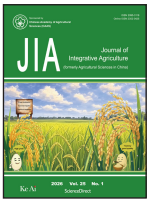
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RESEARCH ARTICLE

Soil nitrogen dynamics regulate differential nitrogen uptake between rice and upland crops

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Highlights

- The characteristics of gross N transformations regulate soil N dynamics.
- Soil N dynamics matching with crop N preference affect crop N uptake.
- Heterotrophic nitrification enhances N uptake in upland systems.
- Autotrophic nitrification constrains N uptake in rice systems.

Abstract

Nitrogen use efficiency in rice is lower than in upland crops, likely due to differences in soil nitrogen dynamics and crop nitrogen preferences. However, the specific nitrogen dynamics in paddy and upland systems and their impact on crop nitrogen uptake remain poorly understood. The N dynamics and impact on crop N uptake determine the downstream environmental pollution from nitrogen fertilizer. To address this poor understanding, we analyzed 2,044 observations of gross nitrogen transformation rates in soils from 136 studies to examine nitrogen dynamics in both systems and their effects on nitrogen uptake in rice and upland crops. Our findings revealed that nitrogen mineralization and autotrophic nitrification rates are lower in paddies than in upland soil, while dissimilatory nitrate reduction to ammonium is higher in paddies, these differences being driven by flooding and lower total nitrogen content in paddies. Rice exhibited higher ammonium uptake, while upland crops had over twice the nitrate uptake. Autotrophic nitrification stimulated by pH reduced rice nitrogen uptake, while heterotrophic nitrification enhanced nitrogen uptake of upland crops. Autotrophic nitrification played a key role in regulating the ammonium-to-nitrate ratio in soils, which further affected the balance of plant nitrogen uptake. These results highlight the need to align soil nitrogen dynamics with crop nitrogen preferences to maximize plant maximize productivity and reduce reactive nitrogen pollution.

Keywords: paddy soil, upland soil, plant nitrogen uptake, N mineralization, nitrification, ^{15}N tracing study

1. Introduction

Reactive nitrogen (N), upon entering the soil, initiates a series of cascades mediated by climate, soil, and microbes (Elrys *et al.* 2023c). These cascades are primarily governed by N transformations, which include processes such as plant and microbial N metabolism in the context of mineralization-immobilization turnover (MIT) (Jackson *et al.* 2008), soil acidification and water contamination governed by nitrification (Rice and Herman 2012; Cameron *et al.* 2013), as well as gaseous N emissions due to processes such as denitrification (Wrage-Mönnig *et al.* 2018). A systematic understanding of N cycling processes in agroecosystems is particularly

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relevant to farm practices, food security, environmental protection, and policy development (Gu *et al.* 2023). Gross N transformation rates in soils are governed by soil property, climate, land use, vegetation type and exogenous N supply (Booth *et al.* 2005; Zhang *et al.* 2018; Song *et al.* 2021). Moreover, N transformation processes are usually a function of the substrate concentrations involved in the reaction, and the individual processes may interact with each other. For example, mineralization provides inorganic N for nitrification and immobilization (Elrys *et al.* 2023b), which subsequently regulate ecosystem N leakage and crop fertilizer N use efficiency (NUE). Non-flooded upland croplands and flooded rice paddies constitute the two important land-use types in agricultural systems receiving large amounts of reactive N. It is imperative that differences in soil N cycling in paddy and upland soils are elucidated, so that effective N management practices for different agroecosystems may be derived.

Large differences in redox potential, soil structure and microbial activity between paddy soils and upland soils are well documented (Kögel-Knabner *et al.* 2010; Wei *et al.* 2021), but uncertainties remain regarding N dynamics. Based on natural abundance investigations, Lim *et al.* (2015) highlighted that the MIT is more pronounced in paddy soils than in uplands, due to limited nitrification in paddy soils. In contrast, Wei *et al.* (2021) suggested that the decomposition of organic matter in paddy fields was slower than in upland soils due to limited oxygen availability. The prevailing consensus is that the MIT is primarily focused on ammonium (NH_4^+) (Geisseler *et al.* 2010). However, some recent findings related to plant nitrate (NO_3^-) mining suggest that the conversion of organic N to NO_3^- can contribute as much to plant N uptake as the conversion of organic N to NH_4^+ (He *et al.* 2022; He *et al.* 2024b). Furthermore, while lower energy costs make microbes generally prefer to immobilize NH_4^+ (Weil and Brady 2017), a growing body of research indicates that microbial NO_3^- immobilization is also widespread in soils (Cheng *et al.* 2017; Tang *et al.* 2024). Moisture is the most important controller distinguishing paddies from uplands. Liesack *et al.* (2000) found that redox potential in paddy soils gradually decreased from 810 to –240 mV with decreasing oxygen concentration. N transformation processes in paddy soils progressively differ from uplands as NO_3 replaces oxygen as the main electron acceptor (Kögel-Knabner *et al.* 2010). It is widely accepted that water saturation slows down the NH_4^+ oxidation rate (Choi and Ro 2003) and leads to higher dissimilatory in NO_3^- reduction to NH_4^+ rates (DNRA, the reduction of NO_3^- to NH_4^+) and denitrification rates (the reduction of NO_3^- to N_2O or N_2) in paddy fields compared to uplands. However, investigations by Yang *et al.* (2016) challenged the idea that oxygen limits NH_4^+ oxidation in paddies because of the wide ecological niche of nitrifiers. Oxygen transport *via* aerenchyma tissue in rice plants enables aerobic root respiration and metabolism in the vicinity of roots (Armstrong and Beckett 1987; Li *et al.* 2008). Unlike the widely distributed uplands, rice fields are concentrated in areas with abundant hydrothermal conditions. Considering that nitrification in soil is also stimulated by temperature and inhibited by rainfall (Li Z L *et al.* 2020), this further exacerbates the uncertainty of NH_4^+ oxidation in both land use types. DNRA is similarly driven by moisture. Huygens *et al.* (2008) observed that DNRA in moist forests dominated NO_3^- reduction. In addition, N mineralization and NH_4^+ oxidation will exacerbate DNRA uncertainty in both agricultural lands due to the direct provision of NO_3^- for DNRA. The current gap in understanding the differences in soil N dynamics between paddy and upland soils, as well as the factors driving these differences, continues to impede the development of tailored N management practices and the realization of co-benefits associated with sustainable agriculture and mitigation of reactive N pollution.

The global NUE of rice is 39%, which is lower than that of upland crops such as maize (46%) and wheat (42%) (Zhang *et al.* 2015). Soil N transformations directly affect the NUE of crops (Zhang *et al.* 2018). For example, pH-mediated nitrification has been recognized as an important process in regulating crop N utilization (Zhang *et al.* 2016). Options to reduce the oxidation of NH_4^+ to NO_3^- have been widely discussed. The argument in favor of biological nitrification inhibitors suggests that inhibition of soil nitrification usually enhances rice N utilization (Sun *et al.* 2016; Coskun *et al.* 2017), while the opposite argument suggests rice stimulates nitrification through oxygen secretion from the root system to promote NUE (Li *et al.* 2008; Xu *et al.* 2020). Zhang *et al.* (2016) observed higher NUE in wheat in soils with rapid nitrification and attributed this to a well-coupled wheat NO_3^- demand with soil NO_3^- supply. Yue *et al.* (2023) also found that wild wheat rhizospheres naturally carry more microbes than domesticated cultivars that mediate nitrification. In contrast, Subbarao *et al.* (2021) showed that activation of nitrification inhibition in wheat increased yield by reducing N losses. However, it is difficult to develop an overarching pattern or explanation of soil N transformations from localized studies that can be widely applied. A major knowledge gap is that of the general linkage between crop N uptake strategies and soil N dynamics.

Soil N dynamics regulate the availability of mineral N and the ratio of NH_4^+ to NO_3^- in soils, which are closely linked to N fate (Zhang *et al.* 2018). In addition, the availability of NH_4^+ and NO_3^- to plants can influence their N source preferences. For example, the previous investigations found that, as the dominant N source changes, plant N preference gradually shifts from NO_3^- to NH_4^+ (Houlton *et al.* 2007; Lai *et al.* 2024). The alignment between the crop N preference and the dominant form of soil inorganic N is fundamental to achieving higher crop yields and NUE. For instance, rice typically absorbs more than 60% of its N as NH_4^+ (Kirk and Kronzucker 2005). Chen J T *et al.* (2024) found that optimal rice growth occurs when N is supplied at a 75:25 NH_4^+/NO_3^- ratio. Thus, it is anticipated that NH_4^+ uptake (U_{NH_4}) and total inorganic N uptake (U_N) of rice benefit from N mineralization but are suppressed by the oxidation of NH_4^+. In contrast, upland crops may benefit not only from N mineralization, but also from direct NO_3^- supply (i.e., the oxidation of organic N to NO_3^-), bypassing the oxidation of NH_4^+, and reducing the risk of N leakage (Gao *et al.* 2023). This mechanism can be a significant driver of NO_3^- uptake (U_{NO_3}) and U_N in upland crops. Furthermore, agroecosystems are often characterized by excessive reactive N inputs. Compared to forests and

grasslands, croplands exhibit slow MIT and rapid autotrophic nitrification, resulting in a low NH_4^+/NO_3^- ratio in soil (Elrys *et al.* 2023b). Considering that rice benefits from NH_4^+ while upland crops benefit from NO_3^-, we hypothesized that: (1) N mineralization in paddy fields will promote U_{NH4} and U_N in rice, while the opposite will be true for autotrophic nitrification; (2) U_{NO3} and U_N in the upland soils are promoted by both N mineralization and heterotrophic nitrification of organic N.

In this analysis, we synthesized 2,044 global observations from 136 studies encompassing eight transformation processes of four N pools (soil organic N, NH_4^+, and NO_3^-, and plant N) in croplands. This represents one of the most extensive datasets on soil N dynamics to date, providing a robust foundation for our analysis. To address the differences in soil N dynamics between paddy and upland soils and their relationship to plant N uptake strategies, we adopted a comprehensive and integrative approach. First, we reviewed measurements of gross N transformations in these contrasting soil types and identified the key drivers of N fluxes with distinct variations. Second, unlike previous studies that primarily focused on plant N preferences (Wang and Macko 2011; Chen J T *et al.* 2024) or examined soil N transformation processes in isolation (Elrys *et al.* 2021a, b), this study uniquely integrated multiple N transformation processes with plant N uptake strategies, providing a more comprehensive understanding of soil N dynamics. We conducted rigorous comparisons and employed linear mixed-effects models to identify global patterns, thereby disentangling the complex interactions between soil processes and crop N uptake strategies. Finally, this study provided actionable insights for global N management by addressing two critical research questions: (1) What are the differences in soil gross N transformations between paddy and upland soils globally and what are their drivers? (2) What are the associations between soil gross N transformations and N uptake in rice and upland plants? By aligning crop N preferences with the predominant inorganic N forms in the soil, we demonstrate pathways to enhance NUE and reduce N losses. This is particularly critical for rice systems, where NUE is often low, and the potential for environmental N losses is high.

2. Materials and methods

2.1. Dataset construction

We collected and screened peer-reviewed papers published before November 2023 in the Web of Science and Google Scholar following the preferred reporting items for systematic reviews and meta-analyses guidelines (Appendix A). Specifically, we considered N transformation processes among the three soil N pools (organic N, NH_4^+, and NO_3^-), namely gross N mineralization (oxidation of organic N to NH_4^+), gross heterotrophic nitrification (oxidation of organic N to NO_3^-), gross autotrophic nitrification (oxidation of NH_4^+ to NO_3^-), DNRA, gross NH_4^+ immobilization (the conversion of NH_4^+ to organic N), and gross NO_3^- immobilization (the conversion of NO_3^- to organic N). Additionally, we took into account plant U_{NH4} and plant U_{NO3}. We used the following search terms: “gross nitrogen rate”, “gross nitrogen mineralization”, “gross nitrification”, “dissimilatory nitrate reduction to ammonium”, “gross immobilization rate”, “plant ammonium uptake”, “plant nitrate uptake”, “cropland”, “upland”, “paddy”, and their combinations.

Publications meeting the following criteria were included in our analyses: (1) The tested soils were from the surface horizon (0–20 cm) of cropland, and the type of cropland was specified, such as upland or paddy; (2) at least one gross N transformation rate was reported; (3) the rate of gross N transformation and the rate of plant N uptake were determined by ^{15}N tracing and the incubation time for the ^{15}N tracing experiment was in the range of 24–96 h. Our dataset includes a portion of observations from pot experiments, in which ^{15}N tracers were typically applied as NH_4NO_3 at concentrations of 60–80 mg N kg^{-1} (i.e., $^{15}NH_4NO_3$ and $NH_4{}^{15}NO_3$, 10% atom). In these experiments, the addition of tracers was considered to simulate the application of fertilizer N. Therefore, the gross N transformations and plant N uptake rates measured in the pot experiments are more representative of scenarios involving fertilizer N application during the growing season. Previous publications related to gross N transformations were also included in our study (Elrys *et al.* 2023b; Chen S *et al.* 2024). After comparing and excluding duplicate studies, 2,044 observations of N fluxes from 136 studies were included in our dataset (Appendix B).

In addition to the above criteria, we set up the following specific data management procedures. First, soil samples were collected from fields or actual cultivated lands, rather than soils subjected to controlled laboratory conditions. Local fertilizer management practices were followed in fields and they were planted with either upland or flooded crops. The soils were not subjected to other artificial interventions or experimental treatments, such as temperature increase, CO_2 enrichment, or organic material addition. Next, all observations were derived from text, tables, graphs and supplementary information. Getdata (version 2.22) was used to extract data from the graphs. Observations (upland/paddy) include N mineralization (334/114), autotrophic nitrification (199/109), heterotrophic nitrification (161/98), NH_4^+ immobilization (210/113), NO_3^- immobilization (194/23), DNRA (150/111), U_{NH4} (76/38), U_{NO3} (76/38). In our dataset, plant N uptake rates were determined using ^{15}N tracing in pot experiments. By simultaneously applying $^{15}NH_4^+$ and $^{15}NO_3^-$, the uptake of NH_4^+ and NO_3^- by plants can be distinguished (He *et al.* 2020). The U_N (76/38) was also calculated as the sum of U_{NH4} and U_{NO3}. In addition, site-specific information on precipitation (mean annual precipitation, 340/118), temperature (mean annual temperature, 337/116), soil pH (353/124), soil total N (324/119), soil organic C (SOC) (278/120), soil C:N (329/122), soil extractable NH_4^+ (185/76) and NO_3^- (197/72), and N_2O emissions (4/50) were extracted accordingly. The dataset had a wide range of precipitation from 152 to 2,365 mm and temperature from 1.5 to 26.7°C. Similarly, soil properties in our dataset exhibited wide ranges: pH ranged from 3.32 to 8.80; total N ranged from 0.12 to 4.80 g kg^{-1}; SOC ranged from 0.17 to 50 g kg^{-1}; the C/N ratio ranged from 2.71 to 22.50; NH_4^+ ranged from 0.03 to 16.06 mg kg^{-1}; and NO_3^- ranged from 0.10 to 121.43 mg kg^{-1}.

2.2. Data analyses

Prior to analysis, we used the interquartile range method to identify and remove potential outliers, determining the dataset for final analysis. For all continuous variables, the upper limit of the observations was defined as the sum of the upper quartile and 1.5 times interquartile range, while the lower limit was defined as the difference between the lower quartile and 1.5 times interquartile range. This approach has been widely applied in many modeling efforts and meta-analyses (Vinutha *et al.* 2017; Elrys *et al.* 2023a). Subsequently, we assessed the normality of the data using histograms and the Kolmogorov-Smirnov test. The vast majority of the indicators did not fit a normal distribution. Therefore, we applied a natural logarithm transformation to standardize the continuous variables.

Statistical analyses were conducted using R (4.3.3). The Two-tailed *t*-test was applied to determine significant differences in each variable between upland and paddy. Differences in N transformations between land uses were reported as mean±standard error (SE). Subsequently, we employed linear mixed-effects modeling (LMEM) to identify potential drivers influencing soil N fluxes in both upland and paddy. The LMEM used the maximum likelihood method, with environmental factors treated as fixed effects and the study treated as a random effect (eq. (1)). The "lme4" package was used to construct the LMEM and the *P*-values were derived from the "lmerTest" package (Bates *et al.* 2015; Kuznetsova *et al.* 2017). After collecting all slopes and *P*-values, we created forest plots using the "ggplot2" package.

$$Ln(Y)=\beta_0+\beta_1(Ln(X))+\pi_{study}+\varepsilon \quad (1)$$

In eq. (1), Y refers to the dependent variable, β_0 denotes the intercept, β_1 represents the fixed coefficient, X is the environmental variable (environmental variables were considered individually), π signifies the random effect, and ε indicates the sampling error. The random effect captures the influence of observations within each study.

Additionally, we used the "randomForest" package to perform random forest analysis to identify important factors related to plant N uptake (U_N, U_{NH_4}, U_{NO_3}, and U_{NH_4}/U_{NO_3}) in cropland. The significance of each variable was ranked based on the increase in mean squared error and reported accordingly. To determine the significance of the variables, we used the "rfPermute" package to estimate *P*-values through 1,000 random permutations, with significance defined at $P<0.05$ (Jiao *et al.* 2018). Similarly, we applied LMEM to explore the association of U_N, U_{NH_4}, U_{NO_3}, and U_{NH_4}/U_{NO_3} with soil internal N fluxes in upland and paddy.

3. Results

3.1. Differences in N dynamics between upland and paddy soils

There were distinct differences between paddy soils and upland soils in gross N transformations (Fig. 1). The mean values of N mineralization and autotrophic nitrification in uplands (2.25±0.11 and 4.49±0.48 mg N kg^{-1} d^{-1}, respectively) were significantly higher than those in paddies (1.79±0.11 and 3.22±0.30 mg N kg^{-1} d^{-1}, respectively). Conversely, DNRA and N_2O emissions were significantly higher in paddies

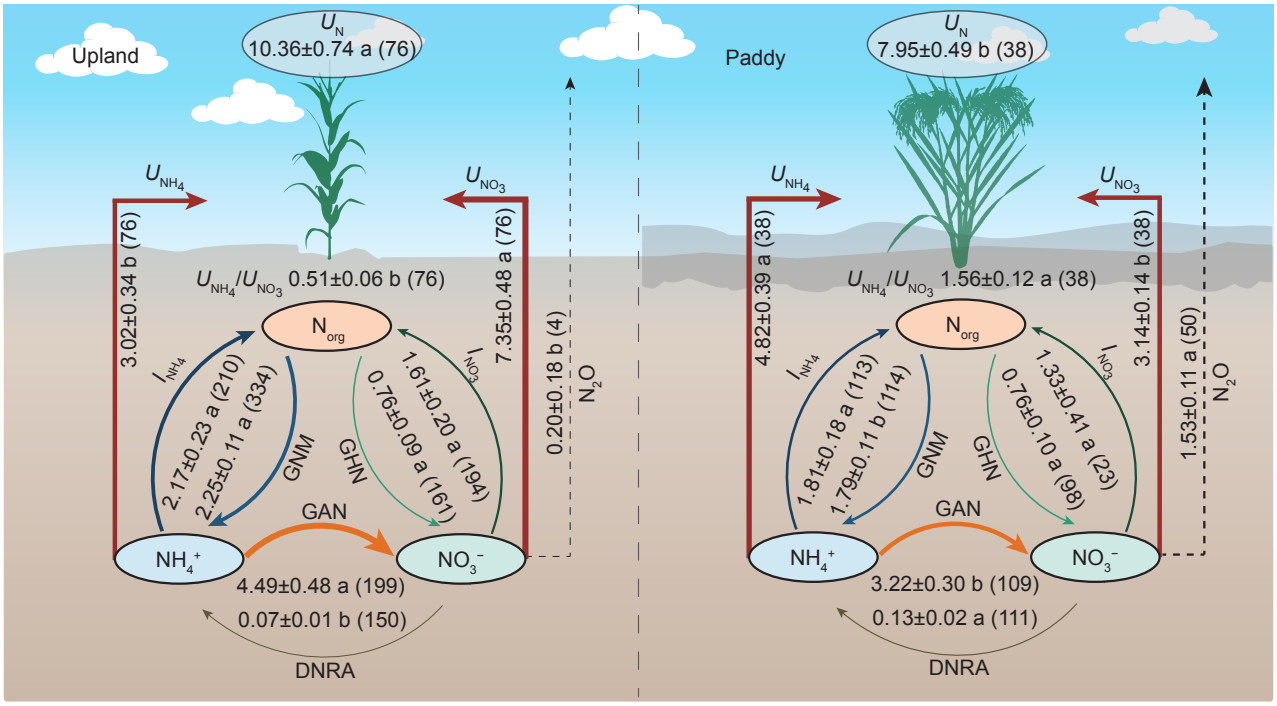


Fig. 1 Differences of nitrogen (N) fluxes between upland soils and paddy soils. N_{org}, organic N; GNM, gross N mineralization; GHN, gross heterotrophic nitrification; GAN, gross autotrophic nitrification; DNRA, dissimilatory NO_3^- reduction to NH_4^+; U_{NH_4}, plant NH_4^+ uptake; U_{NO_3}, plant NO_3^- uptake; I_{NH_4}, gross NH_4^+ immobilization; I_{NO_3}, gross NO_3^- immobilization; U_N, plant inorganic N uptake. The unit of N flux in figures is mg N kg^{-1} d^{-1}. Numbers in parentheses indicate the number of observations. Rate magnitudes are expressed as mean±SE. Different letters indicate significant differences at $P<0.05$ between upland and paddy soils.

(0.13±0.02 and 1.53±0.11 mg N kg^{-1} d^{-1}, respectively) than in upland soils (0.07±0.01 and 0.20±0.18 mg N kg^{-1} d^{-1}, respectively). There were no significant differences in heterotrophic nitrification, NH_4^+ immobilization, and NO_3^- immobilization between the two land uses. Plant N uptake also varied largely between uplands and paddies (Fig. 1). The U_{NH_4} of rice, 4.82±0.39 mg N kg^{-1} d^{-1}, was significantly higher than in upland crops (3.02±0.34 mg N kg^{-1} d^{-1}). However, the U_{NO_3} (7.35±0.48 mg N kg^{-1} d^{-1}) of upland crops was more than twice that of rice (3.14±0.14 mg N kg^{-1} d^{-1}), resulting in a significantly higher U_N by upland crops than by rice. The ratio of U_{NH_4}-to-U_{NO_3} in upland soils (0.51±0.06) was significantly lower than that in paddy soils (1.56±0.12). Our analysis also showed that precipitation and temperature were significantly higher in paddy fields than in upland fields. In contrast, soil total N and extractable NO_3^- concentrations were significantly higher in paddies compared to uplands. However, SOC, C/N ratio, and extractable NH_4^+ concentration did not differ significantly between land uses (Appendix C).

3.2. Drivers of divergence in N dynamics between uplands and paddy fields

Our analysis revealed that increased temperature significantly stimulated N mineralization in paddy fields (slope=0.451, P=0.002) but had no effect in upland fields (slope=−0.032, P=0.854; Fig. 2-A). In upland fields, N mineralization decreased significantly with increasing precipitation (slope=−0.508, P=0.004), whereas the opposite was observed in paddy fields (slope=0.498, P=0.002). N mineralization in both upland and paddy fields increased with rising total N (upland: slope=0.403, P=0.003; paddy: slope=0.604, P<0.001) and SOC (upland: slope=0.229, P=0.046; paddy: slope=0.421, P=0.002). However, C/N ratios significantly suppressed N mineralization in paddy fields (slope=−0.763, P=0.022) and had no effect in upland fields (slope=−0.364, P=0.211). N mineralization was positively correlated with pH in upland fields (slope=0.322, P<0.001) but not in paddy fields (slope=0.001, P=0.980).

Autotrophic nitrification was inhibited by increasing precipitation (upland: slope=−1.033, P=0.002; paddy: slope=−1.532, P<0.001) and was positively correlated with pH (upland: slope=0.552, P<0.001; paddy: slope=0.816, P<0.001) in both upland and paddy fields (Fig. 2-B). However, total N tended to promote autotrophic nitrification in upland fields (slope=0.478, P=0.060), while in paddy fields, total N (slope=−1.131, P=0.010) and SOC (slope=−1.166, P=0.003) were significantly negatively correlated with autotrophic nitrification. Additionally, DNRA increased significantly with pH (slope=0.052, P<0.001), but decreased significantly with increasing precipitation (slope=−0.083, P=0.011), total N (slope=−0.135, P<0.001), SOC (slope=−0.150, P<0.001), and C/N ratio (slope=−0.214, P=0.003) in paddy fields (Fig. 2-C). In contrast, DNRA in uplands was not strongly associated with environmental factors.

3.3. Associations between crop N uptake and soil N dynamics under different land uses

Random forest analyses identified N mineralization as the most critical N flux affecting U_N in croplands (Fig. 3-A). The LMEM analysis also demonstrated that N mineralization contributed to U_N in both upland and paddy soils (upland: slope=0.169, P<0.001; paddy: slope=0.377, P=0.008) (Fig. 4-A). In uplands, heterotrophic nitrification (slope=0.128, P<0.001) promoted U_N, whereas increased autotrophic nitrification (slope=−0.171, P<0.001) and DNRA (slope=−2.165, P<0.001) negatively affected U_N in paddy soils (Fig. 4-A). Autotrophic nitrification was a significant and negative driver of U_{NH_4} in both upland (slope=−0.134, P=0.033) and paddy soils (slope=−0.237, P<0.001) (Figs. 3-B and 4-B). Additionally, in uplands, U_{NH_4} was suppressed by NH_4^+ immobilization (slope=−0.171, P<0.001), but had significant and positive relationships with heterotrophic nitrification (slope=0.270, P<0.001). Conversely, in paddy soils, U_{NH_4} was driven by N mineralization (slope=0.492,

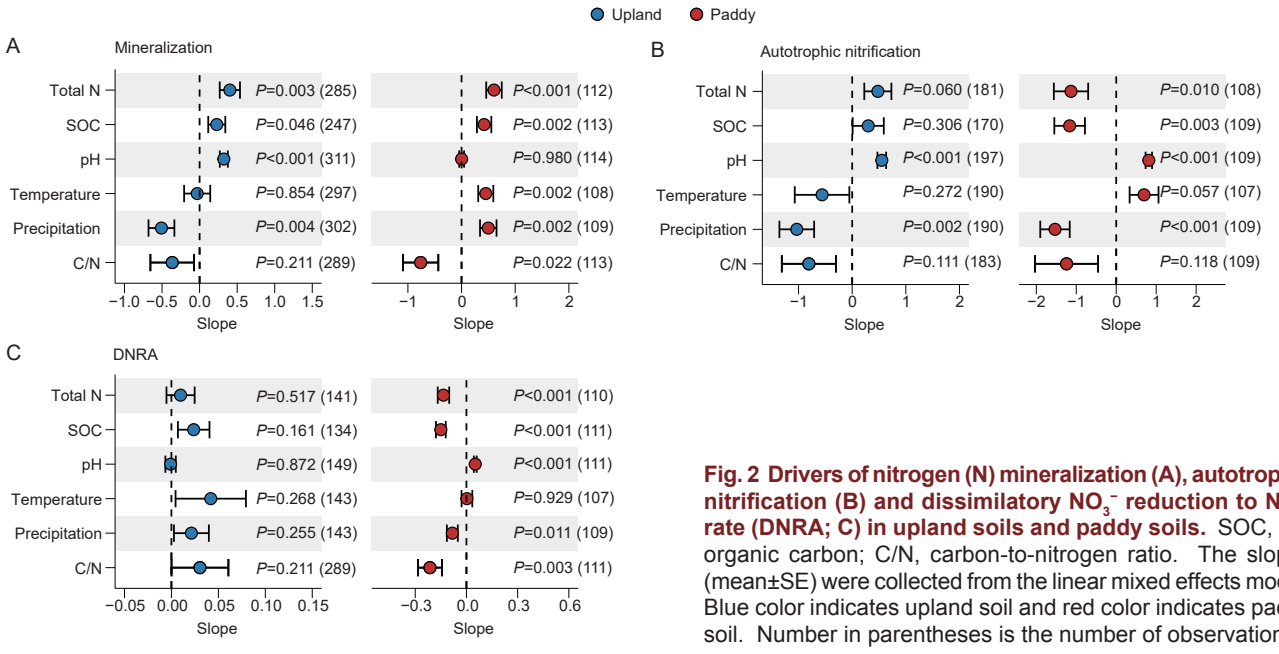


Fig. 2 Drivers of nitrogen (N) mineralization (A), autotrophic nitrification (B) and dissimilatory NO_3^- reduction to NH_4^+ rate (DNRA; C) in upland soils and paddy soils. SOC, soil organic carbon; C/N, carbon-to-nitrogen ratio. The slopes (mean±SE) were collected from the linear mixed effects model. Blue color indicates upland soil and red color indicates paddy soil. Number in parentheses is the number of observations.

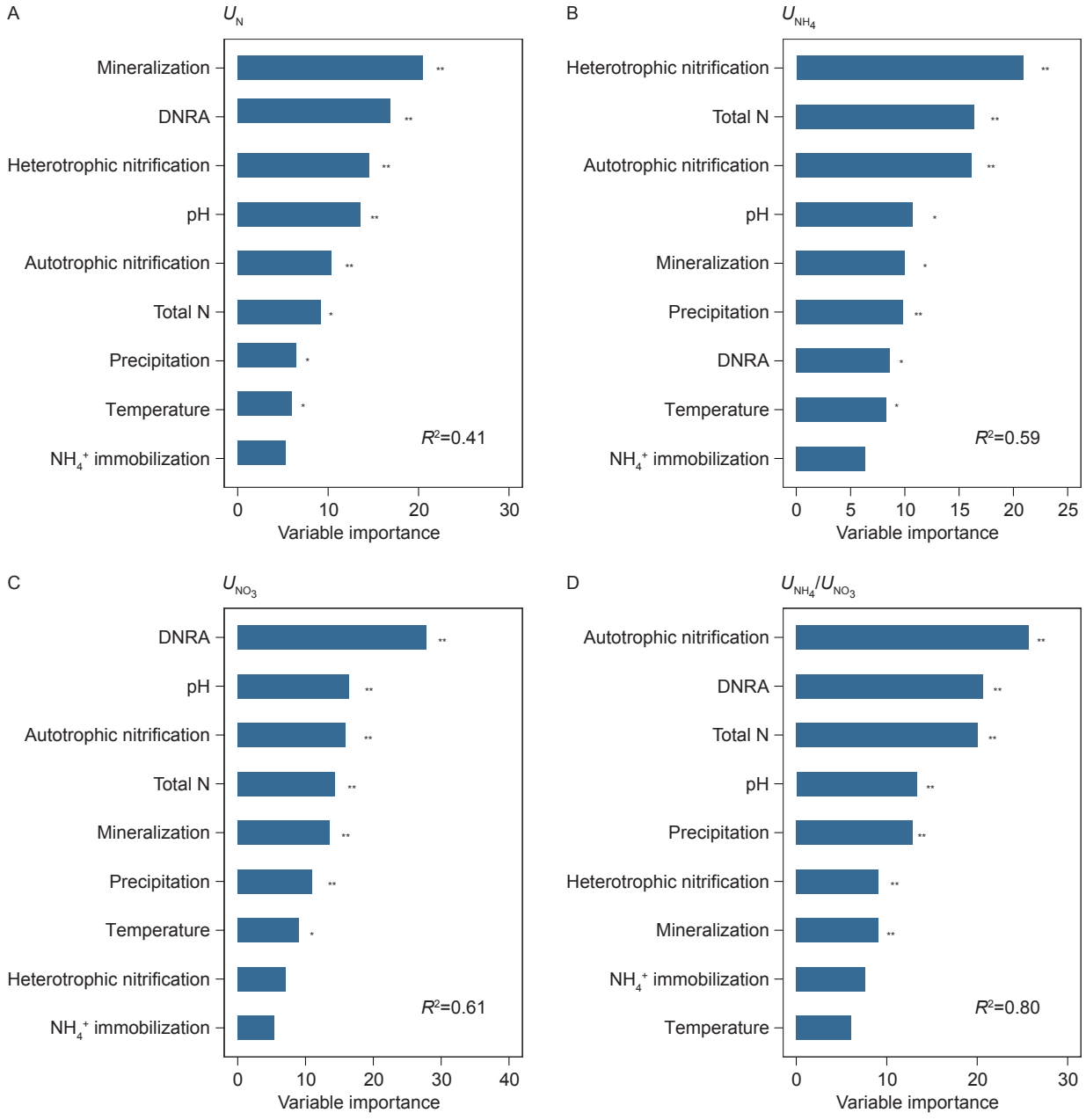


Fig. 3 Important factors affecting plant inorganic N uptake (U_N; A), plant NH_4^+ uptake (U_{NH_4}; B), plant NO_3^- uptake (U_{NO_3}; C) and U_{NH_4}/U_{NO_3} (D) in croplands. DNRA, dissimilatory NO_3^- reduction to NH_4^+ rate. Cropland includes uplands and paddy fields. R^2 denotes the overall explanation of the dependent variable by all covariates. *, P<0.05; **, P<0.01.

P=0.012) (Fig. 4-B).

Random forest analysis indicated that DNRA, autotrophic nitrification, and N mineralization were crucial N fluxes affecting U_{NO_3} (Fig. 3-C). Specifically, in upland soils, U_{NO_3} was driven by heterotrophic nitrification (slope=0.100, P=0.002) and N mineralization (slope=0.183, P<0.001), while in paddies, U_{NO_3} increased significantly with N mineralization (slope=0.256, P=0.016) and decreased significantly with autotrophic nitrification (slope=−0.077, P=0.001) (Fig. 4-C), mirroring the pattern observed for U_N. DNRA also tended to suppress U_{NO_3} in paddies (slope=−0.789, P=0.072). We also found that increased NH_4^+ immobilization (slope=−0.223, P<0.001) and autotrophic nitrification (slope=−0.207, P=0.001) suppressed U_{NH_4}/U_{NO_3} in upland soils, whereas increased heterotrophic nitrification promoted it (slope=0.181, P=0.001). In contrast, in paddy soils, U_{NH_4}/U_{NO_3} increased significantly with increasing N mineralization (slope=0.334, P=0.045) and decreasing autotrophic nitrification (slope=−0.166, P<0.001) and DNRA (slope=−2.649, P<0.001) (Fig. 4-D). In conclusion, autotrophic nitrification emerged as the most important variable regulating U_{NH_4}/U_{NO_3} (Fig. 3-D).

4. Discussion

4.1. Differential drivers of N cycling in upland and paddy soils

N mineralization was significantly lower in the rice fields compared to the uplands (Fig. 1), which challenges the

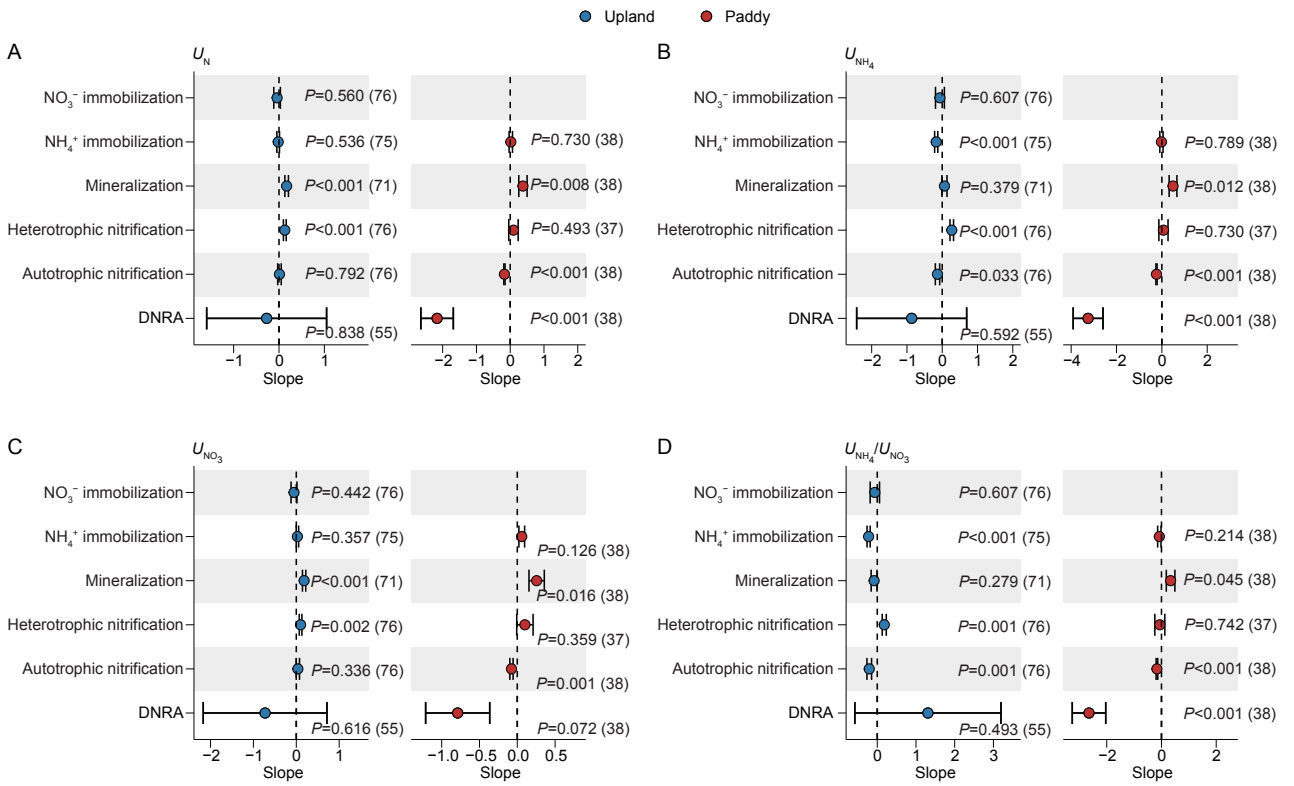


Fig. 4 Drivers of plant inorganic N uptake (U_N; A), plant NH_4^+ uptake (U_{NH_4}; B), plant NO_3^- uptake (U_{NO_3}; C) and U_{NH_4}/U_{NO_3} (D) in upland soils and paddy soils. DNRA, dissimilatory NO_3^- reduction to NH_4^+. The slopes (mean±SE) were collected from the linear mixed effects model. Blue color indicates upland soil and red color indicates paddy soil. Number in parentheses is the number of observations.

opinion that paddy soils are characterized by a faster MIT than upland soils (Lim *et al.* 2015). The low N mineralization in rice paddy was significantly associated with lower total N and relatively high C/N ratios (Appendix C). Soils with abundant substrates generally support high microbial biomass (Li *et al.* 2019), and a low C/N ratio facilitates microbial decomposition and utilization (Bengtsson *et al.* 2003), thereby driving N mineralization (Booth *et al.* 2005; Elrys *et al.* 2021a). The significant increase in N mineralization with rising total N in both upland and paddy fields supports this observation (Fig. 2-A). In addition, total N was higher in the paddy fields compared to the uplands (Appendix C), which is consistent with a previous survey (Wei *et al.* 2021). N mineralization in rice fields would therefore be highly sensitive to substrate quality, as LMEM indicated that N mineralization was significantly suppressed by high C/N ratios in paddy fields, unlike in upland soils (Fig. 2-A). As a result, the significant control of organic N content and the C/N ratio on N mineralization diminishes the effects of other soil properties, such as pH, on mineralization. Thus, despite similar pH levels in upland and paddy fields (Appendix C), N mineralization in upland areas was stimulated by increasing pH, whereas N mineralization in paddy fields showed no sensitivity to pH (Fig. 2-A).

Long-term persistent inundation is the most significant feature distinguishing rice fields from uplands (Kögel-Knabner *et al.* 2010). Reduced oxygen availability directly contributes to the significantly lower autotrophic nitrification in rice fields compared to uplands (Fig. 1), consistent with previous studies (Lim *et al.* 2015). Additionally, NO_3^- concentration in paddies was significantly lower than in uplands (Appendix C), which is attributed to the lower autotrophic nitrification and higher DNRA in paddies. In both paddy and upland soils, increasing pH significantly promoted autotrophic nitrification (Fig. 2-B). In addition, oxygen is required for both N mineralization and autotrophic nitrification. While organic matter improves soil structure and increases soil aggregation and water retention (Rabot *et al.* 2018), it also limits the diffusion of oxygen through soil pores (Asano and Wagai 2014; Totsche *et al.* 2018), which is detrimental to autotrophic nitrification. Moreover, substrate and temperature interactions favor the multiplication and activity of heterotrophic microorganisms (Zimmermann *et al.* 2012; Leifeld and von Luetzow 2014), intensifying the competition for oxygen and further weakening autotrophic nitrification in paddy fields.

In contrast, DNRA was significantly higher in paddies than in uplands (Fig. 1). Our results also showed that the association between DNRA and environmental variables was not clear in the uplands, but DNRA in paddies was stimulated by increase in pH and was related to substrate content and quality (SOC, total N and C/N ratio) and precipitation (Fig. 2-C). As a strictly anaerobic N transformation process (Lam and Kuypers 2011), the prolonged flooding of paddy fields provides ideal conditions for DNRA, with pH being its main stimulator (Fig. 2-C), consistent with previous study (Cheng *et al.* 2022). Many anaerobic microorganisms (e.g., anaerobic bacteria) that

perform DNRA exhibit optimal activity under neutral and slightly alkaline conditions (Li Z X *et al.* 2020; Wang *et al.* 2022). Although DNRA is considered a favorable process for microbial N retention, the higher DNRA in paddy fields compared to uplands does not imply a more conserved N cycle. Investigations by Shan *et al.* (2016) found that denitrification in paddy soils was the primary process of NO_3^- reduction, while DNRA was secondary. This finding aligns with the present study, where we observed much higher rates of N_2O emissions in paddy fields than DNRA (Fig. 1). The analysis also found significantly higher N_2O emissions in paddy fields than in uplands. NH_4^+ produced by N mineralization is rapidly oxidized to NO_3^- in the shallow aerobic zone. Subsequently, rapid denitrification may occur when NO_3^- is transferred to the deep anaerobic zone, resulting in N loss (Ishii *et al.* 2011).

4.2. Differences in N uptake between upland crops and rice are associated with N dynamics

Our analyses revealed that U_{NH_4} was significantly lower in upland crops than for rice, while the opposite was true for U_{NO_3} (Fig. 1). The lower U_N in rice aligns with its lower NUE relative to upland crops. We found that U_N and U_{NH_4} of NH_4^+-preferring rice benefited from NH_4^+-producing processes (e.g., N mineralization) and were inhibited by NH_4^+-consuming processes (e.g., autotrophic nitrification). In contrast, U_N and U_{NO_3} of NO_3^--preferring upland crops benefited from NO_3^--producing processes (e.g., heterotrophic nitrification) and N mineralization. These results confirm our two hypotheses. Specifically, N mineralization and heterotrophic nitrification are the important factors driving U_N in uplands (Fig. 4-A). Conversely, U_N in rice fields is suppressed by autotrophic nitrification (Fig. 4-A). Due to low assimilative energy consumption (Weil and Brady 2017), NH_4^+ is often considered to be a superior N source, with NH_4^+ uptake accounting for more than 60% of U_N in rice (Kirk and Kronzucker 2005). Lower autotrophic nitrification and higher DNRA in rice fields favor U_{NH_4} (Fig. 4-B). Additionally, the release of biological nitrification inhibitors from rice is a crucial mechanism promoting U_{NH_4} (Sun *et al.* 2016). N mineralization also plays a significant role in rice fields by providing substrates for U_{NH_4} (Fig. 4-B). In contrast, many upland crops are less tolerant to NH_4^+ than rice and depend more on NO_3^- availability (Britto and Kronzucker 2013). Although autotrophic nitrification does not promote U_{NO_3} in upland crops, heterotrophic nitrification significantly drives it (Fig. 4-C). Recent studies indicate that plants can activate heterotrophic nitrification through rhizodeposition, with direct oxidation of organic N to NO_3^- without production of NH_4^+ as observed in NO_3^--preferring plants (e.g., wheat and maize) (He *et al.* 2024, 2025).

Differential N uptake strategies between upland crops and rice are closely linked to soil N cycling dynamics. In natural ecosystems, plant N preference shifts from NH_4^+ to NO_3^- under arid conditions, but not under humid conditions (Houlton *et al.* 2007). A similar pattern has been observed in agricultural systems (Fig. 1). However, it has been suggested that faster organic matter decomposition and NO_3^- leaching in wetter regions leads to higher soil NH_4^+/NO_3^- (Wang and Macko 2011). We suggest that autotrophic nitrification is an important process regulating NH_4^+/NO_3^- in agroecosystems. We found that the decrease in autotrophic nitrification from 4.49 mg N kg^{-1} d^{-1} in uplands to 3.22 mg N kg^{-1} d^{-1} in paddy soils corresponded with a reduction in soil NO_3^- concentration from 26.5 to 18.8 mg kg^{-1} (Fig. 1; Appendix C). Concurrently, the U_{NH_4}/U_{NO_3} ratio increased from 0.51 in uplands to 1.56 in flooded paddy fields (Fig. 1). Both random forest and LMEM analyses confirmed that an increase in autotrophic nitrification is a significant factor in suppressing the U_{NH_4}/U_{NO_3} ratio (Figs. 3-D and 4-D). Previous research has indicated that enhanced-efficiency N fertilizer boosts rice yield in neutral and alkaline soils, whereas its benefits in acidic soils are comparable to those of regular urea (Linquist *et al.* 2013). In addition to moisture changes, soil pH also influences plant N uptake strategies (Lai *et al.* 2024). Autotrophic nitrification increases with increasing soil pH (Elrys *et al.* 2021b), and in rice paddies, increased autotrophic nitrification directly reduces the NH_4^+/NO_3^- ratio, leading to mismatches between crop N preferences and soil inorganic N forms. Chen J T *et al.* (2024) demonstrated that rice achieved optimal biomass with a fertilizer NH_4^+/NO_3^- ratio of 75:25, aligning with the rice nutrient uptake strategy. In uplands, autotrophic nitrification reduces the U_{NH_4}/U_{NO_3} ratio primarily by suppressing U_{NH_4} (Fig. 4-B) rather than promoting U_{NO_3} (Fig. 4-C). Many upland crops (e.g., maize and wheat) prefer NO_3^- and perform better when the proportion of NO_3^--N exceeds 50% of total N (Chen J T *et al.* 2024). Liu *et al.* (2019) found that wheat yields were lower in soils with low nitrification rates as NH_4^+ could not be oxidized to NO_3^- quickly enough to meet plant NO_3^- requirements in low-nitrifying uplands. Although rice predominantly absorbs NH_4^+, excessive NH_4^+ uptake may lead to NH_4^+ toxicity and other negative effects, however, these effects are mitigated because rice also absorbs NO_3^- (Britto and Kronzucker 2002).

4.3. Implications and limitations

To enhance crop yields and NUE, agricultural managers can develop rational N fertilizer management strategies based on crop type and soil N dynamics. The spatial variability of soil properties, influenced by differences in organisms, climate, topography, parent material, and formation time (Weil and Brady 2017), creates spatial and temporal heterogeneity in the N cycle and alters nutrient storage patterns. For instance, nitrification is inhibited in acidic soils, leading to a dominance of NH_4^+, whereas in neutral and alkaline soils, nitrification is generally fast, resulting in a NO_3^- predominance (Zhang *et al.* 2018). It is widely accepted that crops originating from NH_4^+-dominated soils, such as rice, tend to prefer NH_4^+ uptake, while crops (such as wheat and maize) from NO_3^--dominated soils, favor NO_3^- uptake (Gigon and Rorison 1972; Falkengren-Grerup and Lakkenborg-Kristensen 1994; von Wiren *et al.* 1997). Matching the form of inorganic N in the soil with crop preferences is crucial for improving yield, enhancing N fertilizer utilization, and minimizing N losses. Planting rice in alkaline soils with rapid nitrification or indiscriminately using nitrification inhibitors without considering soil N dynamics can hinder yield maximization (Zhang *et al.* 2016; Liu *et al.* 2019).

The associations between soil N dynamics and crop N

uptake strategies in uplands and paddy soils identified in this study are instrumental for nutrient management practices in specific agricultural systems. For example, while the application of nitrification inhibitors is generally believed to reduce N_2O emissions and NO_3^- leaching (Akiyama *et al.* 2010; Linquist *et al.* 2012), its impact on crop yield is inconsistent. For instance, Hu *et al.* (2014) found no significant yield effect from nitrification inhibitors in Germany, whereas other experiments showed a positive yield response (Chen *et al.* 2023). This contradiction can be understood by considering soil N dynamics and crop N uptake strategies. For many NO_3^--preferring upland crops, if soil nitrification is not particularly strong, the use of nitrification inhibitors — which prolong the presence of NH_4^+ — can negatively affect crop N uptake and yield (Zhang *et al.* 2016). Conversely, for rice, if the nitrification is rapid or the pH is high, nitrification inhibitors can favor NH_4^+ uptake and enhance yield (Linquist *et al.* 2013; Liu *et al.* 2019). Therefore, nitrification inhibitors that do not take into account crop N preferences and the soil nitrification capacity are unlikely to achieve both environmental benefits and yield improvements. Through the judicious use of nitrification inhibitors, combined with organic fertilizer substitution and 4R nutrient stewardship practices, rice production can be maximized while minimizing the environmental impacts of nitrogen losses (Kong *et al*. 2024).

In intensive cropping systems, pre-sowing mineral N may provide a significant source of plant-available N (Zhao *et al.* 2024). One limitation of the present study is the lack of consideration for application of pre-sowing mineral N during the crop growth season. Future studies integrating environmental and fertilizer management factors with soil N mineralization dynamics could offer a more holistic understanding of N uptake in cropping systems. In addition, the observations from rice fields in this study were concentrated in China while those from drylands were distributed globally. Although China, as the largest rice producer in the world (FAO 2022), has diverse soil and climatic conditions that make it a representative region for studying rice systems, this geographic concentration may introduce potential bias. The results of this study should therefore be interpreted with caution.

5. Conclusion

The characteristics of soil gross N transformations regulated soil N dynamics, e.g., mineral N supply capacity and ammonium to nitrate ratio, which matched with crop specific N preferences could affect NUE. The low supply capacity of ammonium in paddy soil due to low N mineralization rate and the competition of autotrophic nitrification for ammonium with rice that prefers NH_4^+ uptake, as well as the N loss *via* coupled nitrification and denitrification processes, were the key factors resulting in the low NUE of rice. These results highlight that the optimal coupling of crop N preferences with soil available N forms that accord with soil gross N transformations or N fertilizer type should enhance NUE.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

Declaration of generative AI and AI-assisted technologies in the writing process

The authors declare that they did not use AI in the preparation and writing of this manuscript.

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