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RESEARCH ARTICLE

Priming effects of maize growth and photosynthetic substrate supply on soil N mineralization-immobilization turnover

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Abstract

Aims Soil nitrogen (N) mineralization-immobilization turnover (MIT) regulates the inorganic N supply in terrestrial ecosystems. Much research has been done to understand the factors that control the MIT in soils, but how plants-soil-microbe interactions influence the MIT remains to be further explored.

Methods A series of ^{15}N tracing experiments, including with and without maize (*Zea mays* L.) planting, maize shading, and maize root endophytes inoculation, were conducted to investigate the drivers of the change in MIT by the presence of plant.

Results Soil gross N mineralization (*M*), especially the mineralization of recalcitrant organic-N to NH_4^+ (M_{Nrec}, 0.51 mg N kg^{-1} d^{-1}) was significantly improved by maize compared with the control treatment (without maize) (0.07 mg N kg^{-1} d^{-1}). M_{Nrec} significantly decreased after removing maize or covering maize with a black box (preventing photosynthesis). Soil dissolved organic carbon (DOC) concentration significantly decreased after preventing photosynthesis, and showed a significant positive relationship with M_{Nrec}, confirming that photosynthetic substrate

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supply was the dominating factor in stimulating M_{Nrec}. Simultaneously, the release of absorbed NH_4^+ on the cation exchange sites increased with decreasing M_{Nrec} when photosynthesis was prevented. Microbial N immobilization (I), especially NO_3^- immobilization rate (I_{NO3}), was significantly stimulated in all maize treatments compared to the control. The I_{NO3} of unsterilized soil applied with unsterilized plant endophytes was significantly higher than unsterilized soil applied with sterilized endophytes, indicating a close relationship between endophytes and microorganisms on I_{NO3}.

Conclusions M_{Nrec} was stimulated by the photosynthetic substrate supply, and the increasing microbial N immobilization induced by plant significantly increased the ratio of I to M in the presence of maize, which was beneficial to soil N retention and reduced N loss. Our results provide new insights of the MIT for better understanding the productivity of agricultural systems and its driving factors.

Keywords Gross N mineralization · Microbial N immobilization · Root exudates · Plant endophytes · $Ntrace_{\text{Plant}}$ tool

Introduction

Nitrogen (N) is a crucial element for plant growth, as it is a constituent of organic compounds and regulates the synthesis of organic matter in plants. Soil N mineralization and immobilization are two key soil N transformation processes that occur simultaneously. Nitrogen is continually transferred within the soil from organic to inorganic forms and vice versa through N mineralization-immobilization turnover (MIT). Thus, the MIT determine the N availability and the productivity of terrestrial ecosystems (Keuper et al. 2017), and are important to maintain a suitable environmental and ecological N balance (Quan et al. 2021; Zhang et al. 2021; Zhu et al. 2013). The full understanding of the MIT and their controlling factors will shed light on the key drivers to maintain a suitable N balance and predict changes under changing environmental conditions. Nitrogen mineralization serves as the main pathway of inorganic N production, which can provide N nutrition for plants and microorganisms. Microbial N immobilization can temporarily store N in the microbial biomass, thereby reducing soil N loss. Although the immobilization would cause intense competition for inorganic N between microorganisms and plants, it is noteworthy that microbial N turnover is fast and about 70% assimilated N can be re-mineralized and promptly made available for plants (Spohn et al. 2016). Previous studies reported that the MIT was typically related to soil organic carbon (SOC), total N (TN), pH, soil microbial biomass, bulk density, temperature and precipitation, etc. (Elrys et al. 2021; Elrys et al. 2022; Romero et al. 2015). However, previous studies on the MIT are mostly carried out in the absence of plant or conducted by collecting rhizosphere soil and non-rhizosphere soil, thus, there is a dearth of information on MIT under plant-soil-microbe interaction.

Moreover, previous studies investigating the correlation between N processes and plant growth have primarily focused on net N mineralization rate rather than gross rate of N processes (Li et al. 2019; Mueller et al. 2013; Risch et al. 2019). While, the net mineralization rate which resulted from two opposite and concurrent microbial processes (i.e. gross N mineralization and N immobilization), failed to provide insights of the true inorganic N supply capacity. The ^{15}N tracing tool, such as the ^{15}N tracing model described by Müller et al. (2007), has an advantage to determine soil specific gross N transformations rates. Since Inselsbacher et al. (2013) initially attempted to introduce the effects of plants in the ^{15}N tracing model, researches have gradually recognized the significant priming effects of plants on gross N transformation rates. He et al. (2021) observed that gross N mineralization rate was stimulated by the presence of plants compared to a control without plants. Additionally, NH_4^+ preferring plants induced a shift in microbial N uptake from NH_4^+ to NO_3^-, thereby alleviating the competition between plants and microorganism for available N (He et al. 2021). Plants can affect soil N process through N uptake or by rhizodeposition, including root litters and root exudates. On the one hand, plant NH_4^+ and NO_3^- uptake can alter the balance of the inorganic substrate, further promoting or inhibiting N processes (He et al. 2020). On the other hand, approximately 7–11% of carbon (C) from plant photosynthesis could be transferred to rhizosphere soil through root exudates (Pausch and Kuzyakov 2018; Van de Broek et al. 2020). Plants shading can limit the transfer

of photosynthetically fixed C from plants to soil microorganisms (Pfennigwerth et al. 2018), and the humid conditions caused by shading are more conducive to the growth of pathogens (McCarthy-Neumann and Ibáñez 2013), thus leading to negative feedbacks in the plant-soil systems. The input of photosynthate provide C substrates via releasing dissolved organic matter (DOM), thus affecting the activity of microbes involved in inorganic N production (Zhao et al. 2022). It has been demonstrated that plant traits, such as root mass and C:N ratios, exert a greater influence on N mineralization than SOC and TN content (Fornara et al. 2011). Plant traits can directly influence root litters and the photosynthetic substrate supply, thus modifying the fractions of soil organic matter (SOM), e.g. DOM, particulate organic matter (POM). In addition, numerous SOM compounds are chemically recalcitrant or energetically ineffective for microorganisms (Kemmitt et al. 2008), whereas plants can secrete H^+ ions or organic acids to promote the degradation of SOM (Masud et al. 2014), thereby affecting soil N conversion and enhancing N availability. In most studies, direct rhizosphere priming effects could be challenging in the measurement, and root induced changes on the N cycle were often studied by simulating rhizosphere inputs (Drake et al. 2011; Meier et al. 2017). There is little research to investigate the associations between the photosynthetic substrate supply and the MIT in the plant-soil systems.

Apart from the effect of photosynthetic substrate supply, plants might indirectly affect soil MIT via symbiotic microorganism, for example, endophytes. Endophytes, as plant symbiotic microorganisms, can benefit the host plant by facilitating nutrient absorption, disease resistance, insect resistance, and abiotic stress tolerance (Brader et al. 2017). For example, Elsharif (2023) observed the significant increases in the N mineralization rate and the available NH_4^+-N content in the soils inoculated with the endophytic fungus *Phomopsis liquidambari*. Chen et al. (2013) also found that the addition of *Phomopsis liquidambari* to soil could effectively alter the abundance and community structure of microbes in the rhizosphere and enhance the mineral N release in the soils. It seems that the plant endophytes may regulate the MIT in the plant-soil system to promote plant N absorption. However, compared to the previous studies, the effects of plant endophytes on these soil N transformation processes (not only net N mineralization) are not comprehensively and simultaneously studied in the plant-soil systems.

We hypothesized that (1) the growth of maize could potentially promote gross rates of N mineralization and immobilization; (2) photosynthetic substrate supply via root exudates could play a pivotal role in the priming effects of plants on the MIT; (3) plant symbiotic microorganism, e.g. endophytes, could promote gross rates of N mineralization and immobilization, thereby affecting the MIT. A series of ^{15}N tracing pot experiments were established with maize (*Zea mays* L.) in an acidic soil to study the controlling mechanisms of the MIT in the presence of plants. In this study, three treatments, i.e. with and without maize planting, maize shading, and maize root endophytes inoculation, were set up and maize N uptake rates, soil gross N transformation rates, DOC and other soil properties were determined to test our hypotheses.

Materials and methods

Soil samples

An acidic soil (JX) was collected from Yingtan, Jiangxi Province, China (28°14′N, 117°13′E) in June 2022. The sample site was a typical subtropical humid monsoon climate with mean annual precipitation of 1750 mm and temperature of 17.5 °C, and the soil was classified as Ultisol according to soil taxonomy of the USDA. The maize fields have been established more than 50 years, and about 300 kg N ha^{-1} y^{-1} N fertilizer had been applied in the last 10 years. The surface soils (0–20 cm) of four sites were selected randomly, and the soils were mixed with equal amounts. Then the soil was passed through a 2 mm sieved after removing plant litters and stones. Part of JX soil was sterilized with 50 kGy γ-irradiation. The unsterilized soil pH was 4.90, and soil organic carbon (SOC) concentrations and the total N (TN) were 10.65 g kg^{-1} and 1.05 g kg^{-1}, respectively. Soil sterilization did not alter pH, SOC and TN. The initial properties of sterilized and unsterilized soils were presented in Table S1.

Experimental design

Three experiments were conducted in this study.

Experiment 1 was conducted to test hypothesis 1 that plants play an essential role in regulating the MIT in maize-soil systems. 72 pots planted with maize (*Zea mays* L.) were prepared for this experiment. After 20 days of maize growth, 24 pots were selected randomly to conduct a ^{15}N tracing experiment (treatment with maize plantation for 20 d, PM). For the remaining maize pots, 24 pots were selected randomly to conduct another ^{15}N tracing experiment after removing maize plants for 3 days (treatment with maize removal for 3 d, RM3), or after 7 days (treatment with maize removal for 7 d, RM7). A control treatment without maize was set up as well.

Experiment 2 was conducted to test the effects of photosynthetic substrate supply via root exudates on the MIT. Except for PM and the control treatment, 48 pots planted with maize were covered with a black box and put in the dark room to prevent photosynthesis. Then 24 among 48 maize pots were selected randomly to conduct a ^{15}N tracing experiment after 2 days in the dark (treatment with maize in the dark for 2 d, CM2), or 4 days in the dark (treatment with maize in the dark for 4 d, CM4), respectively.

Experiment 3 was conducted to test the potential role of plant endophytes in driving the MIT. Sterilized and unsterilized soils were mixed with or without endophytes, forming four samples: sterilized soil without endophyte (SS-E), sterilized soil inoculated with endophyte (SS + E), unsterilized soil without endophyte (US-E), unsterilized soil inoculated with endophyte (US+E). The endophytes were derived from maize roots. When maize grown in pots for 20 days, maize root was separated and cleaned up, then the root was divided into two parts. One part was sterilized in a high temperature autoclave (121 °C, 20 min) for the sterilized endophytes. For another part, the root surface was sterilized to avoid the interference of microorganisms on the root surface to the endophytes, and the unsterilized endophytes, i.e. the living endophytes, were obtained. The root surface sterilization method was as follows: after washing with tap water, the roots were surface-disinfected by ordered washing with 75% ethanol for 1 min, 2% sodium hypochlorite for 3 min, 75% ethanol for 1 min, followed by rinsing in sterile distilled water for 0.5 min (Ren et al. 2019). Then the sterilized and unsterilized endophytes were ground in the sterilized mortar, and prepared into endophyte solution. Then equal amounts of sterilized endophyte and unsterilized endophyte were added to the sterilized soil and unsterilized soil, respectively. The two +E treatments were mixed with endophytes of maize root, and the two -E treatments were mixed with an equivalent amount of sterilized endophytes of maize root. These four soil samples were used to conduct ^{15}N tracing experiments.

^{15}N tracing experiment

The experiments were conducted in September 2022 in Nanjing, Jiangsu Province, China (32°06′N, 118°54′E). Maize (*Zea mays* L.) seeds of 'Zhengdan 958' were pre-sterilized by 75% ethanol for 5 min and rinsed with the deionized water, then germinated on the moist gauze at 28 °C for 48 h. Maize seedlings were transplanted into 360 mL plastic jars which contained 200 g soil (oven-dry bases). After 3 days, Hoagland solution, urea and potassium dihydrogen phosphate was applied as base fertilizer. N, phosphorus (P), potassium (K) supply were 30, 15 and 24 mg N kg^{-1} soil, respectively. Maize pots were cultivated at 25 °C and 60% water holding capacity (WHC) in a greenhouse under artificial light intensity 5000 Lux (12 h light and 12 h dark cycle) for 20 days at the seeding stage.

The ^{15}N tracing pot experiments of experiment 1 and experiment 2 were established according to He et al. (2020). 12 maize pots were labelled with $NH_4{}^{15}NO_3$ (10.12 atom%), and another 12 maize pots were labelled with $^{15}NH_4NO_3$ (10.12 atom%) for each treatment. 2 mL volume of $^{15}NH_4NO_3$ or $NH_4{}^{15}NO_3$ solution, at a concentration of 40 mg NH_4^+-N kg^{-1} dry soil or 40 mg NO_3^--N kg^{-1} dry soil, was applied with a 4-hole injection technique (Zhu et al. 2023). At 0.5, 24, 48, 72 h after ^{15}N labelling, destructive sampling was carried out with three repetitions for every labeled treatment, and the soil was extracted with 1 M potassium chloride (KCl) (v/w, 5:1) for determining the concentrations and ^{15}N enrichment of NO_3^- and NH_4^+. In the meantime, the collected maize plants were rinsed with 1 M KCl solution and deionized water, then denaturated all enzymes at 105 °C for 0.5 h and dried at 80 °C for measuring the weight. The dried plants were ground and passed through a sieve (0.15 mm) for determining the isotopic

composition and concentrations of maize N. Soil pH and DOC were determined.

In experiment 3, SS-E, SS + E, US-E and US+E treatments were labeled in 250 mL Erlenmeyer flasks, and each flask contained 20 g soil (oven-dry basis). For each treatment, 12 flasks were labelled with $^{15}NH_4NO_3$ (10.12 atom%), and another 12 flasks were labelled with $NH_4{}^{15}NO_3$ (10.12 atom%). 2 mL volume of $NH_4{}^{15}NO_3$ or $^{15}NH_4NO_3$ solution, at a concentration of 40 mg NO_3^--N kg^{-1} dry soil or 40 mg NH_4^+-N kg^{-1} dry soil, was added with a pipette to ensure gas exchange while preventing excessive water evaporation, the flasks was sealed with a membrane featuring small holes. The soil was incubated for 72 h with 60% WHC and incubated at 25 °C incubator. At 0.5, 24, 48, and 72 h after ^{15}N labelling, destructive sampling was carried out with three repetitions for every labeled treatment, and the soil was extracted with 1 M potassium chloride (KCl) (v/w, 5:1) for determining the concentrations and ^{15}N enrichment of NO_3^- and NH_4^+. Soil pH and DOC were determined as well.

^{15}N tracing analysis

The $Ntrace_{\mathrm{Basic}}$ model was employed to determine soil N transformation rates in the soil without maize (Müller et al. 2007) (Fig. S1), and the $Ntrace_{\mathrm{Plant}}$ model was employed to determine the N transformation rates in plant-soil systems (He et al. 2020) (Fig. S2). A Markov Chain Monte Carlo (MCMC) algorithm was applied for parameters based on measured data. The method is well-suited to estimate a large quantity of parameters simultaneously and find the global minimum. By utilizing the probability density function (PDF) for all N processes, the average and standard deviations of each process were quantified. The misfit function of observed values and modeled values in the model took the variance of individual observed values into account. Furthermore, the kinetic parameters of zero-, first-, or Michaelis-Menten kinetics were set to minimize the misfit between the observed and modeled values in ^{15}N analysis. The optimum model version was identified in Akaikes Information Criterion (AIC) based on Matlab (Version 7, The MathWorks Inc.) (Cox et al. 2006). Totally, the ^{15}N excess and concentrations of soil NO_3^-, NH_4^+ and maize N (average ± standard deviation) were provided to the analysis tool. The optimization procedure resulted in a probability density function (PDF) for each parameter, from which parameter averages and standard deviations were calculated (Müller et al. 2007). Each analysis run was carried out with three parallel sequences to identify adequate iteration numbers. Based on the kinetic settings and the final parameters, average N transformation rates of each N processes in Fig. S1 and Fig. S2 were calculated over the 72-hour period and expressed in units of mg N kg^{-1} soil day^{-1}. In Fig. S3-S5, the model and observed values of different treatments are presented.

Analytical methods

Soil pH was measured with the DMP-2 mV/pH (Quark Ltd., Nanjing, China) at a ratio of water to dry soil 2.5:1 (v:w). TN was analyzed with combustion method by a Finnigan FlashEA 1112 elemental analyzer (Thermo Finnigan, Germany). SOC was determined through digestion with H_2SO_4-$K_2Cr_2O_7$. Soil DOC was measured in a water to soil ratio of 5:1 (v:w) by Analyzer Multi N/C (Analytik Jena, Jena, Germany). The concentrations of NO_3^- and NH_4^+ of soil extract were measured with a continuous flow analyser (SA1000, Skalar, Netherlands). Moreover, the NO_3^- and NH_4^+ in extracts were separated via MgO and Devarda's alloy by micro-diffusion methods, then absorbed by oxalic acid, respectively (Zhu et al. 2019). Then, the ^{15}N abundance of NO_3^- and NH_4^+ were measured with Isotope-Ratio Mass Spectrometry (IRMS) (Europa Scientific Integra, Crewe, UK). The ^{15}N abundance of the maize N pools was determined with a Finnigan FlashEA 1112 elemental analyzer with IRMS system (Thermo Finnigan, Germany).

Statistical analyses and calculations

The following equations were used to calculate combined N transformation rates:

Gross N mineralization rate $(M) = M_{Nrec} + M_{Nlab}$.

Total NH_4^+ production rate $= R_{NH4} + M$.

Total maize N uptake rate $(U_{TN}) = U_{NH4} + U_{NO3}$.

where M_{Nrec} was the mineralization of recalcitrant organic-N to NH_4^+; M_{Nlab} was the mineralization of labile organic-N to NH_4^+; R_{NH4} was the release of absorbed NH_4^+; U_{NH4} was maize NH_4^+ uptake rate; U_{NO3} was maize NO_3^- uptake rate.

The least significant difference (LSD) of the 0.05 significance level was calculated for soil N transformation rates according to the three replicates (average and standard deviations) using SigmaStat 4.0 (Systat Software Inc., San Jose, CA, USA). One-way analysis of variance (ANOVA) was used to calculate significant differences of N transformation rates among the different treatments with or without maize plantation and maize shading treatments. A T-test was used to calculate significant difference between treatments with and without endophytes incubation in sterilized or unsterilized soils. Pearson correlation was used to test the relationships between N transformation rates, maize N uptake rates and soil properties in SPSS 23.0 (Inc., USA).

Results

Soil properties

The initial soil pH (i.e., before conducting the maize pot experiments) was 4.90, and the initial SOC and TN were 10.65 and 1.05 g kg^{-1}, respectively (Table S1). In general, during the growing period, maize did not change soil pH, SOC and TN compared to the control treatment (without maize) in different treatments. Compared with the initial DOC concentration of US-JX (196 mg kg^{-1}), and soil sterilization significantly increased DOC concentrations (Table S1). After 20 days of maize planting, DOC concentration in PM (162 mg kg^{-1}) were significantly higher than in the control treatment (137 mg kg^{-1}) ($P < 0.05$) (Fig. 1a). DOC concentrations significantly declined after removing the maize, and DOC concentration in RM7 significantly decreased and showed no significant difference with the control treatment (Fig. 1a). Similarly, DOC concentrations significantly declined after the maize was covered with the black box in the dark room, and DOC concentrations of CM2 and CM4 were no significant difference from the control treatment (Fig. 1b). The DOC concentrations in SS-E and US-E were 335 and 179 mg kg^{-1}, respectively, and the application of maize endophytes did not change DOC concentrations (SS-E vs. SS + E, US-E vs. US+E) (Fig. 1c).

NH_4^+ production rates

Soil gross N mineralization rate (M) in the presence of maize (PM) was significantly higher than that in the control treatment. Specifically, the mineralization of recalcitrant organic-N to NH_4^+ (M_{Nrec}) of PM (0.51 mg N kg^{-1} d^{-1}) was significantly higher than of the control treatment (0.07 mg N kg^{-1} d^{-1}) (Fig. 2a). Compared with PM, M_{Nrec} significantly decreased after maize removal, and M_{Nrec} in RM3 (0.17 mg N kg^{-1} d^{-1}) and RM7 (0.14 mg N kg^{-1}

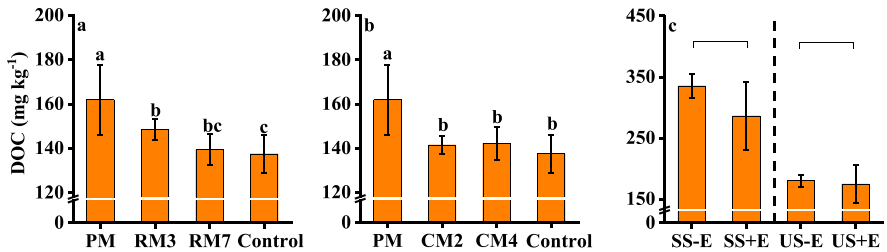

Fig. 1 Soil dissolved organic carbon (DOC) concentration in the different treatments. PM, the treatment that ^{15}N tracing experiment was conducted at the time after 20 days maize growth; RM3, the treatment that ^{15}N tracing experiment was conducted at the time when the maize (20 days growth) was removed for 3 days; RM7, the treatment that ^{15}N tracing experiment was conducted at the time when the maize (20 days growth) was removed for 7 days; CM2, the treatment that ^{15}N tracing experiment was conducted at the time when the maize (20 days growth) was covered with the black box for 2 days; CM4, the treatment that ^{15}N tracing experiment was conducted at the time when the maize (20 days growth) was covered with the black box for 4 days; SS-E, the sterilized soil without endophytes; SS + E, the sterilized soil inoculated with endophytes; US-E, the unsterilized soil without endophytes; US+E, the unsterilized soil inoculated with endophytes. Error bar was standard deviation (n = 3). The different lowercase letters above bars indicated significant differences among the treatments with or without maize planting and the treatments with maize shading or not, and the asterisks above bars indicated significant differences between treatments with and without endophytes incubation in sterilized or unsterilized soil ($P < 0.05$)

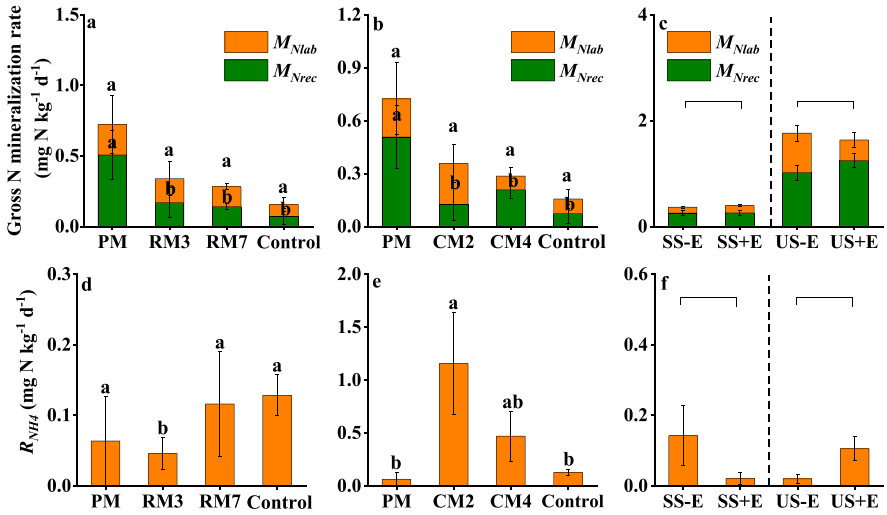

Fig. 2 NH_4^+ production rates in the different treatments. M_{Nlab}, the mineralization of labile organic-N to NH_4^+; M_{Nrec}, the mineralization of recalcitrant organic-N to NH_4^+; R_{NH4}, the release rate of NH_4^+ on cation exchange sites. The meaning of other abbreviation and symbol are same as Fig. 1

d^{-1}) was significantly lower than PM and showing no significant difference to the control treatment. M_{Nrec} in CM2 and CM4 was also significantly lower (< 0.21 mg N kg^{-1} d^{-1}) compared to PM (Fig. 2b), showing no significant difference to the control treatment (Fig. 2b). In the maize planting and shading treatments, M_{Nrec} showed significant positive relationship with soil DOC ($P < 0.01$) (Fig. 5a). Besides, there was no significant difference of the mineralization of labile organic-N to NH_4^+ (M_{Nlab}) between PM, RM3, RM7, CM2, CM4 and the control treatment (0.08–0.23 mg N kg^{-1} d^{-1}) (Fig. 2a, b). The application of plant endophytes did not change M_{Nrec} and M_{Nlab} both in sterilized and unsterilized soil (SS-E vs. SS + E, US-E vs. US+E) (Fig. 2c).

The release rate of adsorbed NH_4^+ on cation exchange sites (R_{NH4}) in PM was 0.06 mg N kg^{-1} d^{-1}, showing no significant difference with the control treatment, and maize removal (RM3 and RM7) did not significantly alter R_{NH4} (Fig. 2d). The R_{NH4} in CM2 was 1.16 mg N kg^{-1} d^{-1}, significantly higher than that in PM (Fig. 2e). R_{NH4} in CM4 (0.47 mg N kg^{-1} d^{-1}) decreased compared to CM2, and showed no significant difference with PM and the control treatment. The application of endophytes did not alter R_{NH4} in sterilized or unsterilized soil (< 0.14 mg N kg^{-1} d^{-1}) (Fig. 2f).

Mineral N consumption rates

Generally, compared with the control treatment without maize, soil gross N immobilization rate (I, both immobilization of NO_3^-, I_{NO3}, and, immobilization of NH_4^+, I_{NH4}) was significantly stimulated in the presence of maize, especially I_{NO3}. The I_{NO3} of PM was 5.82 mg N kg^{-1} d^{-1}, which was significantly higher than in the control treatment (0.26 mg N kg^{-1} d^{-1}) (Fig. 3a). Compared with PM, I_{NO3} significantly decreased in RM3 and RM7 (< 2.67 mg N kg^{-1} d^{-1}). However, I_{NO3} in CM2 and CM4 showed no significant difference to PM (Fig. 3b). Additionally, in unsterilized soil, I_{NO3} of US+E (2.06 mg N kg^{-1} d^{-1}) was significantly higher than that of US-E (0.75 mg N kg^{-1} d^{-1}), and I_{NO3} was negligible in sterilized soil whether endophytes were applied or not (Fig. 3c).

The I_{NH4} of PM was 1.40 mg N kg^{-1} d^{-1}, which was significantly higher than that in the control treatment (0.39 mg N kg^{-1} d^{-1}), and I_{NH4} in RM3 showed no significant difference with PM. However, I_{NH4} significantly decreased in RM7 (0.81 mg N kg^{-1} d^{-1}), and showed no significant difference with the control treatment (Fig. 3a). I_{NH4} of CM2 and CM4 showed no significant difference with PM (Fig. 3b). In maize removal and in the dark, I_{NH4} increased with M_{Nrec} except for RM3 ($P = 0.06$, figure not shown). I_{NH4} of US-E reached 1.19 mg N kg^{-1} d^{-1}, which was significantly higher than US+E (0.67 mg N kg^{-1} d^{-1}), and I_{NH4} in sterilized soil was negligible (Fig. 3c).

The ratio of microbial N immobilization rate ($I_{NO3} + I_{NH4}$) to gross N mineralization rate (I/M) in PM was 9.98, which was significantly higher than that in the control treatment (4.20) (Fig. 3d). The I/M in RM3 and RM7 showed no significant difference

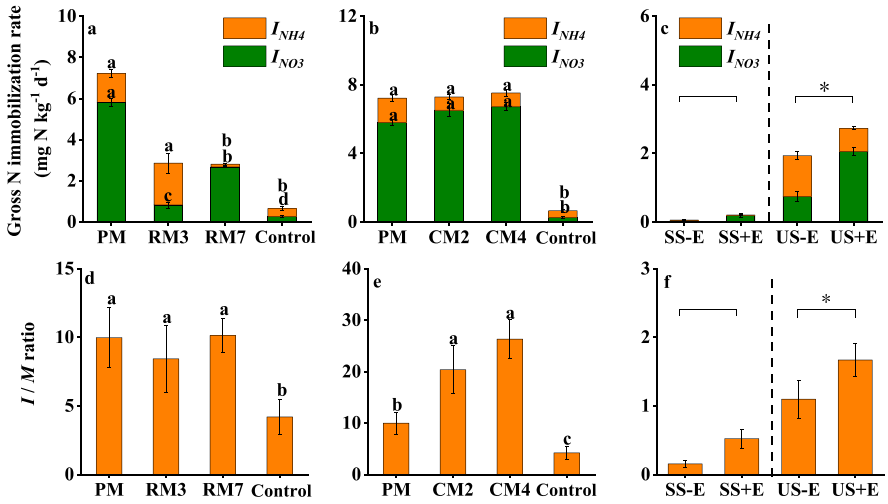

Fig. 3 Microbial N immobilization rates and the ratio of *I*/*M* of the different treatments. I_{NH4}, microbial NH_4^+ immobilization rate; I_{NO3}, microbial NO_3^- immobilization rate; *I*/*M*, the ratio of total microbial N immobilization rates to gross N mineralization rates. The meaning of other abbreviation and symbol are same as Fig. 1

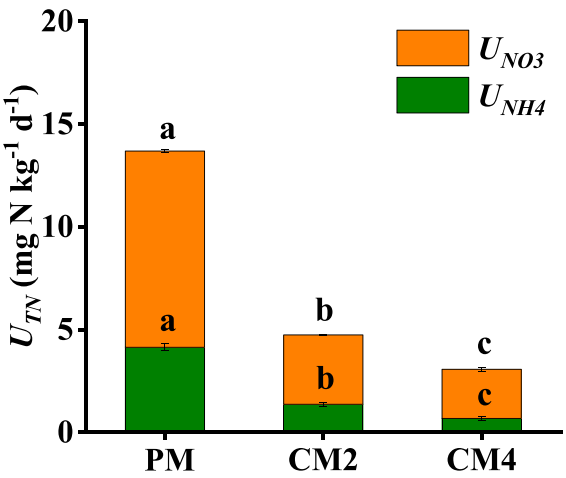

Fig. 4 Maize N uptake rate. U_{NH4}, maize NH_4^+ uptake rate; and U_{NO3}, maize NO_3^- uptake rate. PM, CM2 andCM4 as Fig. 1. Error bar was standard deviation (n = 3), and different lowercase letters above bars indicated significant differences among different maize treatments ($P < 0.05$)

with PM, however, the *I*/*M* in CM2 (20.36) and CM4 (26.32) was significantly higher that PM (Fig. 3e). *I*/*M* of US+E reached 1.67, which was significantly higher than US-E (1.10 mg N kg^{-1} d^{-1}), and there was no significant difference between SS-E and SS + E (Fig. 3f).

Maize NO_3^- uptake rate (U_{NO3}) was 9.55 mg N kg^{-1} d^{-1} in PM, which was significantly higher than U_{NO3} in CM2 and CM4 (3.38 and 2.39 mg N kg^{-1} d^{-1}, respectively) (Fig. 4a). Similarly, maize NH_4^+ uptake rate (U_{NH4}) in PM was 4.14 mg N kg^{-1} d^{-1}, and it was significantly higher than that in CM2 and CM4 (1.37 and 0.68 mg N kg^{-1} d^{-1}, respectively) (Fig. 4a). The U_{NH4} increased with *M* (Fig. 5b) and maize total N uptake rate (U_{TN}) decreased with microbial N immobilization rate ($I_{NH4} + I_{NO3}$) (Fig. 5c).

Discussion

Soil gross N mineralization (*M*) and microbial N immobilization (*I*) rates were altered with the presence of maize. The mineralization of recalcitrant organic-N to NH_4^+ (M_{Nrec}), the immobilization of NO_3^- and NH_4^+ (I_{NO3} and I_{NH4}) were all promoted by maize plantation compared to the control, possibly owing to the photosynthetic substrate supply via root exudates and the interactions between plant endophytes and soil microorganisms. These results indicate that plant activities can affect gross N mineralization and immobilization rates and have an influence on the MIT, which is in line with our first hypothesis.

Maize photosynthetic substrate supply regulates rhizosphere NH_4^+ production

There was a comprehensive effect of soil physicochemical properties in the literature (Cheng et al. 2019; Wang et al. 2016), and their interactions with soil microorganism (Ribbons et al. 2016; Zeng et al. 2014) on soil N mineralization. However, in our study, the short-time (20 days) growth of maize in

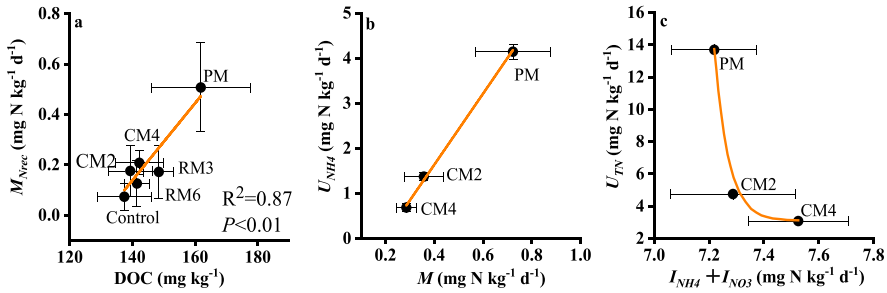

Fig. 5 Relationships among maize N uptake rate, soil gross N transformation rate and soil properties. DOC, soil dissolved organic carbon; M_{Nrec}, mineralization of recalcitrant organic-N to NH_4^+; M, soil gross N mineralization rate; I_{NH4}, microbial NH_4^+ immobilization rate; I_{NO3}, microbial NO_3^- immobilization rate; U_{NH4}, maize NH_4^+ uptake rate; U_{TN}, $U_{NH4}+U_{NO3}$. The meaning of other abbreviation is same as Fig. 1

the greenhouse (temperature at 25 °C, soil moisture at 60%WHC) did not significantly alter pH, SOC and TN. This suggests a direct effect of maize plants activity on M_{Nrec}. This is consistent with the result that M_{Nrec} sharply decreased after maize was covered with a black box for 2 days (preventing plant photosynthesis), which confirmed our second hypothesis. Furthermore, there was a significantly positive correlation between soil DOC concentration and M_{Nrec} ($P<0.01$, Fig. 5a). These results revealed that plant photosynthate input via root exudates may play a crucial role in the priming effects of plants on the MIT, which confirmed our second hypothesis. Generally, 30% even more carbon (C) from plant photosynthesis would be transferred to rhizosphere soil as the C investment for plants nutrients foraging (Van de Broek et al. 2020), thus altering the quantity and quality of soil dissolved organic matters (DOMs). The DOMs can further induce changes of soil biological and physicochemical properties, thus potentially affecting the soil N cycle, e.g. N mineralization (Zhu et al. 2014). As Zhao et al. (2022) reported, plant can recruit N transforming functional microorganisms and assemble the core microbial community though secreting root exudates (sugars, amino acids and organic acid) to produce more mineral N for plant growth. Conversely, microorganisms would release secondary metabolite to stimulate root exudates (amino acids, organic acids) to accelerate the decomposition of organic matters (Phillips et al. 2004). In general, our result revealed the role of photosynthetic substrate supply via root exudates on stimulating M_{Nrec}. Previous studies also reported that plants with strong photosynthesis can exhibit a strong stimulation on mineralization of soil native SOM (Henneron et al. 2020a; Henneron et al. 2020b), possibly owing providing carbon substrates (i.e., root exudates). However, maize removal and maize in the dark did not significantly alter soil mineralization of labile organic-N (M_{Nlab}). So, we further conclude that the plant mainly stimulated soil mineralization of recalcitrant organic-N for improving NH_4^+ availability, which was in line with maize NH_4^+ uptake rates increasing with soil gross N mineralization rates.

The release rate of absorbed NH_4^+ (R_{NH4}) was significantly stimulated with decreasing M_{Nrec} when photosynthesis was prevented. Nitrogen is a crucial element for plant growth, thus during the dark, the plants still need to ingest N for survival. So, the increase of R_{NH4} could make up for the N deficiency caused by the decreased M_{Nrec}. However, the input of photosynthate decreased rapidly under dark condition, suggesting that there might be other factors in stimulating R_{NH4} except the input of maize photosynthate.

Maize root endophytes regulate rhizosphere microbial N immobilization

Our results suggest that maize growth is the main stimulant for microbial N immobilization. Generally, large quantities of native SOM compounds in soil are energetically unviable or chemically recalcitrant as microbial substrates (Kemmitt et al. 2008). Plant growth enhances the soil C availability, and it has been shown that microbes in rhizosphere soil derived more than 50% of biomass C from root exudates (van Hees et al. 2005). Maize root exudates can provide the energy for microorganism growth, but also can act

as signal substances to enhance microorganism activities (Escudero-Martinez and Bulgarelli 2019; Maurer et al. 2021; van der Putten et al. 2016). This is in line with previous studies showing that the activity of microorganism in rhizosphere soil was more than 10 times great higher than that in non-rhizosphere soil (Kuzyakov 2010), and the high specific surface area of microorganisms enabled them to capture inorganic N very quickly (Fischer and Edmeades 2010), which may explain the increasing I_{NO3} and I_{NH4}. Root exudates were originated from photosynthesis, but interestingly microbial N immobilization did not decrease when maize did not undergo further photosynthesis (plant in the dark room). This suggests that the effect of photosynthate input via root exudates might have a hysteresis effect on microbial N immobilization compared with plant photosynthesis. However, microbial N immobilization was significantly inhibited after removing maize, which proved that maize itself, e.g. N uptake from soil, also had an effect on microbial N immobilization. It is noteworthy that soil microbial N immobilization rates were significant accelerated with the application of maize endophytes in unsterilized soil. Meanwhile, there was no priming effect on microbial N immobilization when endophytes applied in sterilized soil. These results further indicated that the activation of gross microbial N immobilization by maize was possibly due to the synergistic effect of maize endophytes and soil microorganisms. However, there was no direct response of the release of absorbed NH_4^+ and soil N mineralization with endophytes applied alone. In our study, the added endophytes were derived from maize, but did not test the effect in the living plant body, so we cannot prove a direct influence of endophytes on soil NH_4^+ production processes with plants. Therefore, more details of endophytes in the living plant should be investigated in future studies for exploring the role of endophytes on soil gross N transformation processes.

The addition of ^{15}N in the experiment may also be a potential reason for the stimulation of N immobilization, especially when the N transformation rates were calculated by the ^{15}N isotopic pool dilution method. The main reason is that the N transformation rates were calculated by zero-order kinetic in the ^{15}N isotopic pool dilution method. In this study, gross N transformation rates were calculated by the ^{15}N tracing tool with zero-, first-order or Michaelis-Menten kinetics. Thus, the stimulating effect by N addition can be greatly weakened. In the control of this study, ^{15}N was also added, but microbial N immobilization and organic N mineralization rates were both low and comparable (0.39 mg N kg^{-1} d^{-1} vs.0.16 mg N kg^{-1} d^{-1}). Therefore, the excitation of microbial N immobilization with maize planting was not caused by the addition of ^{15}N, but by maize growth.

Our findings show that soil microorganisms showed a greater preference for NO_3^- than for NH_4^+ in the presence of maize, and the gross N immobilization was governed by I_{NO3}. This contradicts previous studies that microbes preferentially utilize NH_4^+ over NO_3^- because NH_4^+ can be immobilized directly and it is a more energy efficient process (Romero et al. 2015; Wang et al. 2019). Moreover, in this study, the higher I_{NO3} may be limited by maize NH_4^+ demand. Although maize NO_3^- uptake rates were significantly higher than maize NH_4^+ uptake rates, confirming maize preference for NO_3^- (Wang et al. 2018), there is still be an NH_4^+ demand for maize growth. There was a synergistic effect of maize NH_4^+ uptake and NO_3^- uptake (He et al. 2022; Subbarao and Searchinger 2021), furthermore, maize NH_4^+ uptake is an important nutrient strategy to absorb sufficient N for growth and increasing the yield (George et al. 2016). He et al. (2022) found that even though there was a high NO_3^- production capacity (high autotrophic nitrification) in alkaline soil, maize NO_3^- uptake was limited by low availability of NH_4^+, resulting in low NO_3^- uptake rates. There is a strong competitive relationship between plant NH_4^+ uptake and microbial NH_4^+ immobilization. The rates of NH_4^+ uptake by maize were higher than microbial NH_4^+ immobilization rates, suggesting that plants outcompeted microbial NH_4^+ acquisition. This result in microorganisms can only turn to assimilate another effective N, i.e. NO_3^-, to meet the microbial N demand. This should be one of N acquisition strategies between plant and microorganisms. Most microorganisms switch towards uptake NO_3^- from uptake NH_4^+, saving NH_4^+ is used to meet plant NH_4^+ demand. In addition, our previous studies have shown that maize growth could significantly stimulate the direct oxidation of organic N to NO_3^-, which may provide substrate for microbial NO_3^- immobilization (He et al. 2022).

Large immobilization of available N can be interpreted as a mechanism to protect the applied N fertilizer from being lost from the soil via

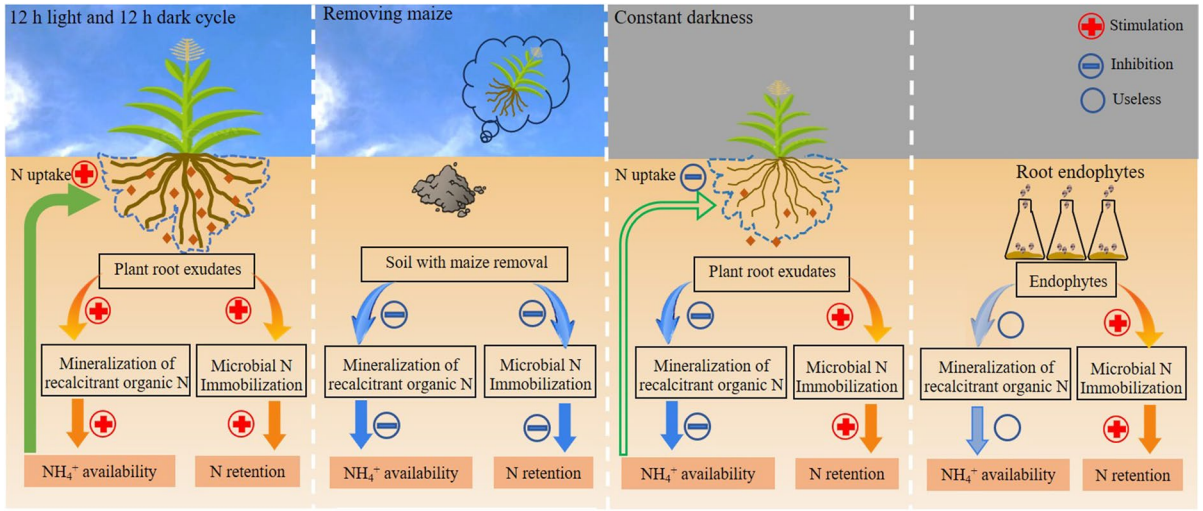

Fig. 6 The conceptual framework of the stimulation of soil N mineralization-immobilization turnover by plants and its potential role. The thickness of the arrows represents the relative importance of each flux

volatilization, denitrification, leaching processes and surface runoff (Kuzyakov and Xu 2013). The N immobilized by microbial biomass will eventually turn into microbial necromass, which provides a SOM stock, and any change of the SOM pool can possibly be related to global change effects (Yang et al. 2022). Although there was competition for N between microorganism and plant, as shown by the negative relationship between maize N uptake rates and microbial N immobilization rates (Fig. 5c), the high microbial biomass turnover rate still supports the N being assimilated and re-mineralized to be available again in supporting the N demand of plant and other biological processes, thus ultimately reducing the risk for N loss (Romero et al. 2015). Therefore, maize has a competitive advantage N competition in the long run owing to the unidirectional flow of N nutrients from soil to plant roots. Plant-microorganism interactions is a strategy to maintain ecosystem stability, and the temporal niche differentiation reflecting plant and microbe generation times lead to mutualistic relationships in rhizosphere. This tight connection between plants and microbes has already been postulated by Hiltner (1904) in his seminal paper when the term rhizosphere was coined for the first time.

Conclusions

Mineral N production and consumption in plant-soil system is controlled by a diverse array of processes that interact with each other. In particular, plants can significantly stimulate the mineralization of recalcitrant organic-N (M_{Nrec}) and microbial N immobilization rates (Fig. 6). The photosynthetic substrate supply via root exudates were identified to be the controlling factors of stimulating M_{Nrec}, thereby producing soil NH_4^+ availability. The increasing microbial N immobilization rate may be accelerated by maize owing to the tight interactions between plant endophytes and soil microorganisms. We conclude that increasing microbial N immobilization can benefit soil N retention and reduce N loss. The results pave the way towards a better understanding of the priming effects on soil N mineralization-immobilization turnover in plant-soil systems.

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Declarations

The authors have no relevant financial or non-financial interests to disclose.

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