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Plant inputs mediate the linkage between soil carbon and net nitrogen mineralization

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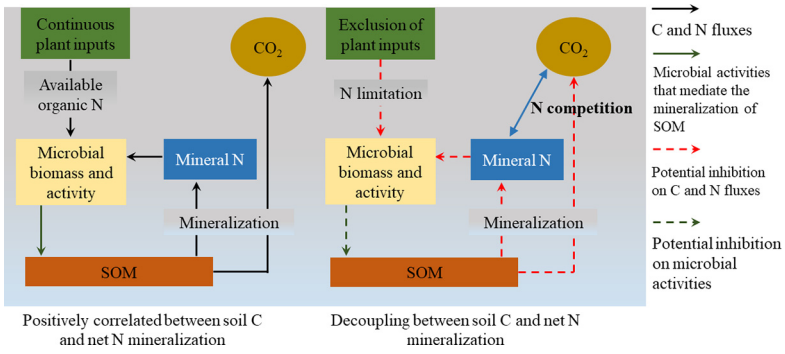
HIGHLIGHTS

- Soil C and net N mineralization (NNM) was decoupled in the bare fallow soil.
- The relationships between soil C and NNM were changed by plant inputs.
- Warming increased soil C and NNM, and changed their relationships.

GRAPHICAL ABSTRACT



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ABSTRACT

Plant residue inputs play a crucial role in regulating soil carbon (C) stock and nitrogen (N) availability in cropland. However, little is known regarding how plant inputs mediate the relationships between soil C and net N mineralization, causing additional uncertainty in predicting ecosystem C and N dynamics. This study investigated the influences of long-term deprivation of plant inputs, short-term addition of maize straw and experimental warming on soil C and net N mineralization and their relationships. We conducted an 815-day laboratory incubation experiment under 10 and 20 °C using soils from a long-term bare fallow plot (without plant inputs for 23 years) and its adjacent old field plot (with continuous plant inputs). Our results showed that long-term deprivation of plant inputs decreased soil net N mineralization (per unit total N or TN) by 56% on average, but had minor effect on soil C mineralization (per unit soil organic C). Soil C and net N mineralization rates were positively correlated in the old field soil under 20 °C. However, soil C and net N mineralization rates were not correlated in the bare fallow soil, mainly due to the low level of net N mineralization. Moreover, soil C and net N mineralization rates were significantly increased by the addition of maize straw in both land-use types. When net N mineralization was <162 (or 159) μg N g^{-1} TN d^{-1}, soil C and net N mineralization rates were negatively correlated due to an increase of microbial N demand during plant litter mineralization. When net N mineralization was >162 (or 159) μg N g^{-1} TN d^{-1}, soil C and net N mineralization rates were positively correlated owing to a greater microbial mining of N from soil organic matter (SOM). Further, elevated temperature increased soil C and net N mineralization rates, and changed the relationships between soil C and net N mineralization. Taken together, this study provides evidence that plant inputs mediate the relationships between soil C and net N mineralization, and is thus critical in controlling ecosystem C and N cycling.

Abbreviations: C, carbon; CO_2, carbon dioxide; SOC, soil organic carbon; SOM, soil organic matter; N, nitrogen; MBC, microbial biomass carbon; C/N, the ratio of carbon to nitrogen; NNM, net nitrogen mineralization; WHC, water-holding capacity; qCO_2, microbial metabolic quotient; CAI, carbon availability index.

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1. Introduction

Plant inputs are the main source of soil organic matter (SOM) contents, providing substrates for microorganisms to mediate a variety of processes that underlie many ecosystem services provided by soils (Paterson et al., 2011). These plant-derived organic inputs determine the stoichiometry of organic material (e.g., carbon/nitrogen (C/N) ratio) and nutrients applied to the soil or biomass harvested from the forest ecosystem (Parolari and Porporato, 2016). In particular, microbial-mediated mineralization of plant residues and associated N mineralization and immobilization fluxes regulate the long-term responses of plant, litter and SOM pools to climate change and management practice (Thornton et al., 2007; Thornton et al., 2009; Du et al., 2018). There is increased recognition that the C-N cycle coupling is invaluable in predicting the future impact of global environmental changes on SOM decomposition in multiple ecosystems (Parolari and Porporato, 2016; Tian et al., 2017). However, our understanding of the effect of C-N interactions on SOM decomposition is rudimentary in agroecosystems.

It is recognized that plant inputs not only determine the chemical composition of SOM (Córdova et al., 2018), but also impact on microbial biomass and activity as well as microbial community structure and functioning (Paterson et al., 2011). Indeed, long-term exclusion of plant inputs altered the preferential functional capacity of microbial communities in mineralizing recalcitrant and labile substrates (Paterson et al., 2011; Nunan et al., 2015). Due to the continuous depletion of more labile SOM pools, the observed soil organic carbon (SOC) dynamics are increasingly dominated by the properties of relatively stabilized SOM pools (Franko and Merbach, 2017), and SOC often exhibits decreased mineralization rate and increased temperature sensitivity in these soils (Lefèvre et al., 2014). While these studies on the effects of plant inputs have mostly focused on the processes of C mineralization, N cycling and its interaction with C mineralization have received little attention.

The relationships between soil C and net N mineralization are generally considered to be soil specific and depending on C and N availability (Mooshammer et al., 2014; Novair et al., 2020; Wang et al., 2021a). Previous studies have found that soil C and N availability are likely to regulate microbial demand and activity, and ultimately influence microbial-mediated C and N mineralization processes (Booth et al., 2005). SOM with high N availability relative to C availability can relieve microbial N limitation and exhibit more gross N mineralization than immobilization, which often results in a net N mineralization and a positive relationship between soil C and net N mineralization (Wild et al., 2015). While in the soil characterized by organic matter containing high C but low N availability, microbes are N-limited and exhibit more N immobilization than mineralization, which results in a negative relationship between soil C and net N mineralization (Cookson et al., 2007; Sun et al., 2020). One of the key factors determining soil C and N availability and the relationships between soil C and net N mineralization is the quality and quantity of organic inputs to the soil (Rummel et al., 2020).

It has been suggested that the supply of labile C through plant residue turnover is an important source of labile C substrates that drive heterotrophic microbial growth and activity (Hooker et al., 2008). The consumption of labile C would result in an increase of microbial N demand and additional immobilization of available N from soil solution during the processes of organic matter mineralization and microbial biomass production (Cookson et al., 2007). On average, the C/N ratio (stoichiometry of proteins) of soil extracellular enzymes is as low as 3.5:1 (Allison, 2005), which is much lower than those of bacterial (5:1) and fungal (15:1) biomass (Sterner and Elser, 2002). Therefore, the requirement of N was even higher for extracellular enzymes production than that for microbial growth, which constrains the allocation of N to mineralization (Lu et al., 2018). With the consumption of the labile fraction of plant-derived organic inputs, some of the activated microbes begin to mineralize the N-rich SOM in order to acquire N (Murphy et al., 2015). As N availability increases relative to C availability, the greater release of dissolved organic N increases the proportion of N-rich microsites to N-poor microsites, which decreases microbial N limitation and causes net N mineralization (Cookson et al., 2007). In contrast, in some specific soil conditions where C is often bound in compounds of low-energy content, microorganisms need to invest more energy to gain the same amount of C. Microorganisms in such conditions are limited in C regardless of C/N ratio of SOM (Wild et al., 2014). These previous studies suggested that energy deficiency may strongly affect the balance between soil C and N availability as well as microbial C and N demand, which then limits net N mineralization and decouples the linkage between C and N mineralization, as proposed in subsoils and clay fractions (Wild et al., 2015; Tian et al., 2017).

In addition, plant inputs constitute the main source of organic N to decomposers that in turn produces inorganic N, and control the long-term soil N availability (Manzoni and Porporato, 2007; Parolari and Porporato, 2016). For example, Tian et al. (2017) suggested that the supply of readily biodegradable organic N derived from plant inputs may provide the direct source of N transformation. Bimüller et al. (2014) suggested that the actual bioavailability of C and N in different particle size fractions of SOM controls the mineralizaiton pattern, thus changing the interactions between soil C and N mineralizaiton. These studies suggested that the relative changes of C and N availability of plant inputs complicate the interactions between C and N mineralization. Therefore, there is an urgent need to further characterize the interactions between plant inputs and microbial processes mediating soil C and N mineralization.

Temperature is one of the most important abiotic factors affecting soil C and N cycling (Liu et al., 2017; Li et al., 2020). It has been suggested that the temperature sensitivity of SOC mineralization varies with its quality (Conant et al., 2008). The recalcitrant SOC is often characterized by higher temperature sensitivity than the labile fraction (Lefèvre et al., 2014; Fang et al., 2017). Recent studies further indicated that higher C availability as well as microbial community response could enhance the temperature sensitivity of SOC mineralization (Karhu et al., 2014; Eberwein et al., 2015; Li et al., 2020). The C quality temperature hypothesis and the microbial response mechanism are also applicable to soil N mineralization (Liu et al., 2017; Salazar et al., 2020). Liu et al. (2017) indicated that the temperature sensitivity of N mineralization is positively correlated with substrate availability. GeoChip microarray analyses revealed significant effects of warming on functional communities, specifically in N-cycling microorganisms (Yergeau et al., 2012). Salazar et al. (2020) also suggested that warming in cold ecosystems increases N mineralization rates and N_2O emissions due to the stimulation of extracellular enzymes that target relatively labile N sources. Although both soil C and N mineralization processes are temperature sensitive, few studies have focused on the interactions between soil C and N mineralization under elevated temperature.

Here we investigated soil C mineralization, net N mineralization, C-N interactions and their responses to external plant inputs in a bare fallow soil which had been deprived of fresh plant inputs for 23 years and its adjacent old field soil with continuous plant inputs. We hypothesized that (1) the long-term exclusion of fresh plant inputs would decrease C availability in the bare fallow soil, resulting in a decrease of microbial activity due to energy limitation; (2) the long-term exclusion of fresh plant inputs would decrease organic N to decomposers in the bare fallow soil, resulting in an inhibition of net N mineralization due to N limitation; and (3) external plant inputs would change the balance between soil N availability and microbial N demand, which in consequence changes the correlation between soil C and net N mineralization. To test these hypotheses, laboratory incubation was applied to isolate treatment effects that arise from changes in the nature of plant inputs to soils from those that arise from changes in the physical environment. Soils from a bare fallow plot and its adjacent old field plot were incubated at 10 and 20 °C to examine soil C mineralization and net N

mineralization. The phospholipid fatty acids (PLFAs), substrate availability, microbial biomass carbon (MBC) and microbial metabolic quotient (qCO_2) were also measured to explore the factors affecting soil C and net N mineralization and C-N interactions.

2. Materials and methods

2.1. Soil collection

Soils were collected from a bare fallow plot and its adjacent old field plot of Shenyang Agricultural experimental station (41°32′ N, 122°23′ E, and 50 m above sea level) of Chinese Academy of Sciences. This experimental station was located in Liaoning province, Northeast China. Soils were taken from the top 20 cm. It is classified as Aquic Alfisol (Soil Survey Staff, 2010) developed from silty sediments (Zhang et al., 2017). The old field and the bare fallow plots (each 3 × 6 m) were established in 1990 and were rice paddy fields before treatments. The old field plot received fresh organic input for 23 years (1990–2012) with freely growing weeds but no anthropogenic interference. The bare fallow plot had been kept free of vegetation by frequent hand weeding for 23 years at the time of soil collection for this study (1990–2012). Soils from these old field and bare fallow treatments were sampled in September 2012. Soil samples were taken from 5 points randomly selected within each plot, and combined into single, composite samples for each plot. These composite samples were relatively homogenous and representative of each plot. They were subsampled to provide uniform replicates ($n = 3$) for chemical analyses of each experimental treatment (Table 1). The composite samples from each plot were analyzed for pH, clay content, SOC, total N, and $\delta^{13}C$. All soils were sieved through 2 mm screen. Fine roots, plant debris and visible stones were removed carefully. All soil samples were air-dried and stored at 20 °C before incubation.

2.2. Experimental design

The bare fallow soil which had been deprived of plant inputs for 23 years and its adjacent old field soil would help us to decipher how plant inputs affect the processes of soil C and net N mineralization. For each soil, 200 g of air-dried soil was weighed in individual polypropylene column (5.2 cm in diameter, 20 cm in length). Both ends of each soil container were closed with one-hole rubber stopper connected to ventilation tubing. A continuous aerobic condition in each plastic container was maintained via automatic timer-controlled aeration with fresh air for 1 h in each 4-hour interval during the entire incubation experiment. All soil columns were divided into two amendment treatments: (1) non-amended control and (2) maize straw-amended treatment. In the maize straw-amended treatment, ground maize leaves (sieved through 2 mm screen) were added at the rate of 30 mg g^{-1} soil. The maize leaves were collected from the Shenyang Agricultural experimental station of Chinese Academy of Sciences (China). These maize leaves contained 379 mg g^{-1} organic C and 13.4 mg g^{-1} N, and the C/N ratio was 28.3. The C-addition rate was within the range of the normal amount of plant input to the soil in local croplands (Liang et al., 2011). The SOC-$\delta^{13}C$ (‰) of the maize leaves was −13.4. Based on the natural ^{13}C isotope tracer technology, we found that at the end of incubation, CO_2 production from SOM decomposition contributed 44–71% of the total CO_2 efflux (Fig. S1). For the maize straw-amended treatment, the soil and ground maize leaves were gently mixed and homogenized. The control treatment did not receive any straw and the soil was mixed and homogenized in the same manner. Each treatment was split into two temperature treatments: a cold treatment with constant temperature of 10 °C and a warm treatment with constant temperature of 20 °C, and were incubated in processor-controlled incubators (SHELLAB LI20–2, Sheldon Manufacturing Inc., USA, with a temperature control accuracy and evenness of ±0.05 °C) for 815 days. During incubation, soil moisture was monitored by weighing and frequently adjusted to reach 60% water holding capacity (WHC) by adding deionized water. A total of 488 columns with soil were incubated in this study, of which 32 were repeatedly used for soil CO_2 trapping at each sampling time (4 replicates for each treatment) and 456 were used for destructive sampling (3 replicates for each treatment and 19 destructive samplings). The fresh soil samples were analyzed for Carbon Availability Index (CAI), Microbial biomass C (MBC) and soil mineral N. Freeze-dried soil samples were analyzed for phospholipid fatty acids (PLFAs).

Table 1
Properties of the two soils. Values are given as mean ± se ($n = 3$ for all analyses).

Property	Old field	Bare fallow
pH (1:2 soil: water)	6.01 ± 0.18	6.10 ± 0.12
Clay (%)	12.6 ± 0.8	10.1 ± 1.8
SOC content (g C kg^{-1})	16.60 ± 0.05	11.44 ± 0.14
Total N (g N kg^{-1})	1.37 ± 0.01	0.94 ± 0.00
C/N	12.1 ± 0.1	12.2 ± 0.1
SOC $\delta^{13}C$ (‰)	−24.2 ± 0.0	−24.0 ± 0.2

2.3. Soil CO_2 trapping

We measured soil respiration using a dynamic CO_2 trapping system with CO_2 trapping efficiency greater than 99% (Lin et al., 2015). The CO_2 trapping was applied at day 8, 14, 28, 45, 60, 75, 90, 128, 144, 158, 187, 202, 240, 263, 299, 330, 360, 410, 480, 550, 585, 630, 670, 702, 756 and 815, respectively. Briefly, we used an air pump to force ambient air through a soda-lime column, thereby, CO_2-free air entered the manifold, from which individual tubing led to individual sample inflow tubing. After an equilibrating period of 2 h, the subsequent CO_2 produced inside the soil columns for 24 h was trapped by the CO_2 trapping bottle containing 12 mL 0.5 M NaOH solution. Blanks were also trapped to correct for inorganic C from NaOH stock solution and sample handling. After CO_2 trapping, the NaOH solution was directly analyzed for total inorganic carbon using multi N/C® 2000 TOC analyzer (Analytik Jena, Germany).

2.4. Lab analysis

Before soil incubation, PLFAs of the old field soil and the bare fallow soil (Table 2) were assayed according to Tian et al. (2013). Briefly, fatty acids were extracted from 8 g freeze-dried soil samples with one phase buffer which contained chloroform: methanol: phosphate buffer (1:2:0.8, *v*/v/v). Phosphatidylcholin-dinonadecanoic acid (19:0) as internal standard 1 was added before extraction. After purification via activated silica, phospholipids were transformed to fatty acid methyl esters (FAMEs) following the derivatization procedure. Tridecanoic acid methyl ester (13:0) as internal standard 2 was added to the sample before transferring the samples to autosampler vials for analyses. PLFA content was measured using gas chromatography–mass spectrometry (GC–MS). PLFAs were divided into four groups (Zhao et al., 2019) as following: Gram-positive bacteria (G+) (i14:0, i15:0, a15:0, i16:0, i17:0, and a17:0); Gram-negative bacteria (G−) (16:1ω7, cy17:0, 17:1ω8c, 18:1ω7, cy19:0); fungi (18:2ω6,9c, 18:1ω9c); and actinomycetes (10Me16:0, 10Me17:0, 10Me18:0).

The ratio of basal respiration rate to substrate-induced respiration (SIR) rate is indicative of the C availability in the soil sample, thus called Carbon Availability Index (CAI) (Gershenson et al., 2009). This technique works by flushing a soil sample with excess glucose to alleviate substrate limitation of microorganisms. Since glucose is a broad spectrum C source, soil microorganisms from different soil treatments were supposed to respond similarly to the excess glucose, and the C availability determined by this method was considered to be comparable. CAI was measured at 8, 14, 28, 45, 60, 90, 128, 158, 202, 240, 263,

Table 2
Amount and distribution of actinomycetic, bacterial, fungal, and total biomass in the old field and bare fallow soils.

Land use	Amount of microbial biomass (μmol g^{-1}C)				Fungal/bacterial biomass ratio	Distribution of microbial groups (%)			
	Total microbial biomass	Actinomycetic biomass	Bacterial biomass	Fungal biomass		Actinomycetes	Fungi	G+ bacteria	G− bacteria
Old field	6.40 ± 0.12 b	0.86 ± 0.01 a	4.55 ± 0.14 b	0.32 ± 0.01 b	0.070 ± 0.005 a	13.53 ± 0.28 a	4.75 ± 0.26 a	25.79 ± 0.40 a	23.21 ± 0.32 b
Bare fallow	5.20 ± 0.19 a	0.76 ± 0.02 a	3.70 ± 0.14 a	0.22 ± 0.01 a	0.061 ± 0.002 a	14.55 ± 0.50 a	4.32 ± 0.14 a	25.33 ± 0.86 a	20.22 ± 0.48 a

Values are given as mean ± se (n = 3). Different letters represent a significant difference between the two land-use types ($P < 0.05$).

330, 410, 480, 550, 630, 670, 702 and 815 days. Briefly, after destructive sampling, 80 g soil samples from each soil column were divided into four 20 g aliquots. Each aliquot was placed in a separate 125 mL Erlenmeyer flask. The flasks were divided among two temperature treatments (10 and 20 °C) and either treated with two glucose treatments (Gl+ for added glucose and Gl− for ambient substrate). We added 2 mL glucose solution (60 g L^{-1}) to each Gl+ sample using a 5 mL syringe with a needle tip. Deionized water was added to ambient substrate replicates in the same manner to avoid confounding influences of soil moisture. After a 1 h stabilizing period in the water bath, the soil respiration in each Erlenmeyer flask was measured using Li-COR 6262 Infrared Gas Analyzer (IRGA) (Li-COR Biosciences, Lincoln, NB, USA) with a mass flow meter according to Gershenson et al. (2009). Respiration measurements on each sample lasted approximately 2 min. The respiration rate for each sample was calculated using the CO_2 concentration, the air flow rate and the exact amount of soil in each pipe. SIR was assayed within 2 h after the glucose addition. During the initial 4 h period after glucose addition no microbial growth was observed and the rate of SIR remained nearly constant (Lin and Brookes, 1999). Care was exercised to ensure even distribution of glucose and deionized water without saturating the soil with liquid, which would restrict CO_2 evolution from the samples.

Microbial biomass C (MBC) was measured using the chloroform fumigation extraction method (Vance et al., 1987) at 8, 14, 28, 45, 60, 90, 128, 158, 202, 240, 263, 330, 410, 480, 550, 630, 670, 702 and 815 days. Briefly, paired 40 g soil samples were either extracted with 80 mL 0.05 M K_2SO_4 or fumigated with chloroform for 24 h in the dark and then extracted in the same way. The extract was analyzed for total organic C using multi N/C® 2000 TOC analyzer (Analytik Jena, Germany). MBC was calculated from the difference of K_2SO_4-extractable C between the fumigated and the non-fumigated soil samples using a k_{EC} factor of 0.38 (Xiao et al., 2015). Microbial metabolic quotient (qCO_2) was calculated as the soil microbial respiration rate per unit MBC (mg CO_2-C g^{-1} MBC d^{-1}) (Pirt, 1975).

Soil mineral N (NH_4^+ plus NO_3^-) was determined by extracting 20 g of fresh soil with 40 mL 2 M KCl solution (Lu et al., 2018) after 28, 45, 60, 90, 128, 158, 202, 240, 263, 330, 410, 480, 550, 630, 670 and 815 days. Samples were shaken for 1 h at 200 rpm, the mixture was filtered through filter paper, and extracts were frozen until analysis. The concentration of NH_4^+ and NO_3^- was measured using a Continuous Flow Analyzer (AA3, Bran+Luebbe, Germany). The cumulative amount of N mineralized was calculated from the changes in mineral N pool size (NH_4^+-N and NO_3^--N) over the course of the incubation period (815-day incubation) in mg g^{-1} TN (Smolander and Kitunen, 2002; Tian et al., 2017; Henneron et al., 2020). Net rates of soil N mineralization were calculated from the changes in mineral N pool size during the incubation divided by the incubation days (Henneron et al., 2020; Song et al., 2011). Soil moisture was measured by oven-drying soil at 105 °C for 24 h.

2.5. Calculations and statistical analysis

The soil respiration data was used for inverse modeling of C pools. The cumulative respired C of each soil sample was fitted individually to the first-order three-pool kinetic model (Collins et al., 2000; Knorr et al., 2005; Paul et al., 2001b):

$$C_{cum}(t) = 1 - a0 \times e^{-k1 \times t} - b0 \times e^{-k2 \times t} - c0 \times e^{-k3 \times t} \quad (1)$$

where $C_{cum}(t)$ is the cumulative amount of C-CO_2 released at time t, which is expressed as a portion (%) of SOC; a0, b0, and c0 are the respective portions of the labile, intermediate and stable C pools in SOC ($a0 + b0 + c0 = 1$); and k_1, k_2, and k_3 (day^{-1}) are the respective decomposition rates for the labile, intermediate and stable SOC pools (Tian et al., 2016). Radiocarbon dating of non-hydrolysable carbon indicated that the residence time of this recalcitrant fraction was about thousand years (Paul et al., 2001a). Statistical analysis also indicated that when k_3 was very small ($<5 \times 10^{-5}$), there was little effect on the first-order three-pool kinetic model (Paul et al., 2001b). To obtain a valid convergence fitting value, we assumed that the residence time of stable carbon pool in the field was on the order of one thousand years, and that k_3 was calculated according the temperature difference between the mean annual temperature (MAT) and our incubation temperature (Collins et al., 2000; Tian et al., 2016). We forced the following constraints: that (a) k_1 was larger than k_2, and (b) that k_1 was larger than 0 (Rey and Jarvis, 2006).

Using the basal respiration rate and the substrate-induced-respiration rate (soil respiration rate in Gl+ treatment), the C availability index (CAI) was calculated as:

$$CAI = R_{Gl-}/R_{Gl+} \quad (2)$$

where R_{Gl-} and R_{Gl+} are the respiration rates in Gl− and Gl+ treatments, respectively (Gershenson et al., 2009; Pang et al., 2015). The R_{Gl-} and R_{Gl+} were calculated using the following formula:

$$Rr = 0.536 \times (C_c \times R_f)/W_s \quad (3)$$

where Rr is soil respiration rate (μg C g^{-1} dry soil h^{-1}) measured using Li-COR 6262 Infrared Gas Analyzer, C_c is the recorded CO_2 concentration (μmol CO_2 mol^{-1}), R_f is the recorded flow rate (mL h^{-1}), and W_s is gram dry weight of the sample.

We used repeated measures ANOVA to test for main effects of temperature (2 levels: 10 °C and 20 °C) and substrate addition (2 levels: control and substrate added), and their interaction on soil C mineralization rate of each land-use type. We used three-way ANOVA to assess the effects of land-use type (old field and bare fallow treatments), temperature (10 and 20 °C), substrate addition and their interaction on cumulative C mineralization, cumulative net N mineralization and the ratio of cumulative mineralized C and N. We also used the Tukey HSD test to assess difference of treatments. We used three-way ANOVA to test the significant effects of land-use type, temperature, sampling date and their interactions on C availability (CAI), mineral N, MBC and microbial metabolic quotient (qCO_2) in control soil. We also used three-way ANOVA to test the significant effects of temperature, substrate addition, sampling date and their interactions on C availability (CAI), mineral N, MBC and microbial metabolic quotient (qCO_2) in each land-use type. Regression analysis was used to analyze the relationships between C mineralization and net N mineralization. We also used non-linear curve fit to find the lowest C mineralization rate based on the net N mineralization rate.

We used one-way ANOVA with a post hoc Tukey HSD test to assess the effects of land-use type, temperature and substrate addition on C decay coefficients (a0, b0, c0, k_1 and k_2). Statistical analyses were performed using SPSS Statistics 20 (SPSS, Inc., Chicago, USA). Differences were considered significant when $p < 0.05$.

3. Results

3.1. Soil C mineralization

In general, soil C mineralization rate from all treatments rapidly declined over time during the early-stage of incubation, and tended to stabilize afterwards (Fig. 1). Soil C mineralization increased with warming and residue addition and fitted three-pool model very well (Table 3). The labile and intermediate C pools in SOC extended for 30 and 518 days on average, while the stable C pools extended for 630 years on average. Though a0 had no significant difference between land-use types and incubation temperatures, k_1 in amended bare fallow soil was increased by warming. Moreover, a0 was increased by substrate addition in both the bare fallow soil and the old filed soil, while k_1 was increased by substrate addition only in the bare fallow soil. Cumulative C mineralization was significantly affected by land-use type, incubation temperature and substrate addition (Table 4). Specifically, the cumulative C mineralization was enhanced by experimental warming ($p < 0.001$) and maize straw addition ($p < 0.001$). The increase of cumulative C mineralization by straw addition was higher in the bare fallow soil (310% and 199% at 10 and 20 °C, respectively) than in the old filed soil (268% and 160% at 10 and 20 °C, respectively). Moreover, under the interaction of warming and substrate addition, the cumulative mineralized C in the old field soil and the bare fallow soil increased by 420% and 450%, respectively (Table 4).

3.2. Soil net N mineralization

Soil net N mineralization from all treatments was pulse-dynamic (Fig. 2). In the control soil from old field and bare fallow plots, the peak values of net N mineralization were observed at day-45 or 60 and day-330 under lower temperature, while the peak values were observed at day-45 or 60 and day-263 under higher temperature. In the control soil, the peak values at these specific sampling times were higher in the old field than in the bare fallow at both low and high temperatures. In addition, experimental warming significantly enhanced the peak values of net N mineralization rate, but the increase occurred transiently. During the initial stage of incubation, maize straw addition decreased net N mineralization except for old field at 20 °C. After then, maize straw addition increased net N mineralization depending on land-use type and incubation temperature (Fig. 2). In general, for both land-use types, the increase of net N mineralization by maize straw addition at 10 °C (ca 410 days) lagged behind that at 20 °C (ca 158–202 days). The cumulative N mineralized was significantly affected by land-use type, incubation temperature and straw addition ($p < 0.001$, Table 4). For the old field soil, straw addition increased the cumulative N mineralization by 61% and 33% at 10 and 20 °C, respectively. While for the bare fallow soil, straw addition increased the cumulative N mineralization by 155% and 200% at 10 and 20 °C, respectively.

3.3. Correlations between soil C and net N mineralization

In the non-amended control treatment, soil C and net N mineralization were positively correlated in the old field soil at 20 °C ($p = 0.044$), where the amount of mineralized C per unit mineralized N was 0.28 (Fig. 3, through linearly fitting the data of soil C and net N mineralization rates). However, there was no significant correlation between soil C and net N mineralization in the bare fallow soil. Maize straw addition changed the relationships between soil C and net N mineralization in both old field soil and bare fallow soil (Fig. 3). For both land-use types at 10 °C, soil C mineralization showed a negative linear correlation with net N mineralization (NNM). However, at 20 °C, soil C mineralization showed a non-linear relationship with the minimum at NNM = 162 μg N g^{-1} TN d^{-1} (for old field) or 159 μg N g^{-1} TN d^{-1} (for bare fallow). Thus NNM = 162 (or 159) was the threshold where soil C–net N mineralization interactions diverged in maize straw amended soil. When NNM was <162 (or 159) μg N g^{-1} TN d^{-1}, soil C mineralization was negatively correlated with net N mineralization. While NNM was >162 (or 159) μg N g^{-1} TN d^{-1}, soil C mineralization was positively correlated with net N mineralization (Fig. 3).

3.4. The dynamics of C availability and mineral N

In the non-amended control treatment, mineral N content was lower in the bare fallow soil than in the old field soil, but C availability (CAI) was higher in the bare fallow soil than in the old field soil (Fig. 4; $p < 0.001$, Table S1). Both CAI and mineral N content were significantly affected by incubation temperature, straw addition and sampling date ($p < 0.001$, Table 5). In general, CAI was highly variable in all soil treatments (Fig. 4a,b). CAI firstly increased during the initial 45–60 days of incubation and then sharply decreased from day 60 to 158, but increased again from day 158 to 480. It was initially higher in the maize straw-amended treatment (before day-330 at 10 °C and day-240 at 20 °C), but ended being lower in the maize straw-amended treatment than in the non-amended control (significant substrate addition × date interaction, $p < 0.001$). In addition, in all soil treatments, CAI was decreased by experimental warming.

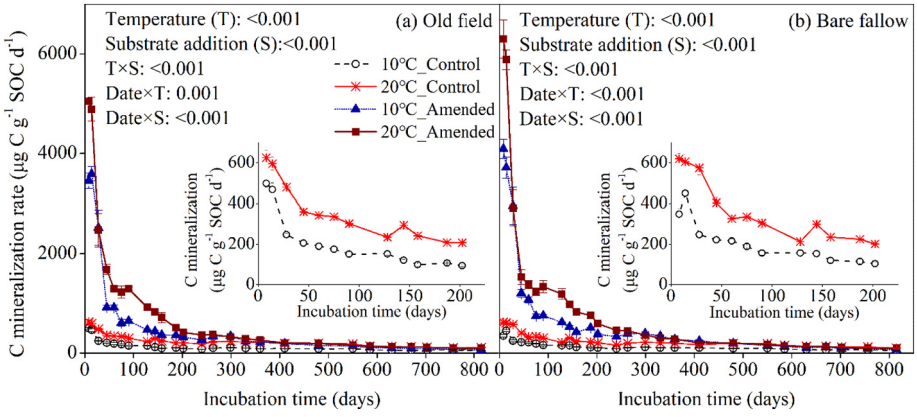

Fig. 1. Dynamics of C mineralization rate in non-amended control and maize straw-amended treatments of old field soil and bare fallow soil at 10 and 20 °C. The inserts show the dynamics of C mineralization rate in the non-amended control treatment over the initial 200 days.

Table 3
Coefficients obtained from fitting the cumulative carbon mineralization data, $C_{cum}(t) = 1 - a0 \times e^{-k1 \times t} - b0 \times e^{-k2 \times t} - c0 \times e^{-k3 \times t}$, where $C_{cum}(t)$ is the cumulative amount of C-CO_2 released at time t, which is expressed as a portion (%) of SOC; a0, b0, and c0 are the respective portions of the labile, intermediate and stable C pools in SOC (a0 + b0 + c0 = 1); and k_1, k_2, and k_3 (day^{-1}) are the respective decomposition rates for the labile, intermediate and stable SOC pools (Tian et al., 2016). Different letters represent a significant difference among treatments ($P < 0.05$). We assumed recalcitrant C residence time was 1000 years, and k_3 was calculated according to the temperature difference between MAT and incubation temperature (Collins et al., 2000). The R^2 of the nonlinear regressions all reached 0.999.

Treatment	Temperature (°C)	a0	b0	c0	k_1 ($day^{-1} \times 10^{-2}$)	k_2 ($day^{-1} \times 10^{-3}$)	k_3 ($day^{-1} \times 10^{-5}$)	*p*
Old field (control)	10	1.3 ± 0.0 a	7.1 ± 0.4 a	91.6 ± 0.4 e	3.2 ± 0.2 abc	1.5 ± 0.1 a	0.326	<0.001
	20	1.3 ± 0.0 a	17.1 ± 0.5 a	81.6 ± 0.5 d	3.6 ± 0.1 bc	1.4 ± 0.0 a	0.652	<0.001
Old field (amended)	10	11.6 ± 0.9 b	20.2 ± 0.7 b	68.2 ± 0.8 c	3.7 ± 0.3 c	3.0 ± 0.0 b	0.326	<0.001
	20	14.3 ± 2.1 b	27.4 ± 1.7 b	58.3 ± 0.6 b	3.5 ± 0.5 abc	4.5 ± 0.3 c	0.652	<0.001
Bare fallow (control)	10	1.2 ± 0.1 a	8.8 ± 0.4 b	90.1 ± 0.3 e	2.5 ± 0.1 a	1.3 ± 0.1 a	0.326	<0.001
	20	1.9 ± 0.0 a	18.8 ± 0.3 c	79.3 ± 0.3 d	2.6 ± 0.2 ab	1.1 ± 0.0 a	0.652	<0.001
Bare fallow (amended)	10	13.0 ± 0.7 b	25.6 ± 0.6 c	61.4 ± 0.6 b	3.6 ± 0.1 bc	3.0 ± 0.0 b	0.326	<0.001
	20	12.6 ± 0.6 b	35.4 ± 1.1 d	52.0 ± 1.6 a	5.2 ± 0.2 d	5.2 ± 0.1 d	0.652	<0.001

In general, soil mineral N gradually increased over time in all soil treatments (Fig. 4c,d). Soil mineral N was initially lower in the maize straw-amended treatment (before day-330 at 10 °C and day-202 at 20 °C), but ended being higher in the maize straw-amended treatment than in the non-amended control (significant substrate addition × date interaction, $p < 0.001$). In contrast to C availability, mineral N was increased by experimental warming in all soil treatments.

3.5. Microbial biomass C and microbial metabolic quotient

Microbial biomass C (MBC) was pulse-dynamic and showed a similar pattern of variation between the bare fallow soil and the old field soil in the non-amended control treatment (Fig. 5). Moreover, for non-amended control treatment, MBC was lower in the bare fallow soil than in the old field soil at both temperatures (10 and 20 °C) (Fig. 5; $p < 0.001$, Table S1). Furthermore, both MBC and qCO_2 were significantly affected by incubation temperature, straw addition and sampling date ($p < 0.001$, Table 5). In both land-use types, MBC was increased by maize straw addition and its dynamic changes showed two distinct patterns during the incubation time (Fig. 5a,b).

Soil qCO_2 was calculated when MBC gradually stabilized (after 45 days of incubation). Soil qCO_2 decreased rapidly during the initial 202 days of incubation, and then gradually stabilized to the end. Maize straw addition significantly increased qCO_2 in both land-use types (Fig. 5c,d). In all soil treatments, qCO_2 was increased by experimental warming.

4. Discussion

4.1. Effect of long-term deprivation of plant inputs on C and net N mineralization

In our study, we found that the long-term bare fallow treatment did not decrease the cumulative C mineralization (per unit SOC) in non-amended control soil (Table 4), suggesting that soil C decomposability was not decreased after long-term deprivation of plant inputs. Our result was in accordance with the finding by Salomé et al. (2010). The constancy in soil texture and the similarity in soil pH and microbial community structure (Fungal/bacterial biomass ratio) (Table 1 & Table 2) likely caused the observed similarity in SOC mineralization rates (Table 4) between the bare fallow soil and the old field soil (Garcia-Pausas and Paterson, 2011; Jackson et al., 2017; Schmidt et al., 2011; Sollins et al., 1996). In contrast to soil C mineralization, soil net N mineralization (per unit total N) decreased after long-term bare fallow treatment (Fig. 2). The positive net N mineralization and the high level of mineral N content in the old field soil suggested that the available N in the soil exceeded the amount required by microorganisms. Instead, the low level of net N mineralization and mineral N content in the bare fallow soil indicated that the microbial communities may be more deficient in N than in the old field soil.

In the old field soil, a positive correlation between soil C mineralization and net N mineralization was observed at 20 °C, but there was no such relationship at 10 °C (Fig. 3). According to Tian et al. (2017), the lack of energy and biodegradable organic N on net N mineralization would be alleviated under warming conditions. Thus, the distinct

Table 4
Cumulative C and net N mineralization in non-amended control and maize straw-amended treatments of old field soil and bare fallow soil after 815 days of incubation.

Treatment	Temperature (°C)	Cumulative C mineralization (mg g^{-1} SOC)	Cumulative net N mineralization (mg g^{-1} TN)	Cumulative mineralization of C/N
Old field (control)	10	86.07 ± 1.47 a	36.62 ± 0.95 bc	28.5 ± 0.5 a
	20	170.58 ± 2.57 b	77.60 ± 2.65 e	26.6 ± 0.4 a
Old field (amended)	10	316.83 ± 7.34 c	59.03 ± 1.61 d	82.3 ± 1.9 c
	20	444.25 ± 4.38 e	103.03 ± 1.34 f	66.1 ± 0.7 b
Bare fallow (control)	10	92.18 ± 2 0.10 a	16.35 ± 0.52 a	68.6 ± 1.6 b
	20	170.13 ± 2.83 b	33.05 ± 0.97 b	62.6 ± 1.0 b
Bare fallow (amended)	10	377.66 ± 5.09 d	41.77 ± 1.88 c	149.3 ± 2.0 d
	20	508.05 ± 16.15 f	99.31 ± 1.35 f	84.5 ± 2.7 c
ANOVA (*p*-values)				
Land use (L)		<0.001	<0.001	<0.001
Temperature (T)		<0.001	<0.001	<0.001
Substrate addition (S)		<0.001	<0.001	<0.001
L × T		0.856	0.025	<0.001
L × S		<0.001	<0.001	0.046
T × S		<0.001	<0.001	<0.001
L × T × S		0.630	<0.001	<0.001

Results are means ($n = 4$ of cumulative C mineralization and n = 3 of cumulative N mineralization) ± standard errors. Different letters represent a significant difference among treatments ($P < 0.05$).

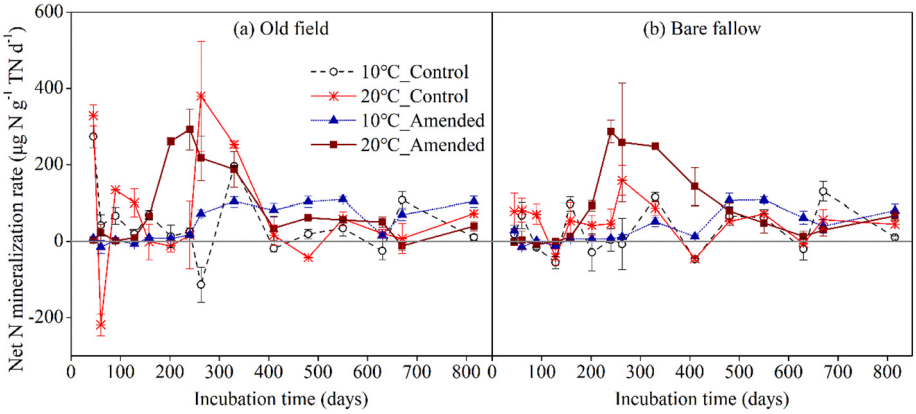

Fig. 2. Dynamics of net N mineralization rate in non-amended control and maize straw-amended treatments of old field soil and bare fallow soil at 10 and 20 °C.

relationships between soil C and net N mineralization at 10 and 20 °C may be related to the difference in available energy and biodegradable organic N at different temperatures. In the bare fallow soil, soil C and net N mineralization were decoupled at both 10 and 20 °C (Fig. 3). Here, the low net N mineralization and the decoupling between soil C and net N mineralization in the bare fallow soil could not be explained by the theory of ecological stoichiometry given the constant soil C/N ratio after long-term bare fallow treatment (Wild et al., 2015). Possibly, there are some other factors that affect the balance between soil N availability and microbial N demand in the bare fallow soil and consequently cause the decoupling between soil C and net N mineralization.

First, the long-term deprivation of plant inputs to soil resulted in a decline in organic matter and microbial biomass contents as well as the proportional abundance of Gram-negative bacteria relative to the old field soil (Tables 1 & 2), likely reflecting decreases of the quantity and quality of substrates available to microbial communities in the bare fallow soil (Paterson et al., 2011). However, the dynamics of CAI indicated that the C availability was not reduced in the bare fallow soil (Fig. 4; Table S1). The lability of SOC in the bare fallow soil was also evident from its similar content of labile organic C fraction as in the old field soil (Table 3). These results rejected our first hypothesis that the long-term exclusion of fresh plant inputs would decrease C availability in the bare fallow soil. Although we did not observe C or energy limitation for microorganisms in the bare fallow soil, the long-term exclusion of plant inputs may affect the structure of microbial communities and their functional diversity (Nunan et al., 2015). Paterson et al. (2011) demonstrated that long-term deprivation of plant inputs to soil diminished the capacity of microbial communities to degrade some certain compounds because of the change of SOM composition, which suggested that C and N fluxes are not directly linked through their gross stoichiometry in SOM. This is due to the heterogeneity and overall passiveness of SOM relative to the dynamic nature of mineralization fluxes and source pools (Murphy et al., 2015). Indeed, the transformation of organic N to mineral form and subsequent mineralization or immobilization of N are also dependent on the composition of SOM (Tiessen et al., 1994). Therefore, the change of microbial community functioning due to long-term deprivation of plant inputs may affect the balance between soil C and N availability as well as between

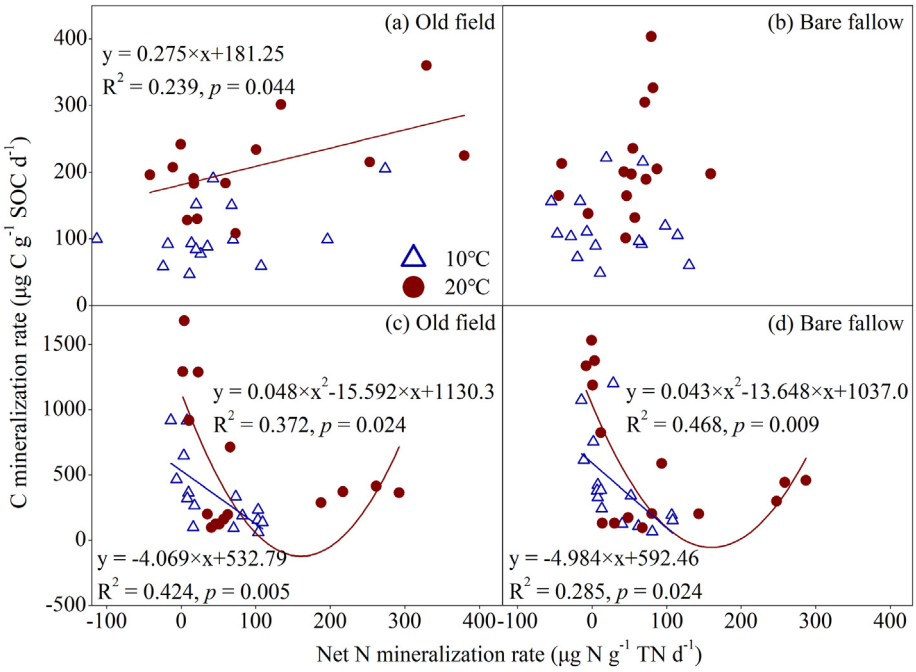

Fig. 3. Correlation between C mineralization rate and net N mineralization rate in non-amended control (a & b) and maize straw-amended (c and d) treatments of old field soil and bare fallow soil at 10 and 20 °C.

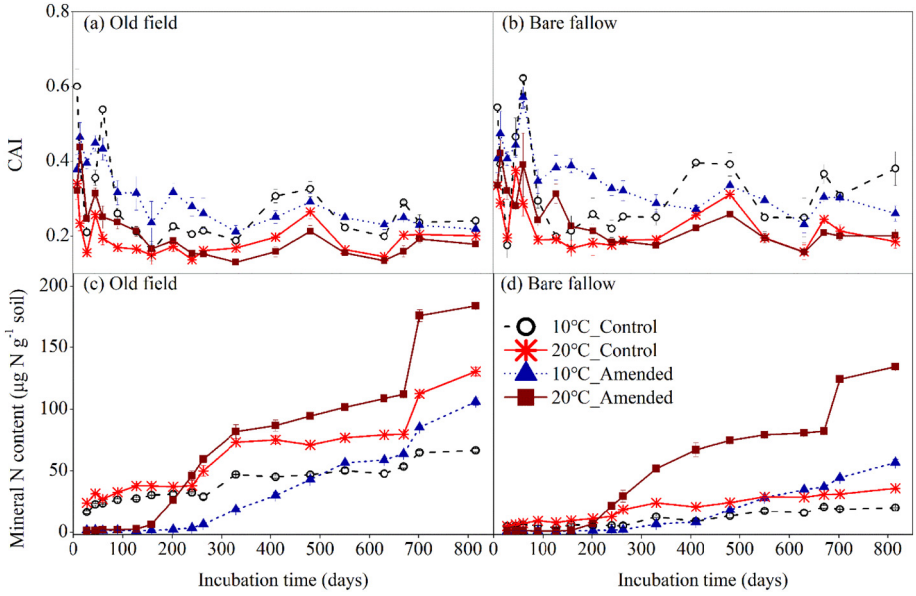

Fig. 4. Dynamics of carbon availability (Carbon Availability Index, CAI) and mineral N (NO_3^--N plus NH_4^+-N) in non-amended control and maize straw-amended treatments of old field soil and bare fallow soil at 10 and 20 °C.

microbial C and N demand, which then limits net N mineralization in the bare fallow soil.

Second, the linkage between soil C mineralization and net N mineralization may be decoupled due to the feedback of N limitation on organic C decomposition in the long-term bare fallow treated soil (Manzoni and Porporato, 2007). N limitation often occurs when the substrate is N-poor, and a large fraction of the microbial community cannot meet their N demand through organic N assimilation (Schimel and Bennett, 2004). Our result showed that the ratio of the cumulative mineralized C/N in the bare fallow soil was 2.4-fold of that in the old field soil (Table 4), which partially reflected the N limitation during SOM decomposition (Mooshammer et al., 2014). Plant litter inputs constitute the main source of organic N to decomposers that in turn produces inorganic N, and control the long-term soil N availability (Manzoni and Porporato, 2007; Parolari and Porporato, 2016). The bare fallow soil in our study had been excluded of fresh plant inputs for 23 years. This was very different from the old field conditions where plant residues and root exudates could provide a continuous source of active N to sustain microbial growth and stimulate mineralization process (Murphy et al., 2003). In some cases, however, plant inputs could also decrease soil N content through priming effect, which usually occurs in soil with low N availability (Wang et al., 2021b). In this study, we found high level of net N mineralization and mineral N content in the old field soil (Fig. 2 and Fig. 4), which indicated that continuous plant inputs did not lead to N limitation for microorganisms in the old filed soil. The significant decrease of the proportion of mineral N in total soil N in the bare fallow soil is caused by a decrease of N mineralization, an increase of N immobilization by microbial community, or the combination of both (Manzoni and Porporato, 2007). Some previous studies demonstrated that reduction of plant residue inputs limited net N mineralization (Khalili and Nourbakhsh, 2012; Tian et al., 2017), and this limitation would be alleviated by available N addition (Tian et al., 2017; Wild et al., 2014).

Table 5
ANOVA table of the effects of temperature (10 °C vs. 20 °C), substrate addition (non-amended control vs. maize-straw amended), sampling date and their interactions on C availability (CAI), mineral N, microbial biomass C (MBC) and microbial metabolic quotient (qCO_2) in each land use.

Source	CAI			Mineral N			MBC			qCO_2		
	df	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
Old field												
Temperature (T)	1	383.3	<0.001	1	3790.6	<0.001	1	178.4	<0.001	1	1870.1	<0.001
Substrate addition (S)	1	16.3	<0.001	1	44.2	<0.001	1	3082.3	<0.001	1	65.8	<0.001
Date (D)	18	50.2	<0.001	16	1342.2	<0.001	18	20.3	<0.001	15	428.6	<0.001
T × S	1	0.2	0.691	1	268.2	<0.001	1	95.3	<0.001	1	0.0	0.924
T × D	18	6.3	<0.001	16	140.5	<0.001	18	2.9	<0.001	15	101.7	<0.001
S × D	18	10.3	<0.001	16	171.6	<0.001	18	15.1	<0.001	15	40.0	<0.001
T × S × D	18	4.1	<0.001	16	22.5	<0.001	18	2.6	0.001	15	15.6	<0.001
Error	152			136			152			192		
Bare fallow												
Temperature (T)	1	376.6	<0.001	1	3247.7	<0.001	1	167.2	<0.001	1	823.9	<0.001
Substrate addition (S)	1	15.8	<0.001	1	2036.3	<0.001	1	3207.4	<0.001	1	354.4	<0.001
Date (D)	18	36.0	<0.001	16	813.9	<0.001	18	30.5	<0.001	15	225.5	<0.001
T × S	1	0.6	0.451	1	1075.7	<0.001	1	115.0	<0.001	1	58.6	<0.001
T × D	18	5.4	<0.001	16	145.9	<0.001	18	4.1	<0.001	15	27.2	<0.001
S × D	18	10.8	<0.001	16	294.4	<0.001	18	23.7	<0.001	15	37.0	<0.001
T × S × D	18	2.8	<0.001	16	78.6	<0.001	18	3.4	<0.001	15	12.9	<0.001
Error	152			136			152			192		

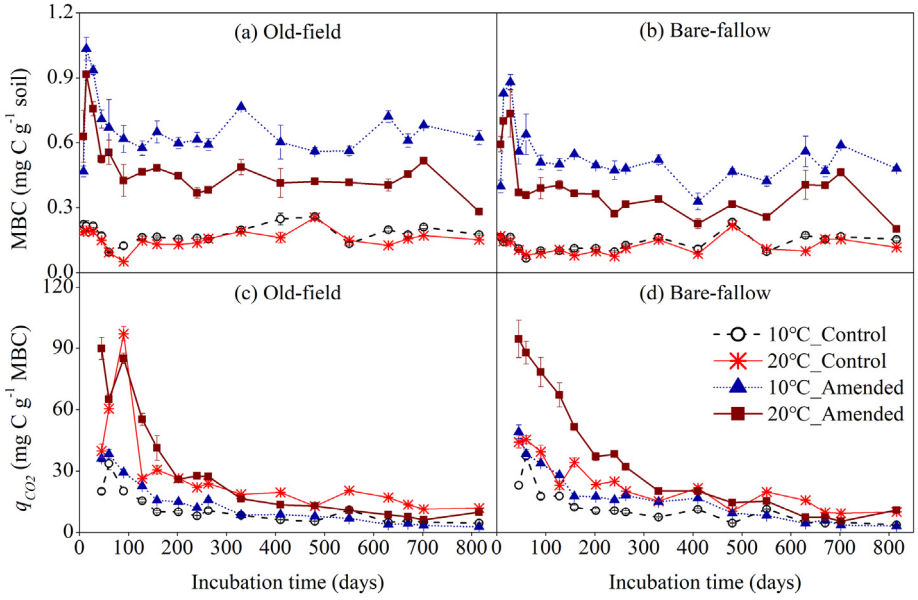

Fig. 5. Dynamics of microbial biomass C (MBC) and microbial metabolic quotient (qCO_2) in non-amended control and maize straw-amended treatments of old field soil and bare fallow soil at 10 and 20 °C.

4.2. Effects of temperature and external substrate addition on soil C and net N mineralization

Both soil C mineralization and net N mineralization were sensitive to elevated temperature. The elevated temperature increased the rate of soil C mineralization and the amount of cumulative C mineralized during the 815-day incubation in both land-use types. Our results agree with most previous studies that elevated temperature stimulates soil C mineralization (Bond-Lamberty and Thomson, 2010; Karhu et al., 2014). Temperature increase also promoted net N mineralization, and this temperature effect has been proposed to be associated with the proportionally larger increase in gross N mineralization than in microbial N immobilization (Hoyle et al., 2006). This is because the increase of microbial activity and the shift of microbial community composition at elevated temperature would stimulate the release of active N from gross N mineralization (Hoyle et al., 2006). In contrast, the rapid assimilation of labile C and the decline of MBC at elevated temperature probably constrain microbial N immobilization (Cookson et al., 2007; Tian et al., 2017). In addition, the elevated temperature would alleviate the limitation of biodegradable organic N on net N mineralization (Cookson et al., 2007). However, this alleviation cannot compensate the lack of active N source in the bare fallow soil. Despite a significant increase of net N mineralization at elevated temperature, net N mineralization was still decoupled with soil C mineralization in the bare fallow soil at elevated temperature.

Maize straw addition significantly increased total organic C mineralization. This increase was likely caused by the rapid utilization of the labile fraction of maize straw due to the vulnerability of plant-derived C to microbial mineralization (Songa et al., 2018; Zhu et al., 2016). The mineralization of labile C during the initial stage after maize straw addition resulted in a decline of net N mineralization compared with the control soil. Similar results has been reported in previous studies (Hoyle et al., 2006; Schaeffer and Evans, 2005). Typically, the addition of labile substrates to soil did not affect gross N mineralization, but markedly increased microbial N immobilization (Schaeffer and Evans, 2005). Therefore, microbial N immobilization gained a larger increment than gross N mineralization, which then caused a decrease of net N mineralization. Microbial N immobilization can be supported by the rapid increase of microbial biomass in the maize straw-amended soil. This transformation may stem from the fact that microbial production of extracellular enzymes during C mineralization would consume much energy and require much N (Lu et al., 2018; Mooshammer et al., 2014), which in consequence constrained the allocation of N to mineralization. When NNM was <162 or 159 μg N g^{-1} TN d^{-1}, soil C mineralization was negatively related to net N mineralization due to an increase of microbial N demand during plant litter mineralization. Our result supports the positive relationship between soil C mineralization and microbial N immobilization during the mineralization of labile substrates.

After the initial dynamic changes following maize straw addition, MBC is stabilized at a relatively low level compared to the initial stage. It is likely that the C (and N) assimilated into microbial biomass during the initial stage gets mineralized during this stage due to the die-out of microorganisms after the initial pulse of growth induced by maize straw addition (Shahbaz et al., 2017). Meanwhile, we observed a positive correlation between soil C mineralization and net N mineralization (when NNM was >162 or 159 μg N g^{-1} TN d^{-1}) in the middle of the incubation (from day-202 to day-330). Moreover, it was also the period when the maximum positive priming effect was observed (Zhang et al., 2017). This positive correlation between soil C and net N mineralization is in accordance with the previous hypothesis that when N mineralization dominates, labile substrate inputs enhance the mineralization of SOM (Lu et al., 2018). Our observation supports the "microbial N mining" hypothesis, which postulates that under N-limitation, microbes use labile-C to catalyze the decomposition of SOM to access the N it contains. Previous studies of long-term bare fallow soils indicated that while microbial activity decrease as available resources are exhausted, that microbial potential remains and can be activated by addition of available substrates (Guenet et al., 2012). But to my knowledge, these studies have not measured microbial activity for such a long period. Our result indicated that the priming effect on native SOM decomposition may be one of the main drivers of a positive relationship between soil C and net N mineralization. Furthermore, maize straw application compensates the loss of active N source during the long-term bare fallow treatment, which in consequence satisfies microbial N demand and stimulates net N mineralization in the bare fallow soil. The positive correlation between soil C mineralization and net N mineralization indicated a shift from N limitation to available C demand during this period.

5. Conclusions

Soil C availability and basal C mineralization rate were similar between the bare fallow soil and the old field soil, while the proportion

of mineral N in total N and basal net N mineralization rate were lower in the bare fallow soil than in the old field soil. This finding supports the hypothesis that long-term deprivation of plant inputs hindered soil net N mineralization due to microbial N limitation. Further, external fresh plant inputs (maize straw) significantly increased net N mineralization in the bare fallow soil, which produced similar rate of net N mineralization as in the old field soil with maize straw addition. These observations highlight the importance of plant-derived organic inputs in mediating soil net N mineralization and its relationship with soil C mineralization. Moreover, experimental warming increased microbial activity, C and net N mineralization rates in both land-use types, but did not alter the decoupling between C mineralization and net N mineralization in the bare fallow soil. This finding suggests that elevated temperature alone did not eliminate the N limitation caused by plant inputs exclusion. Overall, this study suggests that plant inputs play a pivotal role in mediating the relationships between soil C and net N mineralization. The impacts of plant inputs on the dynamics of soil C and N should merit more attention in future experimental and modeling studies of SOM decomposition.

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CRediT authorship contribution statement

Xiuwei Zhang: Data curation, Investigation, Writing – original draft. **Biao Zhu:** Writing – review & editing. **Feihai Yu:** Writing – review & editing. **Weixin Cheng:** Conceptualization, Methodology.

Declaration of competing interest

The authors declare no competing financial interests.

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