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Global plant nitrogen use is controlled by temperature

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Plant nitrogen source in the soil is challenging to track. Compiling the most comprehensive global $\delta^{15}N$ dataset, a new study shows the plant use of various available soil nitrogen forms (ammonium, nitrate, and organic nitrogen) is strongly controlled by temperature.

Background

Nitrogen is a crucial element for plant life. Plants are surrounded by nitrogen since nitrogen accounts for 78% of the atmosphere by volume. However, nitrogen is a major nutrient limiting plant growth[1] because most plants cannot utilize atmospheric nitrogen directly. Only a small group of plants have the ability to fix atmospheric nitrogen through symbiotic association with nitrogen-fixing microbes.

Two chemists changed the plant nitrogen limitation situation fundamentally (at least for agricultural plants) through the invention of an industrial chemical process to synthesize ammonia from hydrogen and atmospheric nitrogen under high pressure. Now called the "Haber-Bosch process", this approach enables us to "fix" atmospheric nitrogen into ammonia as fertilizer at an industrial scale. Currently, anthropogenic nitrogen fixation is much larger than natural biological nitrogen fixation annually[2]. Although the production and wide application of nitrogen fertilizer fuels the Green Revolution, excess nitrogen has also caused serious environmental issues such as eutrophication, water pollution, and biodiversity loss[3].

Plant nitrogen use is complex because nitrogen has multiple forms in soil available for plant uptake (e.g., ammonium, nitrate, organic nitrogen). The stable isotopes (the same element with different numbers of neutrons) of nitrogen are powerful tools to investigate nitrogen transformation and plant nitrogen use. Nitrogen compounds with different nitrogen isotopes function the same chemically, but there is a difference in their physical properties. This allows nitrogen stable isotopes to serve as a natural tracer to study plant-nitrogen relationships. Nitrogen has two stable isotopes, ^{14}N and ^{15}N, and researchers typically use $\delta^{15}N$ to represent the ratio of these two isotopes in plant leaves, stems, roots, and various soil nitrogen forms.

New comprehensive global ^{15}N datasets

There are previous efforts to assemble plant[4] and soil[5] $\delta^{15}N$ separately at a global scale. In a new study, Hu et al.[6] compile the newest and most comprehensive global $\delta\ ^{15}N$ isotope data of both plants (including leaves, stems, roots) and soils (including ammonium, nitrate, organic nitrogen, total extractable nitrogen) in land ecosystems. Based on this dataset, they find whole plant $\delta^{15}N$ values are significantly different between different life forms (i.e., herbs, shrubs, and trees) and between plants that are associated with different mycorrhizal types at the global scale[6]. They also find that there is a significant difference in $\delta^{15}N$ between different plant parts (i.e., leaves, stems, and roots) of the same individual plants with leaf $\delta^{15}N$ being much heavier than the other plant parts, such as roots and stems[6]. The finding of intra-plant $\delta^{15}N$ difference at a global scale is unique and useful to guide future plant sampling for isotope analysis. Recognizing the intra-plant $\delta^{15}N$ difference and mycorrhizal influence on plant $\delta^{15}N$, they propose a new term $\delta^{15}N_{PUN}$ (PUN refers to plant-used nitrogen) to represent the $\delta^{15}N$ of plant nitrogen use[6]. Because this new term uses the whole plant ^{15}N signal, controlled for plant life forms and mycorrhizal types, it has the potential to replace the most commonly used leaf $\delta\ ^{15}N$. As such, $\delta^{15}N_{PUN}$ could serve as a quantitative tool to source the contributions of soil nitrogen to plants.

Plant nitrogen use is controlled by temperature and not by precipitation or atmospheric nitrogen deposition

Hu et al.[6] use $\delta^{15}N_{PUN}$ and $\delta^{15}N$ of various soil components (i.e., ammonium, nitrate, organic nitrogen) to identify plant nitrogen sources in soil, and examine the controlling factors of nitrogen use patterns. They find plant nitrogen use is controlled by mean annual temperature and $\delta^{15}N_{PUN}$ increases linearly with increasing mean annual temperature at the global scale (Fig. 1A). This pattern can be explained by known biogeochemical mechanisms. Higher temperatures would stimulate the soil nitrogen cycle and release more ^{14}N from the ecosystems[7]. Meanwhile, stimulated nitrogen mineralization and nitrification under higher temperatures would cause higher amounts and more direct nitrogen uptake fractions (relative to through the mycorrhizal pathways) of soil nitrogen to plants[8]. The results also show that plant nitrate uptake increases with temperature, organic nitrogen uptake decreases with temperature, and ammonium uptake increases with temperature to reach a peak and then declines with temperature (Fig. 1B).

They also find that atmospheric nitrogen deposition does not significantly affect plant nitrogen utilization[6]. Atmospheric nitrogen deposition refers to the process that reactive nitrogen (i.e., all forms of nitrogen in the environment except for molecular nitrogen) transfers from the atmosphere into Earth's surface through gas forms, particles, and precipitation. This finding is counterintuitive at face value considering the common perception of widespread atmospheric nitrogen deposition. However, several factors likely contribute to their observation. Firstly, not all regions globally experience high levels of atmospheric nitrogen deposition and the proportion of areas with high atmospheric nitrogen deposition remains relatively low on a global scale. Secondly, the amount of atmospheric nitrogen deposited in the ecosystem is likely small compared to the total pool of plant available nitrogen in the soil. This has important implications regarding the debate on whether plant nitrogen availability is declining globally. There are reports showing a decline in foliar $\delta^{15}N$ globally in recent decades and a decline in wood $\delta^{15}N$ across North America[4,9,10].

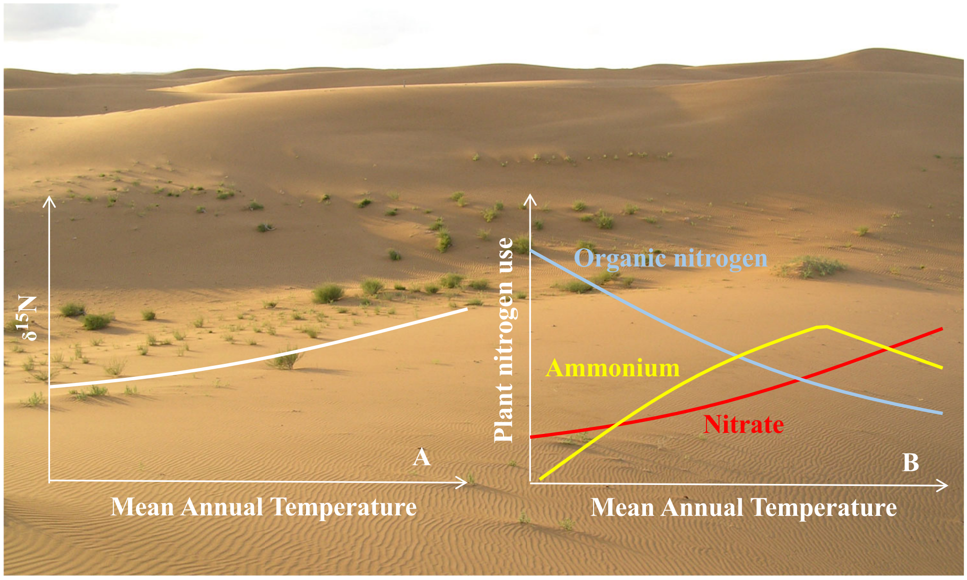

Fig. 1 | The relationships between plant/soil nitrogen and mean annual temperature. The relationship between $\delta^{15}N$ of various components (e.g., plant leaves, stems, roots, soil ammonium, nitrate, and organic nitrogen) and mean annual temperature (not to scale) (**A**). The proportion of plant use of ammonium, nitrate and organic nitrogen (not to scale) with increasing temperature (**B**). The results are from Hu et al.[6].

The decline in foliar $\delta^{15}N$ was used as key evidence to indicate a decline in nitrogen availability[4]. The argument is that higher CO_2 and warmer climates stimulate plant growth and induce nitrogen limitation. Others argue that atmospheric nitrogen deposition is widespread and that both the amount and the isotopic composition of atmospheric nitrogen deposition influence plant nitrogen use[11]. The current study sheds light on this debate by showing that atmospheric nitrogen deposition does not change plant nitrogen use, but it also shows that foliar $\delta^{15}N$ may not exactly represent plant nitrogen use.

The new dataset also shows that annual precipitation does not significantly affect plant nitrogen utilization[6]. This is in contrast with many regional studies showing a significant relationship between foliar $\delta^{15}N$ and mean annual precipitation[12]. However, this lack of relationship is consistent with global soil $\delta^{15}N$ results after controlling for variation in soil carbon and clay concentrations[5]. This suggests that foliar $\delta^{15}N$ is affected by the carbon-nitrogen interaction in soil and highlights the power of the newly proposed $\delta^{15}N_{PUN}$ term.

Organic nitrogen use and nitrogen uptake preference

Hu et al.[6] show that organic nitrogen uptake is almost one-third of total plant nitrogen uptake globally. Such a high degree of organic nitrogen use is surprising and requires verification from extensive field investigations. Hu et al.'s[6] result also gives insight to the plant nitrogen uptake preference. The energy expenditure during the plant ammonium assimilation is much lower in comparison to nitrate. However, an excess of ammonium can be toxic to plants. This makes some plants preferentially utilize ammonium or nitrate or switch nitrogen preference depending on the relative ammonium and nitrite availability[13,14]. Hu et al. identifies a 46% threshold of maximum ammonium contribution to plants globally[6].

Limitations and future perspectives

While Hu et al.[6] are building on biogeochemical theory and extensive observations, the new framework is constrained by the scarcity of simultaneous field observations of $\delta^{15}N$ of plant stems and roots as well as soil components (e.g., ammonium, nitrate, organic nitrogen). When the authors calculate the fraction contributions from different nitrogen sources, the number of observations in each calculation unit has a three-order of magnitude difference. Although the Bayesian statistical approach the authors employ addresses sample size variability to some degree, the data scarcity likely affects the accuracy of estimating source contributions. More field observations of simultaneous measurements of $\delta^{15}N$ of various plant and soil components are required to further test the new framework.

Like other $\delta^{15}N$ synthesis work in the past[4,5], Hu et al.[6] exclude urban and agricultural landscapes in their analyses. However, crops often use nitrogen differently from natural plants. For example, similar patterns of nitrogen uptake preference were found across generations in wild plants[14], but not for crops[15]. Because of the extensive size of agricultural lands and the unique functions of urban areas, data synthesis from urban and agricultural systems is needed in future studies.

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L.W. conceived of and wrote the manuscript.

Competing interests

The author declares no competing interests.

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