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Research progress on isotope labeling in plant-soil-microbe interactions: A case study of forest ecosystem nutrient cycling

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Abstract. In the study of nutrient cycling in forest ecosystems, traditional methods are increasingly unable to meet the researchers' need for understanding the mechanisms of nutrient cycling. Stable hydrogen and oxygen isotope tracing techniques have become important methods for studying the mechanisms of nutrient cycling in forest ecosystems due to their high sensitivity and tracing capabilities. Scholars from both domestic and international backgrounds have conducted research on nutrient cycling in forest ecosystems from various time scales and hierarchical levels. Based on a brief introduction of the principles of hydrogen and oxygen isotope tracing, this paper systematically elaborates on the use of stable 15N isotope dilution techniques and tracing techniques to determine the conversion rate of total N in forest soils and the 15N recovery rate. This aims to reveal the transport and transformation laws and retention mechanisms of forest soil 15N, especially inorganic N. By utilizing stable isotope tracing, isotope ratio mass spectrometry analysis, and other techniques, research on biological nitrogen fixation has been conducted, including the measurement of biological nitrogen fixation, the study of nitrogen fixation mechanisms, and the identification of new nitrogen-fixing species. Isotope labeling, as a key technical means for exploring the biological world, can trace chemical reactions within microbial organisms and their influencing factors. It aims to lay a scientific foundation for further exploration of nutrient cycling in forest ecosystems, especially processes related to nitrogen cycling. Additionally, it provides basic data and theoretical basis for the protection, restoration, and sustainable management of forest ecosystems.

Keywords: Nutrient Cycling, Forest Ecosystem, Isotope Tracing Techniques

1. Introduction

The forest ecosystem is an important component of terrestrial ecosystems. In the process of biogeochemical cycling, the forest ecosystem exchanges matter and energy with the atmosphere, water, and soil at multiple levels, scales, and interfaces. As an important part of green water and clear mountains, the forest ecosystem provides essential ecosystem services, especially in terms of serving as a "green water reservoir" for water conservation, a "green carbon reservoir" for carbon sequestration, a "green oxygen bar" for air purification, and a "green gene bank" for biodiversity conservation. The quality of the forest ecosystem is closely related to human well-being [1]. The vast distribution of forest resources in China plays an irreplaceable role in maintaining ecological balance, improving the

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environment, achieving dual carbon goals, addressing climate change, improving human habitation, and protecting global species diversity [2].

Over the past few decades, due to rapid socioeconomic development and intensive resource exploitation, the degradation of forest ecosystems has become increasingly severe. The research on restoring and rebuilding damaged forest ecosystems has received extensive attention and recognition from the international scientific community and government agencies, leading to rapid development. Stable isotope technology, as a mature technology, has been widely applied in various fields of ecological research. By injecting isotopes into plants and analyzing the changes in isotopic composition, stable isotope technology can be used to study plant physiological processes such as determining plant water sources, water use efficiency, plant elemental absorption, ecosystem gas exchange, climate change, and carbon balance. It plays an important role in maintaining the stability of food chains and food webs, as well as the balance of plant-soil-microbe interactions [3]. Stable isotope tracing studies using stable isotope technology have unique advantages in determining biological nitrogen fixation, studying nitrogen fixation mechanisms, and identifying new nitrogen-fixing varieties. It is the most direct and effective method for measuring biological nitrogen fixation. For example, research conducted by the Institute of Atomic Energy of the Chinese Academy of Agricultural Sciences and other units explored the nitrogen release of Azolla in a designed closed device and found that the nitrogen released by Azolla can be rapidly absorbed by rice. Similar devices were used to assess the nitrogen-fixing capabilities of Alcaligenes faecalis, intestinal bacteria, and Rhizoctonia oryzae, revealing that the nitrogen-fixing ability is much higher when Alcaligenes faecalis and intestinal bacteria are co-cultured compared to individual cultures [4]. At the same time, the symbiotic nitrogen fixation of nodulated crops was estimated using 15N natural abundance, providing a basis for the application of natural abundance measurement of 15N in the field of biological nitrogen fixation. Chen et al. utilized the tracing technique of 15N stable isotopes and directly introduced 15N2 into a seawater culture system, accurately measuring the isotopic tracing level of the culture system substrate. This allowed for the determination of the rate of biological nitrogen fixation in the water, which is of significant importance in studying topics such as new nitrogen sources in the ocean [5]. In recent years, new labeling techniques such as single-cell stable isotope labeling technology provided high-resolution direct solutions to overcome the limitations of uncultured microorganisms.

Due to the limitations of technological equipment, the research and application of stable isotope technology in plant physiological ecology are still in the early stages, with only a few institutions and researchers utilizing this technology. This article focuses on the application and research progress of stable isotope technology in forest ecosystems.

2. Nutrient Cycling in Forest Ecosystems

Since the Industrial Revolution, due to the rapid development of modern industry and the impact of human activities, the concentrations of greenhouse gases such as CO2 and N2O in the atmosphere have been continuously increasing, leading to changes in the global atmospheric environment, such as global warming, which poses a serious threat to human health, as well as the survival of animals and plants [6]. Forest ecosystems play an important role in mitigating climate change by influencing the carbon and nitrogen cycling processes in terrestrial ecosystems. It is estimated that approximately 1.3 TgN is emitted into the atmosphere annually in the form of N2O through forest soils [7]. Therefore, forest ecosystems have an important role in mitigating climate change.

The carbon and nitrogen cycles in forest ecosystems are the most important processes and serve as carriers for matter cycling and energy flow. The use of 15N isotope dilution techniques and tracing techniques to analyze the dynamic migration and transformation of soil nitrogen is currently a research focus in forest ecology. The processes of nitrogen transformation in forest soils, such as N mineralization, nitrification, denitrification, and nitrate ammonification or reduction to ammonium (DNRA), as well as nitrogen immobilization by microorganisms and nitrogen uptake by plants, all exhibit varying degrees of N isotope fractionation effects [8]. Through the study of N isotope fractionation effects, it is possible to effectively reveal the pathways of nitrogen utilization by plants and microorganisms. The 15N isotope dilution technique is an effective method for quantifying the rate of total nitrogen transformation in soils, relying on the labeling, dilution, and enrichment dynamics of a certain form of product with 15N. The 15N isotope tracing technique mainly relies on the labeling, dilution, and enrichment dynamics of a certain form of substrate with 15N [9]. By using stable 15N isotope dilution and tracing techniques to measure the rates of total nitrogen transformation and 15N recovery in forest soils, the transport, transformation, and retention mechanisms of 15N, especially inorganic N, can be revealed. Therefore, the principles of 15N isotope dilution and tracing can not only quantify soil nitrogen transformation rates but also reveal nitrogen production and consumption pathways [10].

Evidence of competition between plants and microorganisms for inorganic nitrogen comes from long-term and short-term 15N isotope tracing experiments. In short-term experiments, with higher labeling abundance of 15NH4+-N and 15NO3--N in the soil inorganic nitrogen pool, the plant, microorganism, and soil inorganic nitrogen pools and their isotopic compositions are determined after short-term cultivation (15 days). In long-term 15N isotope experiments, the same tracing techniques are used, but the measurement time is several weeks or months after cultivation [11]. Based on the results of 15N isotope tracing experiments, the currently popular view is that microorganisms have an advantage in the competition for inorganic nitrogen in the short term, with a preference for NH4+-N, while in the long term, plants are the ultimate winners [12]. In recent years, with the development of 15N isotope tracing techniques, more and more evidence has shown that plant roots, especially those associated with mycorrhizal fungi, can directly absorb organic nitrogen. [13] Frey et al. used isotope tracing techniques and a compartmentalized cultivation system to study the highest N uptake and transport by AM fungal mycelium to host plants, reaching up to 30% of the total N uptake by plants. The absorption of organic nitrogen by plant roots can reduce the dependence of plants on microbial mineralized nitrogen, potentially alleviating the competition between plants and microorganisms for nitrogen. Litter is the link between soil nutrient cycling and the interaction with plants. [14] Du et al. validated the application of dual isotope labeling (13C and 15N) in tree leaf litter, studying the changes in C and N fluxes during the decomposition process of legume and non-legume leaf litter, as well as their responses to different precipitation levels.

Another nutrient that flows in the environment in gaseous form is carbon, and soil organic matter serves as a carbon reservoir. It is closely related to soil structure and fertility, while also profoundly affecting the emission of CO2 in the environment. Isotope tracing technology provides a convenient means for studying the carbon transformation process of soil organic matter in ecosystems [15]. For example, returning straw to the field can increase the organic matter content, improve soil fertility, and enhance soil aeration. Through isotope tracing technology, [16] Zhu et al. observed the different dynamics of 13C and 15N in soil and gas during the decomposition process of corn straw, indicating the differences in carbon and nitrogen. The transformation process of soil organic matter includes several aspects: 1) the presence of carbon isotopes in the environment and its influencing factors. Studies have shown that different substances have different proportions of 12C and 13C, with C3 and C4 plants showing the most significant differences. Different types of plants with different photosynthetic pathways exhibit varying stable carbon isotope fractionation patterns during the process of absorbing CO2 and synthesizing organic matter. This leads to significant differences in δ13C values among different types of plants. The δ13C value range for C3 plants is -0.24‰ to -4%, with an average of -2.7%; for C4 plants, the δ13C value range is -0.9% to -1.9%, with an average of -1.2%; and for CAM plants, the δ13C value range is -1% to -2.3%, with an average of -1.7% [17]. 2) Changes in the content of soil organic matter, including changes in soil organic content, migration, and storage patterns, as well as degradation rates. The changes in soil organic matter content are the result of several factors, including changes in soil density, the degradation capacity of mineral fuels, differences in organic matter structure and composition, and microbial respiration. After the transformation of the ecosystem, the proportion of SOC3 to SOC4 in different soil particle sizes can be calculated, where SOC3 and SOC4 represent organic matter of different ages. Therefore, the new and old ages of organic matter in different soil particle sizes can be determined. The order of migration and distribution of soil organic matter in different soil particle sizes during the degradation process is as follows: fine sand (2000-50 μm) →

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coarse silt (50-5 μm) → coarse clay (2-0.2 μm) → fine clay (< 0.2 μm) → fine silt. Barrios et al. believed that organic matter degradation in the 53-2 μm fraction is the most thorough and has the oldest age [18].

Organisms rely on water as a driving force for nutrient cycling, and isotope technology is widely applied in the study of water cycling. For example, determining the source of plant water, water use strategies encompass a wide range of concepts, including different habitats, different seasons, different growth stages, and the isotopic fractionation process of plant leaf water [19]. Studies have used hydrogen and oxygen isotope values of soil water, xylem, and stem water to observe the water use strategies of different habitats in complex ecological systems. Establishing effective dynamic models can determine the source of plant water. Common methods include two-source or three-source mixing models, multi-source linear mixing models, water uptake depth models, Bayesian mixing models, and dynamic models. In the determination of water sources, it is often difficult to effectively distinguish dew condensation, water vapor evaporation, and rainfall, as the isotopic composition is influenced by the three sources of δ values [20]. To separate evapotranspiration, dew condensation sources, and the water vapor source of precipitation, scientists use modeling, experimental simulation, and laser measurement techniques to determine the water cycling process at a larger scale.

3. Biological Nitrogen Fixation

Nitrogen (N) is a crucial nutrient element required for plant growth. It is a key factor that limits plant growth and carbon fixation in many terrestrial ecosystems [21]. Limited nitrogen availability can reduce the carbon sequestration potential of ecosystems [22]. Biological nitrogen fixation refers to the process in which nitrogen-fixing microorganisms convert atmospheric nitrogen gas into biologically available ammonia. It is the primary source of new nitrogen in the environment and can regulate primary productivity and affect the nitrogen balance in ecosystems. The use of stable isotope labeling techniques, such as 15N2, based on the assimilation or rate of assimilation of 15N by microorganisms, is the most direct method for characterizing microbial nitrogen fixation activity. Stable isotope technology, using isotopic ratio mass spectrometry analysis, has become quite mature in studying biological nitrogen fixation. It has unique advantages in determining nitrogen fixation rates, studying nitrogen fixation mechanisms, and identifying new nitrogen-fixing strains. It is the most direct and effective method for measuring biological nitrogen fixation. To evaluate the biological nitrogen fixation of sugarcane, a 15N isotope dilution method was used in a greenhouse barrel experiment, with cassava as a reference plant. The results showed that the nitrogen fixation of sugarcane plants during the entire growth period was 11.3514% Ndfa, with a nitrogen fixation rate of 0.9269 g per barrel. The nitrogen fixation percentage and nitrogen fixation amount of sugarcane roots, stems, and leaves were in the order of leaves > stems > roots [23]. In a micro-plot experiment conducted on Huangmian soil in northern Shaanxi, the nitrogen fixation of symbiotic bacteria was studied. The results showed that the total nitrogen fixation amount measured by the 15N isotope method was 9.36-18.72 kg/acre, with an average of 13.59 kg/acre. The nitrogen fixation accounted for 73% of the total nitrogen requirement of alfalfa, while the nitrogen fixation amount measured by the total nitrogen difference method was approximately half to one-third of the value obtained by the 15N method [24].

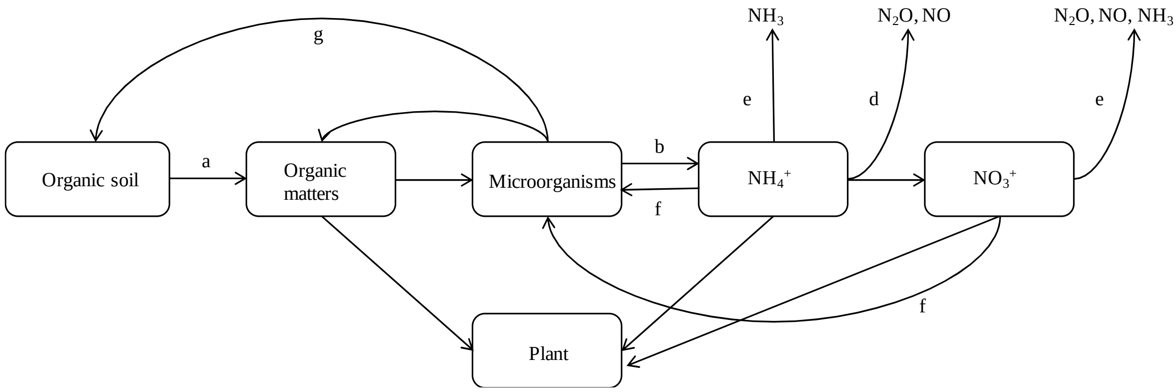

Figure 1. The nitrogen cycle of soil (Schimel and Bennet). Note: a - degradation function; b - total mineralization rate; c - ammonia volatilization; d - nitrification; e - denitrification; f - microbial fixation; g - soil microbial death

4. Evidence of Environmental Toxicology

Isotope labeling is a key technical to explore the biological world and trace the chemical reactions inside microbial organisms, which is often related to nutrient cycling. For example, in 2015, [25] Li et al.used isotope probe technology 13C to label microorganisms related to pentachlorophenol (PCP) in soil. The results showed that earthworms can introduce functional bacteria into the soil, increasing the number of PCP-degrading bacteria and thus accelerating the degradation of PCP in the soil. Nitrate is a major source of water pollution and one of the culprits of eutrophication. Research has used nitrogen and oxygen isotope tracing to identify the sources of nitrate pollution in groundwater in Jishui County. The characteristic values of nitrogen and oxygen isotope δ15N-NO3- and δ18O-NO3- in the water source range from 6.33‰ to 26.60‰ and -0.68‰ to 19.90‰, with average values of 12.38‰ and 7.52‰, respectively. The characteristic values of nitrogen and oxygen isotopes δ15N-NO3- and δ18O-NO3- in the well water range from 2.75‰ to 31.01‰ and 3.18‰ to 16.94‰, with average values of 14.29‰ and 8.75‰, respectively. [26] Xia et al.used a mixing water source isotope identification model to calculate the contribution rate of nitrate sources in groundwater in the study area. The results showed that the main sources of pollution in the water source were manure and sewage, with an average contribution rate of 47.72%. The main sources of pollution in the surrounding wells of the water source were manure and sewage, with an average contribution rate of 58.35%. The main sources of pollution in the wells around the industrial park were precipitation and fertilizers, with an average contribution rate of 39.54%. The main sources of pollution in the wells around the landfill were manure and sewage, with an average contribution rate of 96.92%. Lead is a highly toxic heavy metal element that poses great harm to humans. Tracing the source of lead is a prerequisite for controlling lead pollution. Due to the difficulty of significant fractionation of lead isotopes in natural processes, which retains the characteristics of the pollution source area, it has become a powerful “fingerprint” tool for tracing lead pollution. Li et al. [27] used lead isotopes to identify and analyze the sources of lead in snow and ice. The spatial distribution characteristics of lead pollution (Third Pole > Arctic > Antarctic) and the temporal distribution characteristics (peak concentration of lead in snow and ice mainly occurred around the 1970s) were analyzed. In the same study, Chen et al. [28] used the BCR and 1M HCl separation-extraction techniques to trace the characteristics of lead pollution and lead sources in the sediment of the downstream Xiangjiang River. It was found that the lead content in the riverbed sediment varied greatly and showed significant enrichment. There were distinct regional characteristics. In terms of the forms in which lead existed, the riverbed sediment mainly contained reducible lead (43.76%) associated with iron-manganese oxides and residual lead (41.53%) associated with silicate minerals. When analyzing the source of rare earth elements in the vertical profile of paddy soils and evaluating ecological risks, Cao et al. [29] conducted qualitative analysis of the sources of rare earth elements and used strontium-neodymium isotopes combined with the MixSIAR model to quantitatively calculate the specific

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contributions of potential sources to rare earth elements in the vertical profile of soils. Miao et al. [30] analyzed the Sr, K isotopes of 15 potash rock samples and the Sr, S isotopes of 7 hard gypsum rock samples. The results showed that the Sr, S, and K isotopes of the samples all had characteristics of seawater, indicating that the source of potassium-forming substances in this salt body is seawater.

Table 1. Research Results of Isotope Labeling.

Research Area	Isotope Labeling Content	Main Observational Indicators	Soil Type
	15N	15N enrichment level	
Typical Region of Loess Plateau in Qingyang, Gansu	15N	Nitrogen fixation percentage, plant nitrogen uptake, and soil nitrogen	Yellow soil
	15N	Nitrate Reductase Activity, NRA	
Symbiotic nitrogen fixation in leguminous crops	15N	Natural abundance of nitrogen	
Jinhu National Nature Reserve (30°15’-30°30’N, 116°55’-117°15’E) in southern Anhui Province, China	15N	NH4+ and NO3− extracted using 2 mM KCl and measured using a flow analyzer (AA3, Bran-Luebbe, Germany). Soil glycine content in the extract was also determined using high-performance liquid chromatography (Waters 515, Waters Inc., United States).	Black soil
Sugarcane Research Institute in Guangxi	15N	Percentage of nitrogen derived from the atmosphere (%Ndfa), nitrogen fixation amount (Ndfa), fertilizer utilization efficiency (%FU), and soil nitrogen pool	
Shaanxi	15N	Total nitrogen content and the atomic percentage of 15N in plant samples from the labeled area	Yellow cotton soil

5. Conclusion

In summary, isotope tracing technology plays an important role in ecosystem nutrient cycling, biological nitrogen fixation, and applications in environmental toxicology. It provides an effective approach to explore nutrient sources in the environment and track microbial functions. However, despite significant advancements in existing techniques and computational models, there are still many unexplored questions in the material world.

1) Isotope technology can be applied at a more microscopic level. For instance, the widespread use of single-cell sequencing technology has led to research focusing on the application of isotopes at the cellular level, providing a powerful tool for observing the microcosm.

2) In the application of forest ecosystems, macroscopic analysis is more important. Ecosystems are organic entities composed of biotic and abiotic factors. Current research mostly focuses on material flow, while the interactions among plants-soil-microorganisms, such as how material inputs lead to feedback in plants and even higher trophic levels, are less explored. Combining studies on nutrient cycling in soil-plant systems, atmospheric water cycling processes, and other aspects can further elucidate plant water use efficiency and water-fertilizer coupling mechanisms.

3) Isotope technology is still subject to limitations imposed by various environmental factors. Sampling, pretreatment, and measurement processes are susceptible to evaporation and contamination, leading to large experimental data errors and limitations in in-depth exploration and interpretation of observed phenomena. In conducting isotope research, it is important to consider comprehensive analysis

by combining different soil nutrient conditions in different habitats and plant water physiological characteristics.

4) To avoid interference from natural stable isotopes, it is necessary to explore new approaches, such as artificially adding heavy water enriched with deuterium, to trace different sources of water.

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