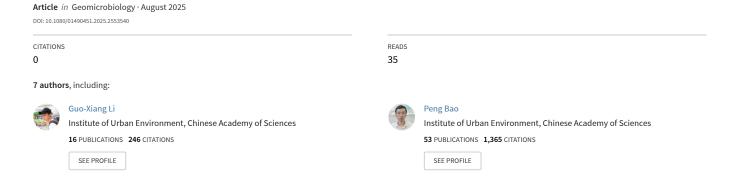
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Impact of Ammonium and Sulfate on Soil Physicochemical Properties and Bacterial Community Structure in Paddy Soils

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ABSTRACT

Sulfate is commonly used to treat polluted paddy soil or suppress methane emissions, but its effects on microorganisms in paddy soil are rarely reported, especially when other common fertilizers such as ammonium fertilizer are applied. To study the influence of ammonium and sulfate fertilizer on bacterial community structure, a field experiment under three treatments: sulfate fertilizer (S), sulfate plus ammonium fertilizer (SN), no fertilizer (CK), was performed. The effects of ammonium and sulfate on soil physicochemical properties, bacterial diversity and structure were comprehensively discussed. The concentration of sulfate, sulfide, and dissolved organic carbon (DOC) was higher in the S treatment samples. The concentration of ammonium, nitrate, and ferrous ions was higher in SN treatment samples. The Bray tree results showed that the bacterial communities in the S and SN samples were similar to each other but not similar to those in the CK groups. In the experimental group with the addition of sulfate only, the bacterial community structure was positively correlated with sulfate, sulfide, and DOC. In the experimental group with both ammonium and sulfate addition, the bacterial community structure was positively correlated with ammonium, nitrate, and ferrous ion. This result indicates that ammonium and sulfate affected the bacterial community structure in rice soils. The residual higher concentrations of sulfur species and nitrogen fertilizer altered the soil solution properties, which in turn changed the bacterial community structure in rice soils.

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Sulfate fertilizer; sulfate-ammonium fertilizer; bacterial community; paddy soils

Introduction

Paddy soil is an important type of cultivated soil in China and its properties are influenced by human activities. In comparison to non-paddy soil, the conventional paddy field management practice of flooding and drainage alternation promotes the development of a distinctive oxidized/anoxic soil profile, leading to the selection of unique bacteria and functions (Li et al. 2021). Diverse soil microbiomes participate in the biogeochemical processes of essential life elements, including carbon, nitrogen, phosphorus, sulfur, and iron. Soil microbial diversity and community composition play crucial roles in nutrient recycling, soil structure maintenance, and various soil ecosystem

processes and functions (Xu et al. 2013). Moreover, soil bacterial communities exhibit highly modularized species-to-species network structures, with climate, and soil factors primarily influencing community patterns by impacting highly connected nodes, known as keystone taxa, within these networks (Li et al. 2021).

Various factors, such as soil carbon, nitrogen, phosphorus, base ions, salinity, and elemental ratios, have been reported to impact bacterial diversity and community composition (Ma et al. 2021). They concluded that soil organic carbon (SOC) plays a primary role in influencing bacterial community composition (Ma et al. 2021). Similarly, Lauber et al. (2009) found a significant correlation between overall bacterial

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community composition and soil pH (r=0.79). This correlation was mainly driven by changes in the relative abundances of *Acidobacteria*, *Actinobacteria*, and *Bacteroidetes* across a range of soil pH levels. Phosphorus was another key factor influencing rice yield and soil microbial communities (Wang et al. 2021). It has been identified that four archaea (belonging to *Thermoplasmata*, *Methanosaeta*, *Bathyarchaeia*, and *Nitrososphaeraceae*) and three bacteria (in *Desulfobacteraceae* and *Acidobacteriales*) that were primarily associated with soil carbon and nitrogen transformation, as well as pH (Wang et al. 2021). These microorganisms may work cooperatively to influence rice yield by regulating soil fertilizer can increase

The application of sulfur fertilizer can increase growth parameters, and improve soil fertility, soil microbial properties, and rice yield in rice-wheat cropping systems (Ram et al. 2017). In general, available sulfur content refers to the amount of sulfur in the soil that crops can absorb and utilize, including sulfates that are soluble in water or adsorbed on soil particles' surfaces, as well as easily decomposable organic sulfur fractions (Uchôa et al. 2021). Sulfate is often used as an amendment for rice soils (Yuan et al. 2021). Soil microorganisms have the ability to incorporate sulfate into cellular components or utilize sulfate as an electron acceptor for organic matter, leading to sulfate reduction through dissimilation (Gupta and Germida 2021). The application of sulfate to paddy soils may lead to some significant long-term effects. It has been revealed that sulfate has the potential to mitigate methane production and emission from paddy soils (Ro et al. 2011). Moreover, sulfate addition may be a promising strategy to reduce purpose diphenylarsinic acid (DPAA) contamination in iron-rich rice soils (Zhu et al. 2023). However, the effect of sulfate application on paddy soil community structure was unclear and needs further research.

Nitrogen is an essential nutrient element for plant growth and development. The ammonium nitrogen absorbed into the body can be directly combined with the organic acids of photosynthesis to form amino acids, which in turn form other nitrogencontaining organics (Giordano et al. 2021). The mineralization and supply capacity of soil organic nitrogen is often the limiting factor of soil productivity. Microorganisms are not only the drivers of soil organic nitrogen mineralization, but also the active repositories of plant nutrients. The discovery of the role of microorganisms in soil nitrogen cycling will provide a scientific basis for further revealing the supply status of soil nitrogen and improving soil nitrogen fertility. In the process of soil organic

nitrogen transformation, soil microorganisms assimilate part of organic nitrogen and some mineral nutrients to form organisms. These nitrogen nutrients fixed by microorganisms can be re-mineralized after their death, becoming effective mineral nutrients for plant absorption and utilization (Jenkinson 1988). Therefore, the content and mineralization dynamics of soil microbial biomass nitrogen directly affect the effectiveness and supply status of soil nitrogen. Studies show that soil microbial biomass nitrogen has a significant positive correlation with mineralizable nitrogen, and its mass fraction is 46%~82% of mineralizable nitrogen (Ali et al. 2021; Zaman et al. 2004). However, it has also been reported that different fertilizer treatments increase the ratio of nitrogen mineralization and soil microbial biomass nitrogen, but there is no significant correlation between soil microbial biomass nitrogen and soil nitrogen mineralization rate (Abrar et al. 2024; Holmes and Zak 1994; Khan et al. 2024).

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The role of microorganisms in the four major transformation processes of nitrogen cycle, namely fixation, ammonification, nitrification and denitrification, has gradually been recognized (Thamdrup 2012; Zhang et al. 2020). Especially in the past decade, with the rapid development of molecular biology technology and its combination with bio-geochemical research methods, some important breakthroughs have been made in the study of nitrogen cycle processes and mechanisms. The diversity distribution characteristics of ammonia oxidizing bacteria (AOB) in typical soils in China and the main factors driving their community structure and population changes. It was found that at the local scale, different land use and management methods, different fertilization measures, and nitrogen fertilizer addition would affect the composition diversity and quantity of AOB (Yao et al. 2011). Conversely, at a larger regional scale soil pH was the main driving factor affecting the composition and distribution of these microorganisms (Hu et al. 2013; Wu et al. 2011). Moreover, in acidic and alkaline soils, AOB had different responses to fertilization and changes in soil physical and chemical properties caused by fertilization. The study of Zornoza et al. (2016) showed that the application of organic-inorganic fertilizer could increase the number of ammonifying bacteria, nitration bacteria and aerobic nitrogen-fixing bacteria.

The balance of nitrogen and sulfur plays a crucial role in the rice growth and development of paddy soil. Hence, this experiment aims to investigate: (1) the effect of sulfur and ammonium nitrogen on soil physicochemical properties; (2) the impact of applying

inorganic sulfur fertilizer and ammonium nitrogen fertilizer on the bacterial community structure of paddy soils during rice cultivation in situ; (3) complex linkages between biogeochemical cycling of sulfur and nitrogen occur in rice fields.

Materials and methods

Experimental site description and soil collection

The experimental site was established in Beilun District, Ningbo (29° 42′ 48.1" N, 121° 50′ 08.2" E). The region experiences a typical subtropical monsoon climate with an annual precipitation of 1480 mm and a mean annual temperature of 16.4°C. The rice field was divided into three equal parts using an impermeable film. Three fertilization treatments were tested: sulfur fertilizer (S), sulfur plus nitrogen fertilizer (SN), and no fertilizer (CK) (Figure 1). The sulfur and nitrogen fertilizers were supplied as sodium sulfate (22.28% S, 0.2 kg/m²) and ammonium chloride (26.19% N, 0.2 kg/m²), respectively. The experimental setups were fertilized twice: before rice planting and before the rice tasseling stage. To analyzed soil properties, soil solutions were collected from three rice fields during the rice tasseling period using a soil solution sampler (DIK-8393, Japan), 23 days after the second fertilization. Additionally, rice soil samples (0-20 cm of topsoil) were collected for microbial community analysis. These samples were carefully placed in self-sealing bags, ensuring the removal of air, and transported back to the laboratory under refrigeration along with the soil solutions.

Analysis of soil physicochemical properties

Analyses of sulfate (SO₄²⁻), ammonium (NH₄⁺), nitrate (NO₃⁻), nitrite (NO₂⁻), sulfide (S²⁻), ferrous ions (Fe²⁺), and dissolved organic carbon (DOC) were conducted using soil solutions. The measurement of SO₄²⁻ was performed using ion chromatography (Dionex ICS-5000+, Thermo Scientific, United States). The NH₄+, NO₃-, and NO₂- were measured using Continuous-Flow Analysis (Auto Analyzer 3, SEAL, Germany). The S2- was quantified using the methylene blue spectrophotometric method. The Fe²⁺ was determined by phenanthroline spectrophotometry. The contents of dissolved organic C (DOC) were determined using an automatic total organic carbon analyzer (Vario TOC, Elementar, Germany).

DNA extraction, PCR amplification and Illumina sequencing

Soil DNA was extracted from 0.5 g of fresh soil samples using the Dneasy PowerSoil Kit (MoBio, Qiagen, Germany). The PCR was performed with primers 341 F and 805 R to amplify the extracted DNA. The PCR cycling conditions consisted of an initial denaturation step at 94°C for 5 min, followed by 33 cycles of denaturation at 94°C for 30s, annealing at 55°C for 30 s, extension at 72 °C for 45 s, and a final extension step at 72°C for 10 min. Samples were sequenced using the Illumina Miseq instrument to obtain the initial sequencing results. Subsequently, the cutadapt software was employed to remove the adaptors, and the PEAR software was utilized to splice the sequences.

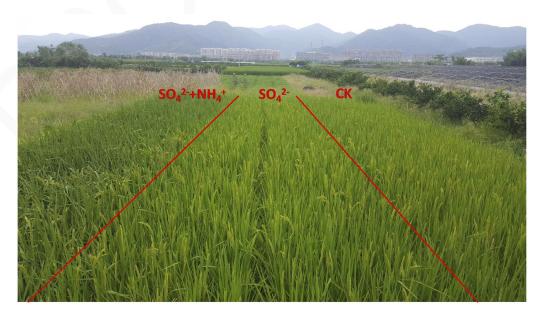


Figure 1. Experimental setup of paddy field. Sulfate plus ammonium fertilizer (SN), sulfate fertilizer (S), no fertilizer (CK).

Following this, the data were compared with the database, and the obtained results were analyzed using MEGAN, R language, and other analysis software.

Data analysis

High-throughput sequencing analysis was used to analyze the differences in the structure of bacterial communities in rice soils under different treatments. The Simpson index was utilized as a measure of bacterial, fungal, and archaeal richness and diversity. Redundancy analysis (RDA) was conducted to illustrate the relationships between major physicochemical properties

of the soil and bacterial community composition at the class and genus levels.

Results

Soil physicochemical properties

The physicochemical properties of the treatment groups were represented by the concentration of $SO4^{2-}$, S^{2-} , NH^{4+} , NO_3^- , Fe^{2+} , and DOC in soil solutions (Figure 2). The ranking of sulfate concentration was S (22.26 mg/L) > SN (16.87 mg/L) > CK (10.01 mg/L). The SN treatment resulted in higher concentrations

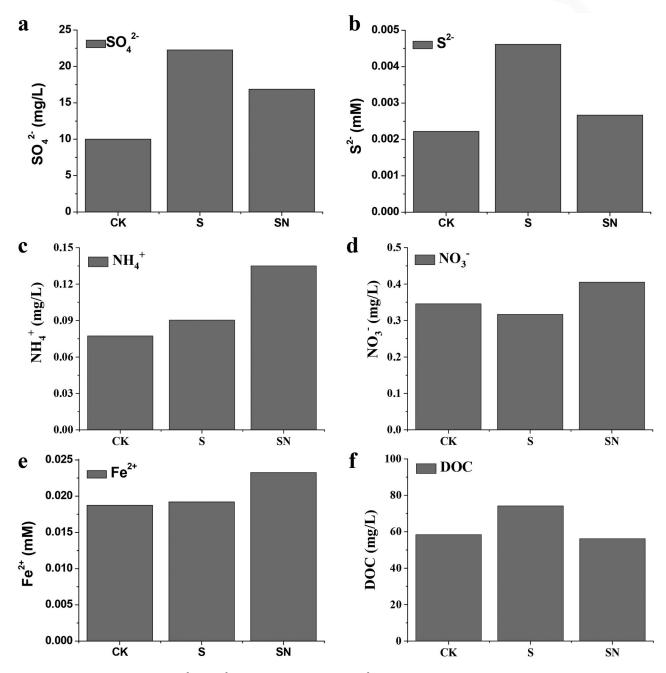


Figure 2. The concentration of SO_4^{2-} (a), S^{2-} (b), NH_4^{+} (c), NO_3^{-} (d), Fe^{2+} (e), DOC (f) in SN, S, and CK fertilization treatments.

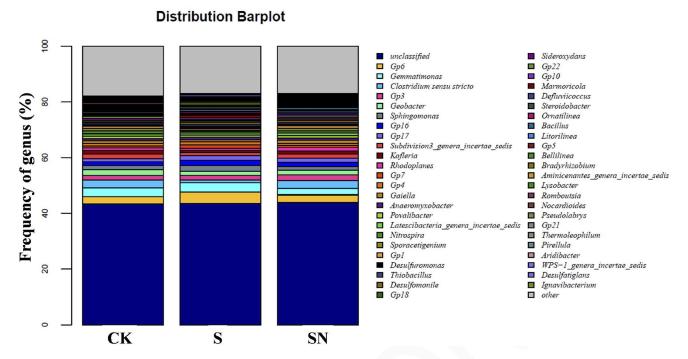


Figure 3. Relative abundance of bacterial genus in CK, S and SN groups.

of ammonium (0.14 mg/L) and nitrate (0.41 mg/L) compared to the other treatments. Additionally, the content of DOC and sulfide in the S treatment was higher than in the SN and CK treatments. The higher concentration of sulfur species (SO42- and S2-) in the S and SN samples and the higher concentration of NH4+and NO3- in the SN samples, compared to those in the CK samples, indicate the remnants of sulfur and nitrogen fertilizers.

Analysis of bacterial community structure

Alpha-diversity analysis was conducted to evaluate bacterial diversity in each treatment. The order of changes in the Simpson index was as follows: S>SN>CK (Figure S1). It was hypothesized that sulfate enhanced the metabolism and competitive ability of various microorganisms (Harrison et al. 2009). The bacterial community in the treatment group with ammonium addition was predominantly composed of nitrogen-fixing microorganisms, resulting in a reduction in overall diversity.

The bacteria from paddy soil samples were distributed in 34 phyla, 71 classes, 91 orders, 197 families and 613 genera, while a large number of unclassified microorganisms were also detected. Excluding unclassified taxa, the five most dominant phyla were Proteobacteria (39.88%), Acidobacteria (14.87%), Chloroflexi (6.3%), Actinobacteria (6.23%), Firmicutes (5.82%) (Figure S2). The dominant genera in S group include Acidobacteria Gp6 (4.24%), Gemmatimonas

(3.26%) and Sphingomonas (1.98%) (Figure 3). The dominant genera in SN group were Clostridium sensu_stricto (2.9%), Acidobacteria Gp6 (2.71%), Gp16 (1.90%), Gp3 (1.74%), and Gp17 (1.53%), Gemmatimonas (3.26%), and Geobacter (1.76%). The dominant genera in CK group were Gemmatimonas (3.23%), Clostridium_sensu_stricto (2.67%) and Acidobacteria Gp6 (2.58%).

Beta-diversity analysis was conducted to evaluate bacterial diversity ampng different treatments. The Bray tree results revealed that the similarity of bacterial communities between the S and SN groups was higher, whereas the control group CK exhibited lower similarity to the bacterial communities of the other two groups. This suggests that sulfate indeed influenced the bacterial community structure in the rice soil, and the nitrogen fertilizer can also affect the bacterial community structures (Figure 4).

It is essential to investigate the correlation between the structure of soil bacterial communities and environmental factors for the CK, S, and SN groups. This investigation will enable us to further analyze the relationship between these three groups of soil bacterial communities and nutrient salts.

Correlation analysis of bacterial community and soil environmental factors

To the correlation between bacterial communities and soil environmental factors in the three treatments, we conducted RDA analysis using Canoco software on

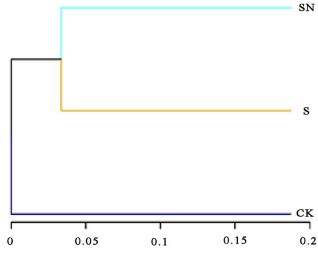


Figure 4. Bray tree plot of bacterial communities in CK, S and SN groups.

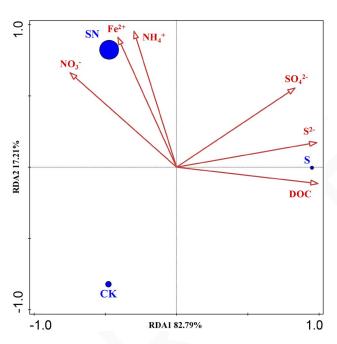


Figure 5. RDA analysis of bacterial communities and environmental factors.

the bacterial communities and environmental factors of the three groups. The findings are presented in Figure 5. The results showed that the bacterial community in the experimental group S, which received only sulfate addition, exhibited a positive correlation with sulfur ions, sulfate, and DOC. On the other hand, the bacterial community in the experimental group SN, which received both sulfate and ammonium addition, displayed a positive correlation with ammonium, nitrate, and ferrous ions. It is worth noting that ferrous ions and other ions present in the soil solution may be involved in the extracellular respiration of sulfate-reducing bacteria (SRB), where sulfur

acts as an electron transporter. As a result, the bacterial community in the SN experimental group shows a certain correlation with sulfate. In contrast, in the control group CK, where no additional nutrients were added, the bacterial community did not exhibit any correlation with the tested environmental factors.

Discussion

Acidobacteria Gp6, members of the Acidobacteria phylum, were generally known for their involvement in the biogeochemical cycling of carbon and were particularly abundant in acidic soils (Sait et al. 2006). In this study, the levels of Acidobacteria were found to be higher in both the S and SN groups compared to the CK group (see Figure 3). More recently, it has been demonstrated that anaerobic members of the diverse Acidobacteria community in wetlands and seafloor environments utilize one or more types of dissimilatory sulfur metabolism (Flieder et al. 2021; Hausmann et al. 2018), thus indicating its fundamental roles in anaerobic water environment sulfur biogeochemical cycling. Acidobacteria played a significant role in the sulfate reducing ammonium oxidation (Sulfammox) process, which involves the coupling of sulfate reduction with anaerobic ammonium oxidation, during an anaerobic cultivation experiment of marine sediment (Rios-Del Toro et al. 2018). The results implied that Acidobacteria was sensitive to sulfate and sulfate/ammonium stress, and might play important role in sulfur and nitrogen cycling in paddy soil. It was noteworthy that the abundance of Planctomycetes was higher in both the S and SN samples than it in the CK samples, indicating their involvement in the Sulfammox process (Dominika et al. 2021; Liu et al. 2021). This result shows that bacterial mediated Sulfammox process occurred in natural freshwater ecosystems, which extends the known process of Sulfammox in marine sediment (Schrum et al. 2009).

Gemmatimonas, which belongs to the phylum Gemmatimonadetes, was widely detected in all three paddy soil samples. This phylum has been found in high relative abundance (0.2-6.5%) in various environments, such as soil and activated sludge (DeBruyn et al. 2011; Zeng et al. 2015; Zhang et al. 2003). These organisms have been specifically enriched for their involvement in the sulfur cycle, nitrogen cycle, and organic biosynthesis (Oshiki et al. 2022). Although, a complete understanding of their metabolic characteristics and environmental functions remains elusive (DeBruyn et al. 2011; Zeng et al. 2015; Zhang et al. 2003), it is possible to infer their

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important role in the nutrient transformation in paddy soil. The abundance of Sphingomonas in the S group (3.32%) was higher compared to the other groups. Sphingomonas, which are ubiquitous in rhizosphere and contain a respiratory benzoquinone (ubiquinone Q-10) (reviewed by White et al. 1996), may be involved in redox activities in the S samples. Additionally, the soil contained a significant presence of Clostridium and Geobacter in the SN soil samples, which were also detected in the SRB community enrichment solution (Li and Bao 2021). These microorganisms exhibited the capability to reduce hydrated ferrite, suggesting their potential role in the elemental sulfur cycling within paddy soils (Campbell et al. 1957; Li et al. 2012b). In this study, the abundance of Clostridium in the S samples was lower than it in the SN samples. These findings suggest that Clostridium is better suited for an environment involving the Sulfammox process.

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For other high relative abundance genus in paddy soil samples, Chloroflexi has been implicated in both biological sulfur reduction and carbon sequestration, as demonstrated by previous studies (Hahn et al. 2022; Li et al. 2023). The involvement of marine Chloroflexi in sulfur cycling has been revealed through single-cell genome and group-specific dsrAB sequencing, as highlighted in the study by Wasmund et al. (2016). Chloroflexi may also involve in light-driven dissimilatory sulfur metabolism (Frigaard and Dahl 2008) in paddy soils. In sulfate-reducing enrichment, Actinobacteria has frequently been observed to be abundant, as reported by Li et al. (2012a).

The bacterial community in each experimental treatment had a positive relationship with the environmental factors (Figure 5). In the S samples, the bacterial community structure was positively correlated with sulfate, sulfur ion, and DOC, while in the SN samples, it was positively correlated with ammonium, nitrate, and ferrous ion. The metabolism of the dominant genera in each treatment was consistent with the environmental factors' results. A very interesting finding was a significant increase in nitrate in SN samples than CK sample. As we known that anaerobic ammonium oxidation to nitrate takes place within the biological Sulfammox process (Eq 1) (Schrum et al. 2009).

$$SO_4^{2-} + NH_4^+ \rightarrow HS^- + NO_3^- + H_2O + H^+$$
 (1)

Therefore, the generation of nitrate provides strong evidence for Sulfammox process SN treatment paddy soils.

Conclusion

In this experiment, the effects of sulfate and ammonium as nutrients on the soil bacterial community structure in rice soils were investigated using in situ culture technique in rice fields. It was found that sulfate and ammonium (if added) remained in the experimental groups with only sulfate and both sulfate and ammonium added until the rice tassel stage. Therefore, different microorganism communisties may have been formed in different experimental treatments. In the control group without the addition of sulfate and ammonium, the dominant genera of microorganisms were Gemmatimonas, Clostridium, Acidobacteria Gp6 subgroup, and Geobacter; in the experimental group with the addition of sulfate only, the dominant genera were Gemmatimonas, Sphingomonas, and subgroups of Acidobacteria; in the experimental group with the addition of both sulfate and ammonium, the dominant genera were Clostridium, Acidobacteria subgroups, Gemmatimonas, and Geobacter. The results of RDA analysis showed that in the experimental group with the addition of sulfate only, the bacterial community structure was positively correlated with sulfate, sulfur ion and DOC; in the experimental group with both sulfate and ammonium addition, the bacterial community structure was positively correlated with ammonium, nitrate and ferrous ion. This indicates that the fertilization of ammonium and sulfate affected the bacterial community structure in rice soils. The simultaneous use of nitrogen fertilizer and sulfur fertilizer can lead to Sulfammox process in paddy soil. This updates our understanding of the coupled sulfur-nitrogen transformation cycle in freshwater ecosystems. The incorporation of sulfur influences soil redox reactions, potentially enhancing nutrient cycling dynamics; however, its effects on crop yield require further investigation. The changes in this microbial community may help with agricultural management and the development of fertilization strategies.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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