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ORIGINAL PAPER

Mineral N suppressed priming effect while increasing microbial C use efficiency and N_2O production in sandy soils under long-term conservation management

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Abstract

Restoring soil organic carbon (SOC) with residue incorporation is an important component of soil health management. In the present study, we investigated the interactive impacts of residue amendment and mineral nitrogen (N) additions on preserving the added residues and SOC in a sandy Ultisols. Soil samples were collected from fields under long-term reduced tillage and incubated with either ^{13}C-labelled crop residues, ammonium nitrate (NH_4NO_3), both, or neither for 55 days. Respiration, microbial biomass C, enzyme activities, and C use efficiency (CUE) were measured along with nitrous oxide (N_2O) production. Residue amendment increased CO_2 production by 206% at the end of the incubation, inducing positive priming effects (PE). Mineral N reduced the positive impacts of residue amendment on CO_2 production and PE, resulting in higher microbial CUE. However, the N addition had no effects on the measured enzyme activities involved in organic C reactions, except for β-glucosidase activity when residues were present. Additions of mineral N reduced residue decomposition by 89% at the end of the experiment. Total CO_2 ($R^2 = -0.56$), residue-derived CO_2 ($R^2 = -0.62$), SOC-derived CO_2 ($R^2 = -0.53$), and the primed production ($R^2 = -0.52$) were all negatively correlated to soil NH_4^+ concentrations. Residue amendment instantly stimulated N_2O production, which was augmented by mineral N addition. Denitrification was seemingly the main N_2O production pathway. The results reinforced the concept that N can regulate SOC dynamics through direct and indirect impacts on soil microbial activities. Combining N fertilization and residue management is seemingly promising to increase SOC stability and preservation in sandy soils. However, the trade-offs of N_2O production need to be considered.

Keywords Residue amendment · Mineral N addition · Carbon use efficiency · Priming effect · N_2O production

Introduction

The storage of soil organic carbon (SOC) is a balance between the inputs from primary production and outputs mainly as heterotrophic respiration (Riggs and Hobbie 2016). Managing SOC in agricultural soils has therefore been focused on increasing organic inputs, while minimizing soil disturbances to protect SOC from microbial decomposition. It has been well demonstrated that increasing organic inputs by applications of animal manure (Maillard and Angers 2014), incorporation of crop residues (Liu et al. 2014), and inclusion of cover crops (Poeplau and Don 2015) increased SOC in a range of production systems. However, the diverse organic sources and their distinguishing physiochemical properties, confounded with varied management practices across temporal and spatial scales, make the desired outcomes less predictable (Brennan and Acosta-Martinez 2017; Redin et al. 2014; Tamura et al. 2017).

Nitrogen (N) fertilization is a standard management practice that can alter SOC dynamics through its direct and indirect impacts on soil microbial communities (Brennan and Acosta-Martinez 2017; Fan et al. 2020; Redin et al.

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2014; Tamura et al. 2017). Recent studies reported that N addition reduced SOC decomposition rates by decreasing microbial biomass (Riggs and Hobbie 2016), induced soil acidification (Averill and Waring 2018), and reduced the decomposition of slowly cycling C pools (Cusack et al. 2010). In contrast, N inputs have also been found to stimulate microbial activities promoting the decomposition of SOC (Khan et al. 2007). In line with the observed inconsistent N impacts through microbial communities, long-term field studies have also demonstrated positive (Seabloom et al. 2021), neutral (Keller et al. 2022; Lou et al. 2011), and negative (Khan et al. 2007) N effects on SOC stocks. These inconsistent observations suggested our improved but incomplete understanding on microbial controls over SOC dynamics and their interactions with N management, especially when plant residues were simultaneously introduced (Cui et al. 2020; Gougoulias et al. 2014; Kallenbach et al. 2015).

Introducing organic materials into the soil can stimulate SOC decomposition, i.e. priming effects (PE) (Kuzyakov et al. 2000), which has often been used to explain why long-term incorporations of crop residues did not always increase SOC stocks (Khan et al. 2007; Mulvaney et al. 2009). Despite the fact that the exact mechanisms of PE remain unsolved, the microbial biomass is widely considered the key component of PE (Bernard et al. 2022; Fontaine et al. 2003; Kuzyakov 2010). There are two competing hypotheses relating PE to N availability, "stoichiometric decomposition" and "microbial N mining" (Chen et al. 2014; Liu et al. 2020). The first theory believes that if the C to N ratio of the organic inputs matches microbial stoichiometric C to N ratio, the decomposition would be maximal. At the same time, the latter suggests that if soils are low in N availability, organic inputs are to stimulate microbial decomposition of SOC to acquire N contained. Both hypotheses have been tested with clear lines of evidence, reinforcing the importance of N in regulating microbial functions and SOC dynamics (Chen et al. 2014; Cui et al. 2020; Liu et al. 2020). However, similar studies also suggested the importance of energy supplies from the organic inputs and decoupling of PE and microbial N mining, highlighting the necessity to consider both C and N availability in understanding microbial controls over SOC stability (Fan et al. 2020; Mason-Jones et al. 2018; Schroeder et al. 2020; Wild et al. 2019).

There is increasing interest in adopting conservation practices to maintain or improve soil health of the production agriculture (Bünemann et al. 2018; Kaye and Quemada 2017; Palm et al. 2014; Turmel et al. 2015). However, changing crop management practices (e.g. crop rotation and cover cropping) is likely to change the quality and quantity of crop residue returns to soils (i.e. C inputs) and nutrient management strategies (i.e. N inputs). These crop and nutrient management changes also raise the fundamental question of how such changes would further affect the preservation of the organic inputs and the stability of native SOC. In the present study, we collected soil samples from a 40-year research plot, where conservation tillage has resulted in significant SOC accumulations in topsoil (Novak et al. 2007; Parajuli et al. 2021a). Recent studies also indicated that rotating crops with high biomass production is seemingly the best additional management option to promote long-term SOC accretion in the bulk soils (Nash et al. 2018; Novak et al. 2020). However, how the associated changes of organic C and N inputs due to the changes of rotation crops would affect microbial activities and the accumulated SOC in these soils remain elusive. Therefore, we incubated the soils with ^{13}C-label rice residues (a proxy of changing crop residue chemistry due to rotation) and mineral N to investigate how they collectively affected the stability of residues and SOC. A better understanding of this question could lead to better management strategies to optimize C sequestration while minimizing N losses in agricultural soils. Given that these sandy soils are intrinsically low in N availability (Ye et al. 2021), we hypothesized that (1) both the additions of crop residue and mineral N stimulate microbial activities promoting the decomposition of native SOC and (2) the additions of mineral-N retard the decomposition of added crop residues and SOC. The goal is to understand the importance of mineral N in improving C sequestration potentials of the sandy Ultisols, where reduced tillage and residue incorporation are commonly applied.

Materials and methods

Site description and soil sampling

The field is located at the Pee Dee Research and Education Center, Clemson University, Florence, SC, USA (34°18′ N, 79°44′ W). The 40-year research plot was established by USDA-ARS scientists from the Coastal Plain Soil, Water and Plant Conservation Research Center in mid-1979 to investigate tillage impacts on SOC dynamics. The soils are primarily Norfolk loamy sand (fine-loamy, siliceous, Thermic Typic Kandidults) with 6–7% clay and 80–85% sand. In mid-1980s, rotation was adopted with periodic transitions between corn-winter wheat (*Triticum aestivum* L.)-soybean (*Glycine max* L.) and corn-winter wheat-cotton (*Gossypium* L.) systems. Wheat was replaced with cereal rye (*Secale cereale* L.) cover crop in 2003 to determine its rooting effects on SOC accumulation, which was removed from the rotation in 2008 (Novak et al. 2020). More details about the cropping systems and management practices can be found in Campbell et al. (1984), Bauer et al. (1997, 2006), Hunt et al. (2004), and Nash et al. (2018).

Recent studies have suggested that 40-year conservation tillage resulted in accumulations of organic matter in the top 5 cm of soils, which, however, is approaching the equilibrium state (i.e. C inputs equal to the outputs) (Nash

et al. 2018; Novak et al. 2009; Parajuli et al. 2021b). In this study, a soil incubation was conducted to test how the SOC will respond to changing C and N inputs. Ten soil cores at 5-cm depth were randomly collected from each of five conservation tillage plots in 2021 (a total of 50 cores). The soils were composited and transported on ice to a nearby laboratory, then sieved (2 mm) to remove rock and plant materials, and stored at 4 °C until used. On average, the soils had 13.9 ± 1.6 g kg^{-1} total C and 1.18 ± 0.09 g kg^{-1} total N with a pH of 5.8. Potassium chloride (1 *M*) extractable NO_3^--N and NH_4^+-N were 4.1 and 1.2 mg kg^{-1}, respectively.

Laboratory incubation

The incubation trial was conducted as a fully crossed factorial design including two factors (i.e. residue amendment and mineral N addition) with four replicates. ^{13}C-enriched rice residues ($\delta^{13}C = 636‰$, C/N = 52) was used as the C source and introduced in small pieces (< 1 cm) at a rate simulating winter rye (*Secale cereal* L.) cover crop production on adjacent fields (~ 4000 kg ha^{-1}) (Bauer and Reeves 1999; Ye et al. 2019). Details about preparations of the residues can be found in Bird et al. (2003) and Ye and Horwath (2017). Mineral N was added at a rate similar to fertilizer N applied for cotton production (~ 80 kg ha^{-1}) in these soils using ammonium nitrate (NH_4NO_3) as the source. Field soil bulk density was used to calculate the amounts of residue and N addition.

Approximately 30 g soils (dry weight equivalent) and 60 mg residues were mixed in a 1 L Mason jar with a spatula. Mineral N was added in deionized (DI) water solution (1067 mg N L^{-1}) to assure the soils were incubated at 70% of the soils' water holding capacity. The jar was closed with a cap equipped with a rubber septum allowing headspace gas collection and incubated in the dark at room temperature (20 ± 1 °C). Controls without residue and mineral N were also included in the study, in which similar amounts of DI water were added, replacing N solutions. Additional sets of samples were prepared for destructive sampling during the incubation.

CO_2 and N_2O analyses

On days 1, 2, 4, 6, 9, 12, 16, 21, 27, 34, 41, 48, and 55 of incubation, 2 mL headspace gases were drawn from each Mason jar and diluted in a pre-vacuumed 12-mL glass vial with 13 mL pure N_2 gas. After each gas sampling event, jars were opened and allowed to refresh in a fume hood for 5 min, after which the jars were closed and returned to the incubation conditions described above. Blanks were prepared to measure background air CO_2 concentrations and their ^{13}C abundance, which were used to calibrate CO_2 production and following partitioning. The gas samples were analysed for CO_2 and N_2O concentrations with a gas chromatograph (Shimadzu, Columbia, MD). On days 2, 6, 12, 21, 34, and 48, gas subsamples were prepared and analysed for ^{13}C-CO_2 at the Stable Isotope Facility of the University of California Davis.

Soil analyses

After gas sampling on days 2, 6, 12, 21, 34, and 48, a set of parallel incubation samples was randomly sacrificed and used for the additional analyses. Subsamples were extracted with 1 *M* KCl), centrifuged, and filtered with Whatman No. 42 filter paper. The filtrates were analysed for exchangeable ammonium (NH_4^+) (Verdouw et al. 1978) and nitrate (NO_3^-) (Doane and Horwáth 2003) colorimetrically. The second set of subsamples were used to quantify microbial biomass C (MBC) with fumigation-extraction methods (Vance et al. 1987). The extracted liquid samples were analysed at the Stable Isotope Facility of the University of California, Davis, for the concentration and ^{13}C abundance of the dissolved organic C (DOC). The MBC was calculated as the difference in DOC between the fumigated and unfumigated samples using a conversion factor of 0.37 (Wu et al. 1990).

Enzymatic activities associated with C-cycling, i.e. β-D-cellubiosidase (CBH), β-glucosidase (BG), N-acetyl-β-glucosaminidase (NAG), and β-xylosidase (XYL), were measured using fluorescence assays as described by Ye et al. (2019). In brief, 1 g of soil was gently mixed with 10 ml of DI water for 20 min in a reciprocating shaker and allowed to settle in a fridge at 4 °C for 30 min and centrifuged at 4 °C. Approximately, 200 µl supernatant was incubated with 50 µl of 200-µM substrate solution in a 96-well microplate for 24 h at room temperature (20 ± 1 °C). Changes of fluorescence intensity were measured at 0, 12, and 24 h after incubation with a standard quenching curve, most of which increased linearly during the incubation (data not shown). The enzyme activities were then estimated by linear changes of fluorescence intensity against time and expressed as µmole product g^{-1} h^{-1}.

CO_2 production partitioning and priming effect

On days 2, 6, 12, 21, 34, and 48, the fraction of CO_2 production derived from residue was calculated as follows:

$$F_{CO2,\,residue} = \left(\delta^{13}CO_{2,\,residue} - \delta^{13}CO_{2,\,control}\right) / \left(\delta^{13}C_{residue} - \delta^{13}C_{control}\right) \quad (1)$$

where $F_{CO2,\,residue}$ is the fraction of total CO_2 production derived from ^{13}C-labelled residue. The $\delta^{13}CO_{2,\,residue}$ and $\delta^{13}CO_{2,\,control}$ are δ^{13}C values of the CO_2 production in soils incubated with and without ^{13}C-labelled residue, respectively. The $\delta^{13}C_{residue}$ and $\delta^{13}C_{control}$ are the δ^{13}C values of the residue and soil, respectively.

Table 1 Results of repeated measures ANOVA on residue amendment, mineral N addition, and time effects and their interaction on selected measured variables. Significant level was set at $\alpha = 0.05$

Variables	Residue	N	Residue*N	Time	Time*residue	Time*N	Residue*N*time
CO_2 production	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.98
N_2O production	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
MBC	< 0.0001	0.16	0.95	< 0.0001	< 0.0001	0.50	0.62
β-D-cellubiosidase activity	< 0.0001	0.92	0.41	< 0.0001	< 0.0001	0.73	0.89
N-Acetyl-β-D-glucosaminidase activity	< 0.0001	0.83	0.16	< 0.0001	< 0.0001	0.64	0.25
β-Glucosidase activity	< 0.0001	0.43	0.001	< 0.0001	< 0.0001	0.23	0.25
β-Xylosidase activity	< 0.0001	0.89	0.02	< 0.0001	< 0.0001	0.13	0.44
NO_3^--N	< 0.0001	< 0.0001	< 0.0001	< 0.001	< 0.0001	< 0.0001	< 0.0001
NH_4^+-N	< 0.0001	< 0.0001	0.46	< 0.0001	0.03	< 0.0001	0.03

The SOM-derived CO_2 ($CO_{2,\ SOM}$) production was determined as follows:

$$CO_{2,\ SOM} = CO_{2,\ total} \times (1 - F_{CO2,\ residue}) \quad (2)$$

where $CO_{2,\ total}$ was total CO_2 (mg C g^{-1}) production in soils with residue.

Primed CO_2 production and the priming effect were calculated as follows:

$$\text{Primed production} = CO_{2,\ SOM} - CO_{2,\ control} \quad (3)$$

$$\text{Priming effect} = \text{primed production}/CO_{2,\ control.} \quad (4)$$

where $CO_{2,\ control}$ was CO_2 (mg C g^{-1}) production in soil without rice residue.

^{13}C-Microbial biomass C and C use efficiency

The $\delta^{13}C$ values of MBC were determined as follows (Wu et al. 2019):

$$\begin{aligned}\delta^{13}C - MBC =& (\delta^{13}C - DOC_{fumigated} \times DOC_{fumigated} \\ &- \delta^{13}C - DOC_{unfumigated} \times DOC_{unfumigated}) \\ &/ (DOC_{fumigated} - DOC_{unfumigated}).\end{aligned} \quad (5)$$

where $\delta^{13}C$-$DOC_{fumigated}$ and $\delta^{13}C$-$DOC_{unfumigated}$ were $\delta^{13}C$ values of extractable DOC in fumigated and unfumigated soil samples, while $DOC_{fumigated}$ and $DOC_{unfumigated}$ were the concentrations (mg kg^{-1}), respectively.

Residue-derived MBC (mg kg^{-1}) in soils incubated with residues was further calculated according to the following equation (Wu et al. 2019):

$$\begin{aligned}Residue - derived\ MBC =\ & MBC_{total} \times (\delta^{13}\ C - MBC_{total} - \delta^{13}\ C - MBC_{control}) \\ &/ (\delta^{13}\ C_{residue} - \delta^{13}\ C - MBC_{control})\end{aligned} \quad (6)$$

where MBC_{total} and δ^{13} C-MBC_{total} were the amounts (mg kg^{-1}) and δ^{13} C values of total MBC in soils incubated with residues and δ^{13}C-$MBC_{control}$ was δ^{13} C values of MBC in soils without residue additions.

Microbial C use efficiency (CUE) was calculated on days 12 and 34 of the incubation, according to the methods described by Sauvadet et al. (2018),

$$\begin{aligned}CUE\ =\ & Residue - derived\ C - MBC \\ &/ (Residue - derived\ C - MBC\ +\ Residue - derived\ C - CO_2)\end{aligned} \quad (7)$$

Data analyses

Repeated measures ANOVA was used to determine the effects of residue amendment, mineral N addition, incubation time, and their interaction at $\alpha = 0.05$. The significant difference between treatment levels was tested by Students' t-test on least-square means. The data were examined for heterogeneity and normality with residue plots and log-transformed when such transformation improved the normality (including NH_4^+-N concentrations, MBC content, and BG activities). The relationship between measured variables was analysed by pairwise correlation analysis and a linear regression model. All analyses were performed with JMP 14.1 statistical software (SAS Institute, Cary, NC).

Results

CO_2 and N_2O production

Both residue amendment and mineral N addition affected CO_2 production, the direction and magnitude of which were different and changed over time (Table 1; Fig. 1a). Regardless

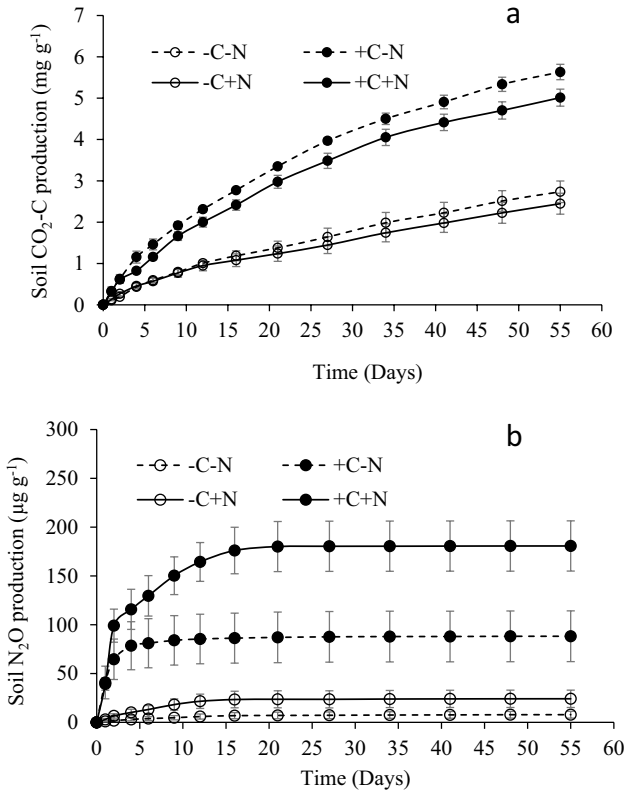

Fig. 1 Cumulative CO_2 (**a**) and N_2O (**b**) production in soils incubated with either residue, mineral N, both, or neither. Bars indicate one standard error of the means ($n=4$). −, without; + with; C, residue amendment; N, mineral N addition

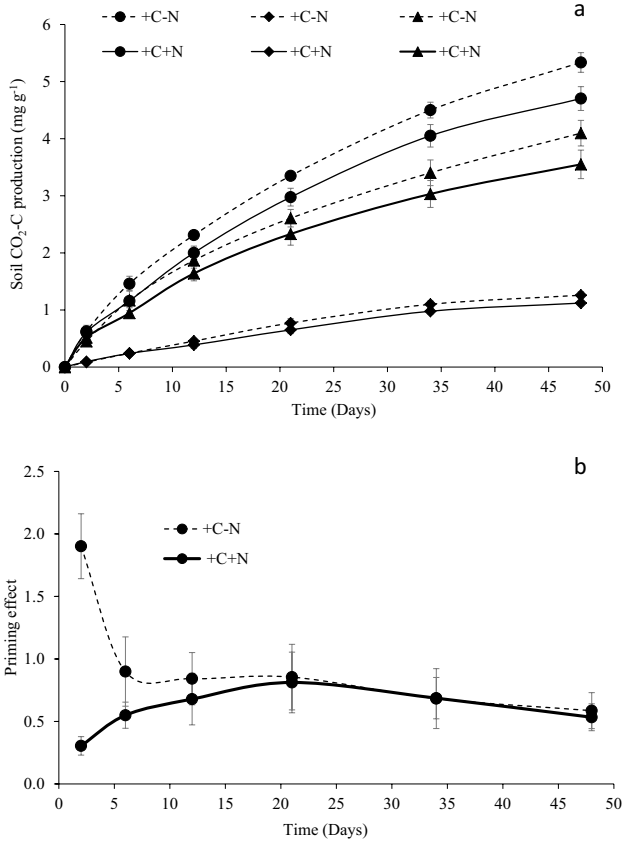

Fig. 2 Partition of total CO_2 production into its sources (**a**) and calculated priming effects of residue amendment (**b**) in soils incubated with residue alone or residue plus mineral N. Bars indicate one standard error of the means ($n=4$). −, without; + with; C, residue amendment; N, mineral N addition; total, total CO_2 production; SOM, soil organic matter

of N addition, residue amendment increased CO_2 production on day 2, and the stimulatory effects continued to the end of the experiment (Fig. 1a). In contrast, when residue was absent, mineral N addition significantly decreased cumulative production on days 48 and 55. This inhibitory effect was also observed when N was added together with residue, starting from day 4 to the end of the experiment.

Basal cumulative N_2O production was consistently low (<10 μg g^{-1}) during the entire period of the experiment (Fig. 1b). The introduction of mineral N alone did not change N_2O production. In contrast, sole residue amendment promoted N_2O production from days 2 to 4, after which the production levelled off. Additions of mineral N magnified the stimulatory effects of residue amendment on N_2O production (Table 1; Fig. 1b). At the end of the experiment, the N_2O production in soils with both N and residue additions was 105% higher than that in soils with residue only.

Partitioning CO_2 production and priming effects

Regardless of mineral N addition, total CO_2 production in soils with residue amendment was dominated by SOM-derived production during the experiment, ranging from 70 to 85% (Fig. 2a). Mineral N addition affected both the SOM- and residue-derived pools (Table 2). Starting on day 12, the SOM-derived production in soils with both residue and mineral N was less than that in soils with residue only (Fig. 2a). Similarly, the residue-derived production in soils incubated with both mineral N and residue was also less than that in soils with residues only, which was only significant on days 21, 34, and 48.

Residue amendment promoted SOM decomposition resulting in positive PE, the intensity of which deceased from days 2 to 6 and plateaued from day 6 to the end of the experiment (Table 2; Fig. 2b). Additions of mineral N reduced the PE of residue amendment by 524% on day 2, but the inhibitory effect diminished and disappeared on and after day 6.

Microbial biomass C and C use efficiency

The MBC was averaged 86 mg kg^{-1} prior to the incubation (Fig. 3a). Residue amendment increased MBC, which was only observed on day 34 (Table 1; Fig. 3a). Regardless of residue amendment, mineral N addition had no effects on MBC on both

Table 2 Repeated measures ANOVA analysis of the effects of mineral N addition and time and their interaction on selected measured variables. Significant was set at $\alpha = 0.05$

	N addition	Time	N addition*time
Total CO_2	< 0.0001	< 0.0001	0.06
Reside-derived CO_2	0.001	< 0.0001	0.17
SOM-derived CO_2	0.0001	< 0.0001	0.08
Primed effect	0.001	0.03	0.005
C use efficiency	0.004	< 0.0001	0.6

days 12 and 34. Total MBC was dominated by the SOC-derived pool (Fig. 3b). Mineral N additions did not change the dominance of the SOC-derived over residue-derived.

When mineral N was not added, microbial CUE was averagely 0.04 on day 12, increasing to 0.31 on day 34 (Fig. 4). Mineral N addition increased the CUE by 200% on day 12 (Table 2; Fig. 4). This stimulatory impact was also observed on day 34, on which N addition increased the CUE by 22%.

Potential enzyme activities

Basal CBH activities were mostly lower than 1 μmol g^{-1} h^{-1} and did not change during the entire period of the experiment (Fig. 5a). Additions of mineral N, either with or without residue, did not change CBH activities (Table 1; Fig. 5a). In contrast, residue amendment increased CBH activities from days 2 to 48, which was not affected by N addition. Similar stimulatory impacts of residue amendment and neutral effects of N addition were also observed for the activities of XYL and NAG (Fig. 5b and c) (Table 1). Furthermore, sole addition of mineral N did not change BG activities. However, when added together with residues, mineral N amplified the positive impacts of residue amendment on BG activity on days 21, 26, 34, and 48 (Table 1; Fig. 5d).

NO_3^--N and NH_4^+-N concentrations

The NO_3^--N concentrations in control soils (without N and residues) ranged from 4 to 15 mg kg^{-1}, which increased slightly from days 2 to 12 and then remained unchanged to day 48 (Table 2; Fig. 6a). Regardless of N addition, residue amendment decreased NO_3^{-1}-N concentrations, becoming consistently lower than 0.4 mg kg^{-1} after day 2 (Fig. 6a). Sole N addition increased NO_3^{-1}-N concentrations from days 2 to 16, after which it remained unchanged.

Additions of residue and mineral N increased soil extractable NH_4^+-N concentrations, also affected by incubation time (Table 1). The extractable NH_4^+-N concentrations increased from days 0 to 2 in all soils, being the highest in soils incubated with both residue and N

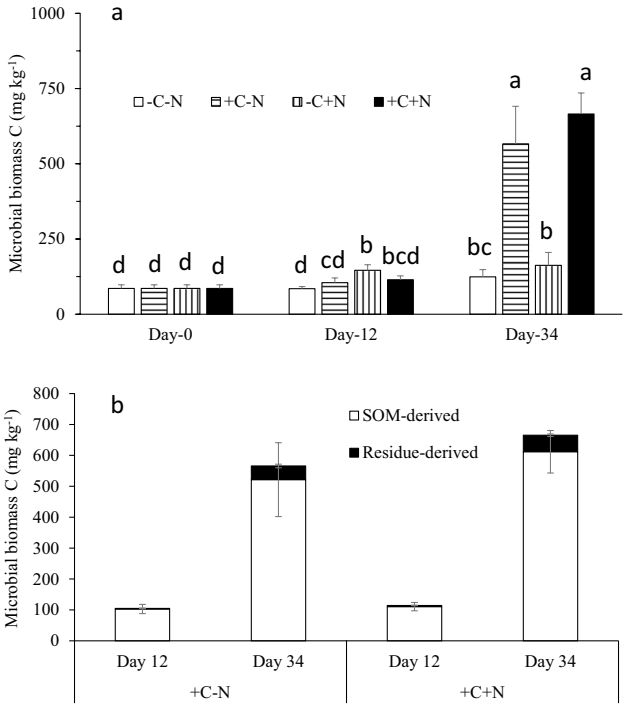

Fig. 3 Total microbial biomass C on days 0, 12, and 34 of the incubation (**a**) and the partitions of microbial biomass C into its sources (**b**). Bars indicate one standard error of the means ($n = 4$). −, without; + with; C, residue amendment; N, mineral N addition. Different letters over the bar indicate significant difference at $\alpha = 0.05$

(24 mg kg^{-1}), followed by N alone (18 mg kg^{-1}), residue alone (8 mg kg^{-1}), and control (3 mg kg^{-1}) (Fig. 6b). However, the concentrations in all soils decreased gradually after day 2. On day 26 and thereafter, soil exchangeable NH_4^+-N concentrations were minimal, and there was no difference between the treatments.

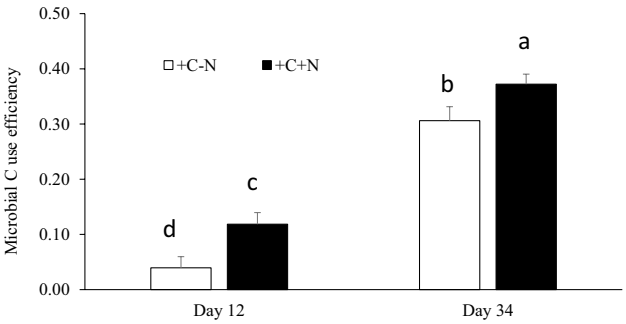

Fig. 4 Microbial C use efficiency of soils incubated with either residue amendment or additions of both residue and mineral N. Bars indicate one standard error of the means ($n = 4$). −, without; + with; C, residue amendment; N, mineral N addition. Different letters over the bar indicate significant difference at $\alpha = 0.05$

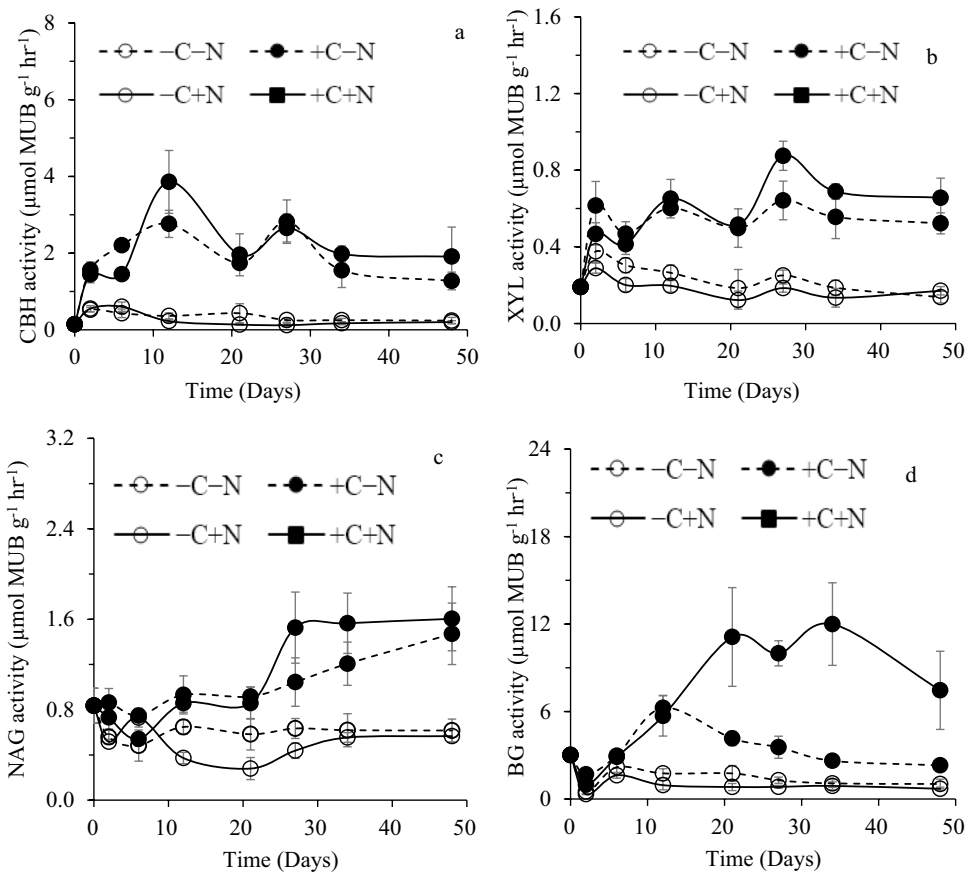

Fig. 5 Potential activities of β-D-cellubiosidase (CBH) (**a**), β-xylosidase (XYL) (**b**), N-acetyl-β-glucosaminidase (NAG) (**c**), and β-glucosidase (BG) (**d**) in soils incubated with either residue, mineral N, both, or neither. Bars indicate one standard error of the means ($n=4$). −, without; + with; C, residue amendment; N, mineral N addition

Relation between measured variables

There was no significant relationship between NO_3^--N concentration and the measured enzyme activities and CO_2 production, including total, SOM-derived, and residue-derived CO_2 and the primed production (Table 3). In contrast, exchangeable NH_4^+-N concentration was negatively correlated to the total, SOM-derived, and residue-derived CO_2 and the primed production, which also negatively correlated to NAG activities (Table 2; Fig. 7). In addition, NAG activity was positively correlated to total, SOM-derived, and residue-derived CO_2 and the primed production.

Discussion

Priming effect (PE) of residue amendment and N impacts

Residue amendment readily accelerated SOC decomposition resulting in positive PE (Fig. 1a; Fig. 2b) (supporting hypothesis 1). This positive PE has also been reported in a range of agricultural soils (Fontaine et al. 2003; Kuzyakov 2010; Mason-Jones et al. 2018; Wild et al. 2019). Even though the exact mechanisms of PE remains unsolved, microbes are believed to play the key role (Fontaine et al. 2003; Kuzyakov 2010; Liu et al. 2020). One of the many hypotheses suggested that when supplied with an abundance of C sources, soil microorganisms may become N-limited and therefore use the organic C as the energy source to decompose soil organic matter (SOM) for N contained while inducing PE (i.e. microbial N mining theory) (Cui et al. 2020; Fang et al. 2020; Mason-Jones et al. 2018). In the present study, the increased SOC decomposition was accompanied by enhanced activities of all the measured C-cycling enzyme activities with no increase of MBC observed until day 34 (Fig. 3a; Fig. 5). Therefore, it is plausible that higher microbial enzyme production was induced upon residue amendment leading to the PE but apparently with higher respiratory costs (i.e. higher qCO_2 or the ratio of mineralization production of CO_2 to MBC) (Sauvadet et al. 2018). The results were in line with the microbial N mining theory, which was further supported by the observation that N addition reduced the decomposition of SOC and PE (Fig. 2) (supporting hypothesis 2).

Inhibitory effects of N additions on residue and SOC decomposition have recently been documented (Liu et al. 2020; Mason-Jones et al. 2018; Meng et al. 2017). In the present study, this suppressive effect can be further

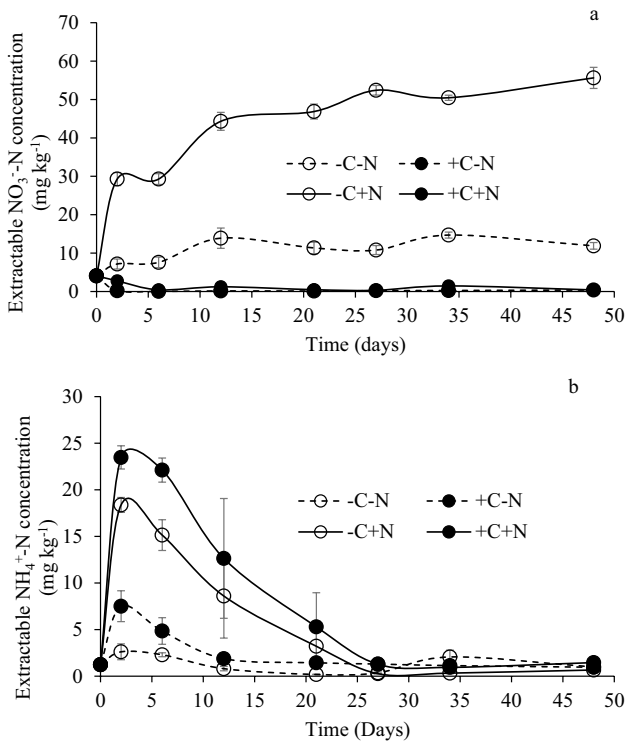

Fig. 6 The concentrations of NO_3^--N (**a**) and exchangeable NH_4^+-N (**b**) in soils incubated with either residue, mineral N, both, or neither. Bars indicate one standard error of the means ($n=4$). −, without; + with; C, residue amendment; N, mineral N addition

depicted by negative linear regressions of soil NH_4^+ concentrations against total, SOC-derived, residue-derived, and primed CO_2 production, respectively (Table 3; Fig. 7). A recent study described a negative relation between mineral N addition and PE in an exponential function, which summarized results from many similar studies (Zang et al. 2016). Interestingly, the negative relationship was not observed for soil NO_3^- concentrations in the present study (Table 3), suggesting the type of N sources may also have different impacts on SOC decomposition. Other recent studies have demonstrated that, in contrast to NH_4^+, both labile organic N (i.e. amino acids) (Mason-Jones et al. 2018) and NO_3^- addition (Liu et al. 2020) induced positive PE on residue amendments. It has been suggested that the difference was likely attributable to the amounts of energy needed to assimilate the N (Liu et al. 2020; Mason-Jones et al. 2018). Soil microbes may prefer to utilize N in the form of NH_4^+ (reduced state) over NO_3^- (oxidized state) and organic N to save energy (Christie and Wasson 2001; Romero et al. 2015), mainly when exogenous organic C was supplied (Cheng et al. 2017). Therefore, it is not surprising that the gradually decreasing NH_4^+ concentrations in soils amended with residues were not accompanied by increasing NO_3^-, while consistently higher NO_3^- concentrations were observed in soils without residue amendments (Fig. 6).

Residue C use efficiency (CUE) and N effects

The estimated CUE in soils with sole residue amendment ranged from 0.04 to 0.31 (Fig. 4), which was within the lower range of the commonly observed values in soils (Manzoni et al. 2012; Soares and Rousk 2019). Lashermes et al. (2016) demonstrated that CUE was highly dependent on the content and stoichiometry of soluble organic compounds. In the present study, high C/N ratio (52:1) of the added residues (vs. soil C/N ratio of 14:1) likely explained the observed low residue CUE (Fig. 4), because more significant investment in enzyme production may be required (Sauvadet et al. 2018; Soares and Rousk 2019), which may also describe the dominance of SOM-derived CO_2 production (Fig. 2a) and MBC (Fig. 3b) over the residue-derived pools. This low CUE residue found in our study was further

Table 3 Pairwise correlation of selected measured variables. Values are correlation coefficient R

	Total CO_2	Residue-CO_2	SOM-CO_2	Primed CO_2	CBH	NAG	BG	XYL	NO_3^--N
Residue-CO_2	0.98**								
SOM-CO_2	0.997**	0.96**							
Primed CO_2	0.85**	0.82**	0.86**						
CBH	−0.24	−0.28	−0.22	−0.10					
NAG	0.57**	0.57**	0.56**	0.45**	−0.05				
BG	0.18	0.13	0.20	0.15	0.52**	0.18			
XYL	0.12	0.07	0.13	0.29	0.34*	0.49**	0.28		
NO_3^--N	−0.23	−0.21	−0.24	−0.27	0.16	−0.19	0.19	−0.1	
NH_4^+-N	−0.67**	−0.67**	−0.65**	−0.68**	−0.16	−0.43**	−0.28	−0.23	0.39*

*, $p<0.05$; **, $p<0.01$; Total CO_2, cumulative CO_2 production; Residue-CO_2, residue-derived CO_2 production that contributed to the total CO_2; SOM-CO_2, soil organic matter-derived CO_2 production that contribute to the total CO_2; CBH, β-D-cellubiosidase activity; NAG, N-acetyl-β-glucosaminidase activity; BG, β-glucosidase activity; XYL, β-xylosidase activity

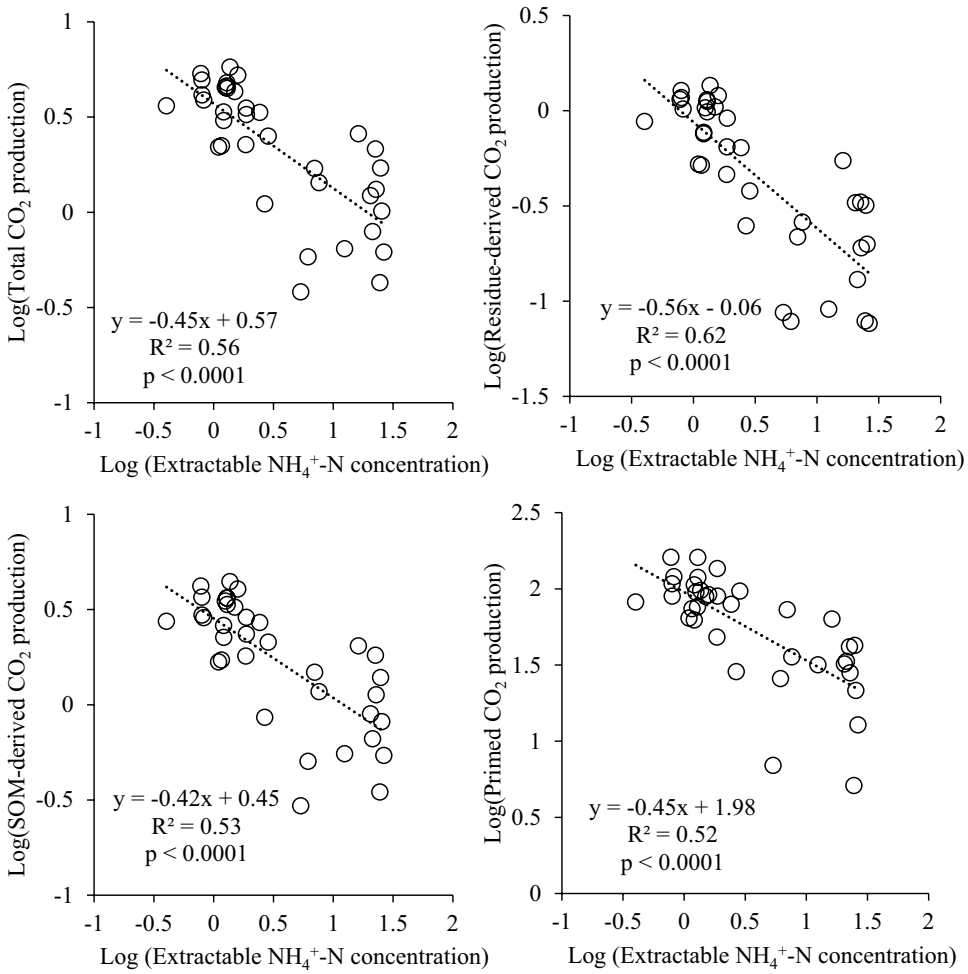

Fig. 7 Relationship of exchangeable NH_4^+-N concentration with total, SOM-derived, and residue-derived CO_2 and the primed production. Equations are linear regression models with coefficients (R^2) and *p* values

supported by the increased enzyme activities upon residue amendment (Fig. 5).

Maximal CUE occurs when the costs of obtaining C and N are minimal (Moorhead et al. 2012). Therefore, nutrient limitation can result in uncoupling of anabolism and catabolism, reducing microbial CUE (Liu 1998). In the present study, mineral N addition increased CUE on days 12 and 34 (Fig. 4). However, this positive effect was not found in total MBC and the residue-derived MBC during the same period (Fig. 3b). It is therefore apparent that the increased CUE was mainly caused by reduced C losses and energy drain through respiration (e.g. investments for maintenance, extracellular enzyme synthesis, and overflow mechanisms) but rather than enhanced microbial growth (Manzoni et al. 2012; Soares and Rousk 2019). The observation likely suggested the decoupling of anabolism and catabolism, which explained why residue amendment alone stimulated enzyme activities but did not increase MBC on day 12 and why total MBC was primarily derived from SOC (Fig. 3b). However, regardless of N additions, higher MBC was found in soils amended with residues than the controls on day 34 (Fig. 3a), on which the contributions of residue-derived MBC increased from day 12 (Fig. 3b). The results were in line with the statement that the costs associated with enzyme production or maintenance could be compensated for overtime by new compounds made available by enzyme during the decomposition processes (Lashermes et al. 2016; Soares and Rousk 2019).

Enzymes activities are often considered measurable proxies for microbial decomposition (Burns et al. 2013), which can be optimized with minimum incubation time to minimize microbial growth and production of enzyme during the measurement (Nannipieri et al. 2018). In the present study, we incubated the soils for 24 h because of their intrinsically low enzyme activities (Fig. 5), likely attributable to their low N availability (Fig. 6). Interestingly, NAG activity (associated with both C and N cycling) was the only enzyme activity that positively correlated to CO_2 production from different pools and also the sole enzyme that was negatively correlated to soil NH_4^+ concentrations (Table 3). Microorganisms direct their resources to different enzymes to acquire available forms of C and N that can meet their stoichiometric demands (Lashermes et al. 2016; Moorhead et al. 2012). The amounts of enzyme required

for substrate decomposition can vary substantially, which may at least partially explain why enzyme activity was not always responsive concurrently with microbial residue CUE as observed in the present study (Figs. 4 and 5) (Lashermes et al. 2016; Sauvadet et al. 2018).

Residue and N amendment impacts on N_2O production

As expected, additions of mineral N (NH_4NO_3) increased both concentrations of extractable NH_4^+ and NO_3^- in soils (Fig. 6). It was also apparent that the NO_3^- continued to increase from days 5 to 25 in soils with sole N addition, which coincided with decreasing extractable NH_4^+ concentrations during the same period, indicating the occurrence of nitrification (Li et al. 2018). However, the addition of N and following nitrification did not increase N_2O production throughout the entire experiment (Table 1; Fig. 1b), which was previously reported by Lehtinen et al. (2014). The minimal initial extractable NH_4^+ availability and ambient air in the soils likely created a favourable condition for the nitrification of the added mineral N allowing rapid and complete oxidation processes to eliminate intermediate products (i.e. NH_2OH and NO_2^-), supressing N_2O production (Zhu et al. 2013).

Residue amendment also increased soil NH_4^+ concentrations at the beginning of the incubation (Fig. 6b), because of microbial N mineralization of the residue (Akkal-Corfini et al. 2010). In contrast, regardless of N additions, residue amendment readily exhausted soils NO_3^- (Fig. 6), with simultaneous rapid increases of N_2O production within the first 5 days (Fig. 1b). It has been suggested that crop residue can modify soil aeration by enhancing soil aggregations and increase microbial O_2 demands creating an anaerobic environment in soil microsites favourable for denitrification (Chen et al. 2013; Li et al. 2016). Energy supplies from the residue may further encourage denitrification. Therefore, it is possible that denitrification was the primary source of N_2O production in the present study, as suggested by similar studies (Köster et al. 2011; Li et al. 2016). In addition, the decreasing NH_4^+ concentrations from days 5 to 25 in soils with both residue and mineral N additions did not lead to increases of either NO_3^- concentrations (Fig. 6a) or N_2O production (Fig. 1b). The disconnections between NH_4^+ depletion and NO_3^- and N_2O production were also observed in the soils with residue amendment alone but with fewer magnitudes (Figs. 1b and 6). These results further supported the statements that denitrification was seemingly the major pathway for N_2O production in the present study, while the depletion of soil extractable NH_4^+ was attributed to microbial assimilation or nitrification (Chen et al. 2013; Moran et al. 2005).

N addition, SOC preservation, and trade-offs

In contrast to the conventional view of SOC formation, growing lines of evidence have indicated that microbial materials or necromass is important constitutions of SOC and can play a key role in regulating C accumulation in agricultural soils (Kallenbach et al. 2016, 2015). Recent studies further demonstrated that N addition facilitated the integrations of residue C into microbial biomass and stable organic pools, improving their stability and preservation in soils (Kallenbach et al. 2015; Moran et al. 2005; Sauvadet et al. 2018; Soares and Rousk 2019), all of which raised the importance of mineral N in sequestering C. In the present study, mineral N addition did increase the stability of the added residue and SOC but mainly through reduced respiration and PE (Figs. 1a and 2). No increased integrations of residue to microbial biomass were observed (Figs. 3b and 4). Despite the discrepancy, the results agree with many similar studies that integrated nutrient, and residue management can be an excellent strategy to increase C sequestration and SOC preservation in agricultural soils (Fang et al. 2018; Kallenbach et al. 2015; Meng et al. 2017). In addition, it has been suggested that combined additions of mineral N and residue also enhanced the transforms of N into organic pools, promoting their retentions in soils (Meng et al. 2017; Moran et al. 2005). In the present study, the production and completion patterns of NH_4^+ in soils amended with both mineral N and residues also suggested its assimilation into unidentified pools in the tested soils (Fig. 6). However, significant pulses of N_2O production were also observed when the two were added together (Fig. 1b). New strategies to combine the additions of organic materials and fertilizer N in agricultural soils should consider this trade-off (Bai et al. 2020).

Conclusion

Crop residue amendment and mineral N addition had distinct impacts on microbial decomposition of SOC in the tested sandy soils. Residue amendment instantly induced C-cycling enzyme activities and microbial respiration promoting positive PE, which was not observed when mineral N was added alone. Mineral N did not augment the residue impacts on enzyme activities involved in organic C reactions, except on BG activities after a lag period. Instead, N addition reduced the positive impacts of residue amendment on respiration and PE while increasing microbial CUE. Nonetheless, mineral N did not facilitate the integrations of residue C into microbial biomass during the entire period of the experiment. The PE of residue addition was induced mainly by the supplies of energy

and subsequent enzyme production to acquire N (in line with microbial N mining theory of PE). In addition, mineral N addition reduced microbial mining of organic N and the decomposition of the added residues. The results highlighted the importance of N application to improve C preservation and N retention in sandy soils. It is apparent that rotating crops with high biomass production potentials along with effective N management can be an appealing strategy to increase C sequestration potentials in agricultural soils. However, research is further needed to understand long-term N fertilization impacts on SOC/SOM formation and the trade-offs between C sequestration and N_2O production, especially under the changing management practices and climate.

Declarations

Conflict of interest The authors declare no competing interests.

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