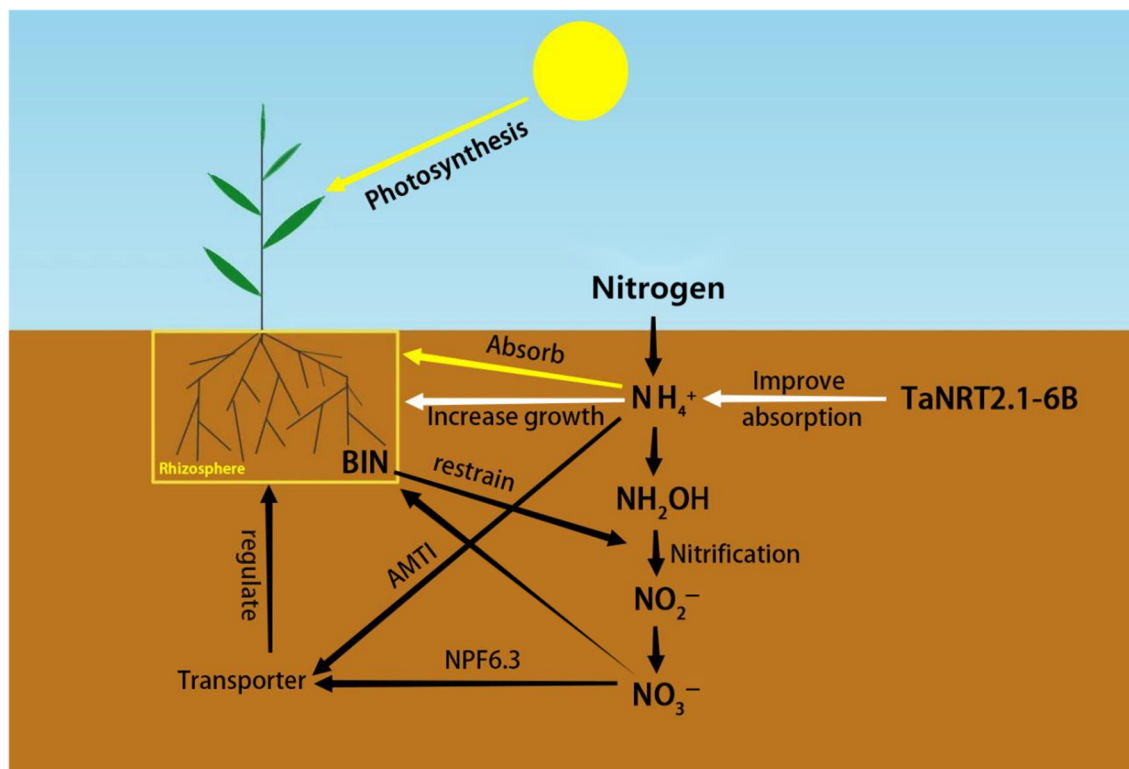


Figure 2. Transformation process of nitrogen in soil and root system.

Plant nitrogen utilization is affected by the long-distance transport and distribution of NO_3^- in plants [72]. The reduction in the vacuolar isolation ability of NO_3^- in roots enhances NO_3^- transport to the aboveground plant and contributes to the improvement in nitrogen use efficiency by promoting NO_3^- distribution to the aboveground plant [73]. The *OsNPF7.2* protein localized in the *NRT1* family of rice vacuolar membrane may regulate the short-distance distribution of NO_3^- in root cells. *NRT1.5* and *NRT1.8* proteins are found in plants, such as *Arabidopsis* and oilseed rape. NO_3^- induces the expression of *NRT1.5* in the root column cells, loading NO_3^- into the root xylem from the pericycle cells, and *NRT1.8* is responsible for NO_3^- removal from the root xylem. The strategy of rapeseed varieties with high nitrogen absorption and utilization to cope with low-nitrogen stress is to increase *NRT1.5* and reduce the expression of *NRT1.8* so that more NO_3^- is transported to the aboveground plant [74]. From this, it can be seen that promoting root nitrogen absorption and aboveground transport is an important way to improve nitrogen absorption efficiency in rice.

Recent studies have found that the rhythm clock gene *Nhd1* (*OsCCA1*) can directly activate the transcription of the high-affinity ammonium transporter *OsAMT1.3* and the double-affinity nitrate transporter *OsNRT2.4* [75]. Therefore, under the condition of low nitrogen in the field, the flowering period and growth cycle of the *Nhd1* mutant are prolonged, thus accumulating more nitrogen. The nitrogen absorption efficiency is improved. Promoting root nitrogen uptake and aboveground nitrogen transport is an important strategy for rice plants to cope with low-nitrogen stress. At the same time, we observed different rhizosphere microbiota between indica and japonica rice, and the presence of *NRT1.1B* in indica rice made its rhizosphere bacterial community more diverse, including more genera with nitrogen metabolism functions [76]. This provides new information for breeding strategies to improve crop nitrogen utilization. *OsTCP19* also regulates the expression of nitrogen utilization genes in rice [77]. On the one hand, *OsTCP19* mediates nitrogen-triggered developmental processes by regulating the expression of tiller-promoting genes. On the other hand, *OsTCP19* further regulates nitrogen uptake by regulating the expression of nitrogen utilization genes to meet the increased demand for nitrogen. The frequency of *OsTCP19* nitrogen-efficient variation in rice varieties was significantly negatively correlated with the nitrogen content in paddy soil [78]. The results show that the allelic variation in *OsTCP19* improves the geographical adaptability of rice to areas with low soil fertility, and it is retained in low fertility areas during rice domestication. The research on *OsTCP19* has laid the foundation for cultivating rice with low nitrogen fertilizer application and high yield in the future.

4.2. Root Nitrogen Assimilation

Nitrogen assimilation is a process in which plants transform inorganic nitrogen into available organic nitrogen through various physiological and biochemical reactions. NO_3^- absorbed by plant roots from soil is usually reduced to NH_4^+ . After NH_4^+ is absorbed by plants, amino acid and protein metabolism is completed through nitric acid reductase (NR), glutamine synthase (GS), glutamate synthase (GOGAT), glutamate dehydrogenase (GDH), and other enzymes [79]. NR and GS activities tend to be higher in varieties with high nitrogen absorption and utilization efficiency, which are key enzymes and multifunctional enzymes in plant nitrogen metabolism [80,81], and can maintain high NR, GS, and GDH activities under low-nitrogen conditions [82]. Root nitrogen assimilation enzyme activity affected the nitrogen assimilation behavior of rice and was also related to nitrogen transport to shoots. It was found that *OsGS1* was treated with a GS inhibitor. In rice mutant plants with gene 2 deletion, ^{15}N transport to the shoot was reduced and accumulated in the roots, and a large amount of free NH_4^+ accumulated in the roots, significantly reducing the biomass and yield [83,84]. The simultaneous overexpression of *OsAMT1* and *OsGOGAT1* could significantly improve rice yield and nitrogen uptake and utilization under low nitrogen [85–87]. Japonica near-isogenic family plants containing *OsNR2* alleles of indica rice had a significantly enhanced nitrogen absorption capacity under low-nitrogen levels

and had greater root NR activity, yield, and nitrogen uptake efficiency [88]. Therefore, high nitrogen assimilation enzyme activity is an important root physiological characteristic of high nitrogen uptake and utilization rates in crop.

4.3. Root Respiratory Metabolic Pathway

Under stress, plants can adapt to stress through a variety of respiratory metabolic pathways and electron-transport chain pathways. For example, under low-nitrogen stress, plants can increase the pentose phosphate pathway (PPP) and decrease the glycolytic-tricarboxylic acid cycle (EMP-TCA). Increasing alternate pathways (APs) and decreasing cytochrome pathways (CPs) can reduce the impact of stress [89,90], and infertile varieties can maintain better EMP-TCA and CP pathways and maintain greater respiratory productivity efficiency [91]. When the EMP-TCA pathway is blocked, glucose-6-phosphate dehydrogenase (G6-PDH) and 6-phosphogluconic acid dehydrogenase (6-PGDH) catalyze the operation of the PPP pathway, replacing normal aerobic respiration to ensure plant growth, development, and adaptation to the environment [92]. Crop varieties with a high nitrogen absorption efficiency have greater root cytochrome oxidase activity and ATP content, which can absorb more nitrogen. Therefore, high root respiratory productivity efficiency is an important physiological mechanism of high nitrogen use efficiency in crops [93].

4.4. Root Secretion

Root exudates can not only activate insoluble nutrients in the soil and improve fertilizer efficiency [94], but can also increase the absorption and transport of NO_3^- by roots by reducing the soil pH value, improving nitrogen utilization efficiency, and reducing the impact of low-nitrogen stress [95,96], including inorganic ions, organic acids, amino acids, and phenolic compounds [88]. At the same time, crop roots can also improve the absorption efficiency of NH_4^+ by secreting the nitrification-inhibitor 1,9-sebacediol [97]. Crop root exudates are affected by the nitrogen supply level, and a moderate nitrogen application can increase amino acid and organic acid secretion [98]. It was found that improving the soil environment could help increase plant root exudates, which would affect the rhizosphere microbial community and improve nitrogen use efficiency in the field. In the soil improved by compost, the amount of residual nitrogen uptake by high exudate genotypes (Snowmass) was 1.8 times that of low exudate genotypes (Byrd), and more rhizosphere microbial groups were associated with high exudate genotypes (Snowmass) [99]. These advances contribute to improving resource utilization and reducing fertilizer and pesticide inputs by utilizing root exudates from different species to achieve interspecific promotion, providing a theoretical basis for building sustainable ecosystems.

Hormones are the key signaling molecules in plant responses to external nutrient conditions and internal nutrient requirements to coordinate their growth and development. Ethylene, as an important stress hormone, plays an important role in the plant response to nitrogen stress. As an important cellular signal, ethylene mediates root structure adaptation, nitrogen absorption and transport, ammonium toxicity, anthocyanin accumulation, and premature aging thus enable plant growth and development to adapt to external nitrogen conditions [100]. Under hydroponic conditions, the total amount of organic acids secreted by the roots of crop varieties with high nitrogen absorption and utilization efficiency was lower than that of nitrogen-inefficient varieties under different nitrogen treatments, and the contents of oxalic and aspartic acids in the secretion were significantly negatively correlated with the nitrogen utilization efficiency [101]. Therefore, rice varieties with high nitrogen absorption and utilization efficiency reduce assimilation loss and improve nitrogen absorption and utilization efficiency by reducing the secretion of organic and amino acids by the root system.

5. Rhizosphere Microorganisms and Nitrogen Uptake and Utilization

The parts of plant roots in close contact with soil are collectively referred to as the rhizosphere environment [102]. Plants tend to recruit microbial communities that are more conducive to their growth and development from the rhizosphere. Rhizosphere microorganisms are an important way for plants to obtain essential nutrients, affecting plant growth and development, nitrogen use efficiency, and ecological adaptability [103]. Rhizosphere microorganisms have direct and indirect effects on nitrogen uptake and utilization in rice [104]. Rhizosphere microorganisms were able to convert inorganic phosphorus and other nutrients not readily available to plants to meet their essential nutrient uptake [105]. At the same time, by affecting the growth and distribution of the root system, nitrogen absorption and utilization were indirectly enhanced.

5.1. Effects of Interrhizosphere Microorganisms on Root Configuration

Rhizobia can form nodules symbiotic with leguminous plants and fix nitrogen in the air into ammonia, which can be absorbed by the plant (Figure 3). The nitrogen fixation ability of legumes enhances the rhizosphere excitation effect by promoting photosynthesis and rhizosphere deposition [106]. In acid soil, the roots of leguminous plants symbiotic with Rhizobia and mycorrhizal fungi can improve their adaptability to acid soil by adjusting root architecture [107]. Inoculation of rhizobium can increase root biomass and root length, for example, *Rhizobium* sp. POA3 can increase the root dry weight of rice [108]. The biomass of apple rootstock inoculated with ARR11 increased significantly (12.6–36.1% higher in root, 14.3–18.8% higher in stem, and 11.9–22.6% higher in the leaf than control, respectively), and the nitrogen concentration in the root and leaf was significantly higher than that in control [109]. The increase in root biomass provided a larger living space for rhizosphere microorganisms. Compared with uninoculated soil, inoculated ARR11 promoted the growth of apple seedlings in low-nitrogen soil.

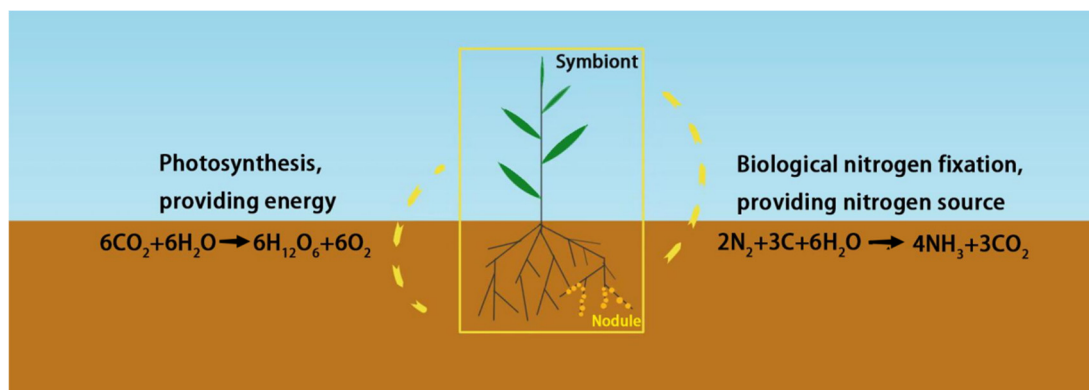


Figure 3. Nitrogen fixation effect of rhizobium.

Arbuscular mycorrhizal fungi (AMFs) can combine with plants to form symbionts, which not only directly provide nutrients to plants but also indirectly enhance the utilization of nutrients and disease resistance of plants by regulating root growth [110]. Arbuscular mycorrhizal fungi coexist with terrestrial plants, which can promote nitrogen absorption by plants but have a limited organic nitrogen absorption capacity. In addition, the synergistic effect of AMF and other microorganisms promoted organic nitrogen absorption and increased the overall nitrogen concentration in wheat grains [111]. At the same time, nitrogen enrichment also caused environmental changes, thus damaging the ability of plants to obtain organic nitrogen, and the synergistic effect between AMF and other microorganisms was also affected [112]. AMF can improve lateral root growth through direct contact or transmission of molecular signals. Studies have shown that the root biomass of both wheat and maize was significantly increased after inoculation with AMF [113], and the lateral root development of rice was activated after inoculation with AMF in rice seedlings [114].

An AMf-induced ammonium transporter *ZmAMT3* was identified from maize 1. Nitrogen is transported from fungi to plants by mediating ammonium nitrogen transport at the plant–mycorrhizal symbiotic interface [115], which contributes to the efficient acquisition of soil nitrogen by plants. The discovery of this mechanism provides a new idea for improving crop nitrogen efficiency through plant–microbial interactions.

5.2. Combined Effects of Corooting Microorganisms on Root Configuration

PGPR (plant growth-promoting rhizobacteria) act through a different mechanism to promote the plant growth of a group of beneficial rhizosphere microorganisms, including phosphate solubilization, nitrogen fixation, plant hormones, VOC volatile compounds, etc. [116]. PGPR can regulate root density, biomass, root length, branch number, lateral roots, and other aspects of plant roots. After inoculation with PGPR, the length, diameter, and branches of the rice roots increased [117]. Although *Pseudomonas* PS01 isolated from the maize rhizosphere inhibited the growth of primary roots, it promoted the formation of lateral roots and root hairs [118]. The inoculation of *Arabidopsis* with *Pseudomonas* also triggered the same response, while in *Azospirillum brasiliensis*, there was a greater proliferation of lateral roots rather than growth [119]. Common PGPRs include *Bacillus* and *Pseudomonas*, among others. *Methylobacterium* *Bacillus* can increase the root density and branching degree of *Arabidopsis*. After inoculation with *Bacillus*, the length of the primary roots, the number of lateral roots, and the root biomass of alfalfa increased [120]. All these studies prove that rhizosphere microorganisms can regulate the growth and development of plant roots.

5.3. Effects of Rhizosphere Microorganisms Directly Promoting Crop Growth

There is a high quantity of organic nitrogen in the soil that cannot be directly absorbed and utilized by crops. It can be utilized only by converting it into inorganic nitrogen through mineralization by rhizosphere microorganisms (mechanisms of nitrogen fixation and phosphorus dissolution) [121]. Functional microorganisms participating in the nitrogen cycle in paddy field ecosystems drive multiple complex processes, such as nitrogen fixation, nitrification, and denitrification, to maintain the nitrogen budget balance [122]. It is an important way to regulate soil nitrogen supply, transformation, and loss. The nitrogen absorption and utilization rate can be influenced by two aspects: increasing the levels of rhizosphere nitrogen fixation and ammonium fixation microorganisms can increase soil nutrient availability and promote nitrogen absorption by rice, and reducing the activity of rhizospheric nitrification/denitrification microorganisms can reduce soil nitrogen loss and improve crop nitrogen absorption and utilization efficiency [123]. Indica rice had higher nitrogen use efficiency than japonica rice because the presence of the nitrate transporter gene *NRT1.1B* enriched more microbial communities involved in nitrogen metabolism in the rhizosphere of indica rice than japonica rice, and the *NRT1.1B* gene was associated with specific enrichment of root microorganisms in indica and japonica rice [111]. These microorganisms can convert organic nitrogen into ammonia nitrogen and improve the nitrogen utilization efficiency of rice [124]. Field experiments showed that rice genotypes enriched specific bacterial communities in the rhizosphere at the classification and functional levels, and fewer denitrifying bacteria led to reduced rhizosphere nitrogen loss, thus increasing available nitrogen and improving rice yield [125]. In addition, soil microorganisms can alleviate plant stress phenotypes by synthesizing ACC deaminase. Alternatively, through resource competition, the synthesis of antibiotics or dissolution of pathogenic bacterial structures inhibits the pathogenic ability of pathogenic bacteria and maintains normal crop growth [126].

5.4. Composition and Influencing Factors of Rhizosphere Microorganisms

The composition of rhizosphere microorganisms is influenced by many factors [127], such as the interaction between host plant genes and rhizosphere microbiota on host plant nutrient uptake [128]. It was found that, in unsterilized low-nitrogen soil, the nitrogen concentration of apple seedlings with a high expression of *MdNRT2.4* was higher than

that in sterilized low-nitrogen soil [129]. Apple seedlings overexpressing *MdNRT2.4* could recruit more bacterial groups with the nitrogen metabolism function. At the same time, the symbiotic pattern and aggregation process of bacterial communities in rhizosphere and common soils were different under nitrogen treatment; these secretions specifically stimulate or inhibit different microbial members in the soil [130].

The interaction between agricultural management and plant selection processes also affects the formation of rhizosphere microbial communities [131]. The application of biochar had a significant impact on the bacterial community in the rhizosphere soil [132]. There is a significant difference in the microbial community between rhizosphere and non-rhizosphere soils, and the bacterial community and core microorganisms in the rhizosphere soil play a key role in the formation of maize root architecture. By changing soil microorganisms, increasing nitrogen fixation, and reducing nitrogen loss, straw returned to the field increased the plant nitrogen supply. Especially in flooded paddy soil, crop-straw return to the field significantly increased the relative abundance of Firmicutes and decreased the relative abundance of Proteobacteria. This changed the composition of the microbial community [133]. The $^{13}\text{C}/^{15}\text{N}$ double-scale method was used to study whether acquisitive species with higher photosynthetic rates, rhizosphere carbon deposition, and nitrogen uptake promoted soil nitrogen cycling through the excitation effect of rhizosphere organic matter decomposition, making them absorb more nitrogen and distribute it to the aboveground plant to promote photosynthesis, thus maintaining a faster growth rate [134]. However, long-term fertilization inhibited the growth and function of specific *Azotobacter* clusters in the rhizosphere. High nitrogen application rates increased the abundance of root exudates and soil bacteria, leading to a decrease in fertilizer utilization efficiency and systematic nitrogen loss [79], and long-term fertilization inhibited the growth and function of specific nitrogen-fixing bacterial clusters in the rhizosphere. The research found that key nitrogen-fixing microbial communities, such as oligotrophic geobacterium, are phylogenetically aggregated under long-term no-fertilization conditions, and fertilization results in a random state of their phylogeny, indicating that the soil environment under long-term fertilization management can no longer actively select key nitrogen-fixing microbial communities closely related to nitrogen-fixing activity, resulting in the irreversible loss of the soil nitrogen-fixing function [135].

6. Summary and Prospects

In studying the relationship between plant root biology and nitrogen, whether from the perspective of microorganisms or root architecture, root anatomical structure, and root physiological and biochemical characteristics, the growth and development status of plant roots and different nitrogen application treatments have a significant impact on nitrogen absorption and utilization. The impact of plant root biology on nitrogen absorption and utilization efficiency and its interaction mechanism are international cutting-edge research fields and key research directions. However, the physiological mechanisms of root characteristics affecting efficient nitrogen absorption and utilization in rice, as well as the combination of root microbiome and crop breeding, are still insufficient. In response to China's agricultural development strategy of "less investment, more output, and environmental protection", China should focus on the following aspects to lead the international development of this field.

- (1) The ideal root architecture of rice should be constructed. The ideal root configuration guarantees the growth of a healthy aboveground plant and is an important characteristic for breeding high-yield and high-quality rice varieties. However, due to the lag in root research and the diversity of paddy fields in different regions, the definition of ideal plant is very different. The construction of an ideal root configuration via breeding and cultivation regulations is an important component of rice root research in the future.
- (2) The functions and growth-promoting mechanisms of root microorganisms at the community level should be studied. Although the research on plant growth-promoting

bacteria dates back to 300 BC and biobiotics have been widely used in the form of biofertilizers, their growth-promoting effects on plants vary, depending on crop varieties or soil environments. This variance results from a failure to fully understand the dynamic construction of the microbial community and its function at the community level. Future microbial comparative genomics studies may help us systematically understand the functional composition of root microorganisms on an unprecedented scale and elucidate the effects of microbe–microbial interactions on the construction and function of root microbial communities.

- (3) Some microorganisms have been applied to production practice; however, most beneficial microorganisms are still in the research stage, mainly due to the complex and variable environment. It is reported that the inoculation of Brazilian nitrogen fixing spirillum Ab-V5 under greenhouse conditions significantly increased the dry weight, volume, and biomass of maize and wheat roots; however, under field conditions, the strains had no significant impact on plant growth [136]. Therefore, when preparing microbial agents, the experiments on natural environments should be increased to improve the stability of microbial inoculants in different environments. PGPR, AMF, and rhizobia can play a synergistic role in promoting growth, and the limitations of single strains or single types of bacteria can be broken during microbial agent preparation to realize the application of a comprehensive microbiome system [137]. In conclusion, the regulation of rhizosphere microorganisms on plant root configuration has broad application prospects in production practice, and the multiomics association research method can fully elucidate the mechanism of the role of microorganisms and provide research direction for the selection of strains.

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