Long-term continuous farmyard manure application increases soil carbon when combined with mineral fertilizers due to lower priming effects

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ABSTRACT

Organic and synthetic fertilizers not only increase soil fertility and crop productivity but also enhance soil organic carbon (SOC). However, the priming effect (PE) leads to increased soil carbon (C) loss through native SOC mineralization. To date, the mechanisms by which long-term (>66 years) synthetic and/or organic fertilization alters net SOC sequestration remain a matter of debate. This study aimed to assess the effects of different fertilization practices on SOC decomposition and PE in agricultural systems subjected to long-term annual synthetic and/or organic fertilizer application. This aim was achieved by collecting topsoil samples (0–20 cm) from four long-term fertilization practices, i.e., unfertilized, synthetic supplemental (+s), cattle farmyard manure (+m, similar nutrient amount to +s), and synthetic fertilizer with farmyard manure (+s +m, the highest nutrient amount). The soil samples were incubated for 33 days with and without ^{13}C-glucose addition, and a CO_2 isotope analyzer combined with a modeling approach was used to establish a real-time method to monitor CO_2 and $^{13}CO_2$ production rates during the incubation period. Overall, +m increased the cumulative SOC-derived CO_2 (SOC-CO_2) by 107, 74, and 24 % compared to the unfertilized, +s and +s +m, respectively. The higher SOC-CO_2 in +m treatment was associated with the greatest priming effect (PE, 390 ± 21 mg C kg soil^{-1}), which corresponded to a 30 % increase compared to the average of the treatments that involved synthetic fertilizer (+s and +s +m) and a 137 % increase compared to the unfertilized control. The results were explained by the lower dissolved nitrogen (N), a proxy of available mineral N, in +m compared to +s +m, thus enhancing microbial mining for additional N via increasing SOC mineralization. However, the combined application of synthetic fertilizer and manure in the +s +m treatment provided enough easily accessible nutrients for microbial growth and activities from the applied synthetic fertilizer, leading to lower SOC mineralization than manure (+m) alone. Nevertheless, the treatments with manure application (i.e., +m and +s +m) significantly increased net SOC compared to the synthetically fertilized treatment and unfertilized control, suggesting greater C inputs than outputs and leading to high SOC accumulation over time. These results indicated that organic manure has a great potential to mitigate climate change by increasing SOC over time, which can be fostered by the addition of synthetic fertilizer; however, caution still needs to be taken regarding the quality and quantity of the added fertilizer.

1. Introduction

Soil organic matter (SOM) is a primary component of soil quality, agricultural sustainability, and environmental conservation (Carter, 2002; Fageria, 2012; Navarro-Pedreño et al., 2021; Page et al., 2020). From an agricultural perspective, applying organic manure to soils has long been promoted as an efficient practice for improving soil health by increasing SOM. In a global meta-analysis study, O'Brien and Hatfield (2019) reported an increase of 17 % in SOM under organic manure application compared to synthetic fertilizer. In another meta-analysis, Chen et al. (2018) reported an increase from 23 % to 49 % of soil carbon (C) after long-term (≥10 years) organic amendments application.

Liu et al. (2020) reported an increase (of 27 %) not only in the stable soil organic C (SOC), but also in the C pools with fast turnover reflecting the acceleration of C and nitrogen (N) cycles following manure application.

Similarly, from an environmental perspective, the application of organic manure can be considered an effective tool to reduce the threat of climate change by enhancing SOC sequestration in which atmospheric CO_2 is stored within the soil matrix (O'Brien and Hatfield, 2019; Reeves, 1997; Scialabba and Müller-Lindenlauf, 2010). Despite this expectation, as SOM increases with organic manure application, it may accelerate native SOM mineralization, reducing SOC stocks (Fontaine et al., 2004; Jenkinson et al., 1985; Shahbaz et al., 2017). The priming effect (PE) is frequently mentioned as a mechanistic explanation for such negative effects of manure applications. The PE refers to a sequence of processes that boost respiratory activity and microbial decomposition of the native SOC due to the supply of readily available organic substances (Blagodatskaya and Kuzyakov, 2011; Kuzyakov, 2010). The incorporation of organic materials from manure into the soil may stimulate microbial activity and extracellular enzyme synthesis to mine SOM for access to the microbes' required nutrients, notably N, resulting in the acceleration of SOM mineralization (known as positive PE) (Chen et al., 2014; Fontaine et al., 2011). If the SOM mineralization rates exceed the accumulation rate of SOC due to manure application, it may yield negligible SOC gains or even a loss in soil SOC stocks (Balota et al., 2010; Schmatz et al., 2017; Shahbaz et al., 2018). Conversely, the application of organic manure can reduce SOM mineralization (known as negative PE), since microorganisms preferentially utilize the abundant source of available C and nutrients from organic manure (Chowdhury et al., 2014; Zimmerman et al., 2011).

The above-mentioned mechanistic considerations suggest that the final net SOC balance between C inputs and outputs via mineralization determines the potential of organic manure application for soil C sequestration (Fontaine et al., 2003; Jacobs et al., 2020). Therefore, SOM mineralization and manure C inputs should be considered simultaneously to evaluate C sequestration resulting from farmyard manure application. However, despite the intensive research on the response of SOC dynamics to long-term organic manure and synthetic fertilizer application, the underlying mechanisms by which C is sequestrated in soil still need further investigation (Shahbaz et al., 2017; Su et al., 2006; Wu, 2019).

SOM mineralization is controlled by soil type, climatic conditions, and the amount and type of fertilizer (Dungait et al., 2012; Huang et al., 2014; Zhou et al., 2016). Long-term fertilization changes soil nutrient levels and alters the soil physiochemical properties, and microbial community and activities (Gautam et al., 2020; Su et al., 2006; Wu, 2019). For instance, nutrient status affects SOM mineralization by altering microbial composition and microbes' associated activities (Mohanty et al., 2013; Nett et al., 2010). Moreover, organic and/or mineral fertilizer applications can increase C and nutrient availability and consequently alter the stoichiometry of microbial substrates, such as the C:N ratio of the dissolved organic matter pool. This stoichiometric imbalance between microbial biomass and its substrate may control microbial processes of C and N cycling. Therefore, the interactive effects of soil C and nutrient availability, microbial community, and microbial activity regulate the C sequestration response to organic manure addition into soils (Dong et al., 2014; Ma et al., 2020; Tong et al., 2020).

Several previous studies investigated the independent effect of synthetic or farmyard manure fertilization on soil C sequestration (e.g., Huang et al., 2014; Liang et al., 2012; Neff et al., 2002; Sarma et al., 2017). Few existing studies have investigated the effects of mixed-source fertilizer application—i.e., farmyard manure and synthetic fertilization—on SOC (Ghosh et al., 2018; Liu et al., 2020; Manna et al., 2007; Nett et al., 2010). The existing studies are mostly short and mid-term, with some rare cases with up to 44 years of continuous farmyard manure and mineral fertilizer application (e.g., Ghosh et al., 2018). However, fertilizers are usually added annually for longer periods—up to centuries (Deubel and Merbach, 2007; Kidd et al., 2017). The soil C

mineralization rate in response to persistent fertilization for more than several decades, particularly in light of underlying microbial mechanisms such as PE, is still a matter of debate.

The current study aimed to assess the impacts of different fertilization practices on SOC in agricultural systems subjected to over 66 years of annual fertilizer applications. The specific objectives were: (i) to quantify SOC mineralization under different synthetic and/or organic fertilization; (ii) to evaluate the direction of PE in response to synthetic and/or organic manure fertilization; and (iii) to understand how changes in available C and N, in response to different fertilizer applications, affect the soil microbial biomass and subsequently SOC mineralization and PE. The study hypothesized that long-term continuous application of farmyard manure with and without synthetic fertilizers would enhance microbial activity and biomass, increasing SOC mineralization due to the positive PE. However, greater SOC mineralization and higher PE was expected under farmyard manure only, because combined synthetic and organic fertilizers decrease the necessity for microorganisms to mine N from SOM and hence decrease SOC mineralization rates.

2. Materials and methods

2.1. Study site and experimental setup

In 1904, a static long-term fertilizer field experiment was established at the Dikopshof research farm, Germany (50°48′ 21″ N, longitude: 6°59′ 9″ E, altitude: 62 m a.s.l.) on a Haplic Luvisol developed from loess. The soil has a silty loam texture with a silt content of up to 63 % in the upper 30 cm (Table S1). The climate at the study site has a mean annual temperature of 10 °C and mean annual precipitation of 630 mm (1906–2014) (Hadir et al., 2021). The five year crop rotation includes sugar beet (*Beta vulgaris* L.), winter wheat (*Triticum aestivum* L.), winter rye (*Secale cereale* L.), and a fodder legume crop. The initial fodder crop was red clover (*Trifolium pratense* L.), later replaced by lucerne (*Medicago sativa* L.) and, after 1967, mainly Persian clover (*Trifolium resupinatum* L.). Each of the five crops was cultivated every year in one of the designated strips (five strips in each treatment) (Fig. S1). The experimental design had three factors (crop species, fertilizer type, and fertilizer amount) and comprised six main treatments. Five treatments were based on the presence or the absence of one of the primary macronutrients, i.e., N, nitrogen; P, phosphorus; K, potassium; and Ca, calcium (added as CaO) as follows: NPKCa, PKCa, NKCa, NPCa and NPK: all being compared to an unfertilized control.

In 1953, each plot was subdivided; one strip received an additional supply of synthetic fertilizer compensating for nutrients supplied by manure, allowing for a direct comparison of synthetic and organic fertilization effects, and one strip had no supplemental mineral fertilizer applied. Each strip was thus divided into unfertilized control, base-fertilized, and fertilized with additional synthetic fertilizer (s), fertilized with manure (m), and fertilized with both additional synthetic fertilizer and with manure, leading to 24 treatments in each strip since 1953. The total plot size was 15 m × 18.5 m, with a core plot size, that was eventually sampled and harvested, of about 9 m × 10 m. In the rotation, farmyard manure (+m treatments) from cows was applied to winter rye, sugar beet, and potato. Each crop received 20 tonnes ha^{-1} year^{-1} of fresh matter manure, thus 60 tonnes ha^{-1} per rotation, with 20–30 % dry matter and a C:N ratio of about 25:1 (Hadir et al., 2021). Since 1909, the soil has been regularly ploughed to a maximum depth of 30 cm. Crop residues were removed during the entire period, except for roots and senesced potato leaves. More details about the experimental site, design, and treatment layouts were reported previously by Ahrends et al. (2018), Rueda-Ayala et al. (2018) and Seidel et al. (2021).

The fertilization rates of the four treatments—unfertilized control, fertilized with additional synthetic fertilizer (+s), fertilized with manure (+m), and fertilized with additional synthetic fertilizer and with manure (+s +m)—considered in the current study are given in Table 1. The

Table 1

Application rate per element (kg ha^{-1} year^{-1}) for each treatment, by crop and fertilization sources at Dikopshof. Treatments were fertilized either with mineral (synthetic) fertilizer (+s) or cattle farmyard manure (+m), or the combination of both synthetic and manure fertilizer (+s +m). Since 1953, treatments were fertilized with supplementary synthetic fertilizer (+s) to compensate for the amount of nutrients supplied by manure (+m) were established. Thus, treatments +s and +m are fertilized with the same amounts of NPK but with either synthetic or with organic fertilizer.

Treatments	Fertilizer	N—P—K-Ca applied (kg ha^{-1} year^{-1})				
		Winter wheat	Winter Rye	Sugar Beet	Potato	Persian clover
Unfertilized control	Base	0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0
	Manure	0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0
	Synthetic	0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0
Synthetic fertilizer (+s)	Base	0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0
	Manure	0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0
	Synthetic	0-0-0-0	40-22-83-0	40-22-82-0	40-22-83-0	0-0-0-0
Manure (+m)	Base	0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0
	Manure	0-0-0-0	40-22-83-0	40-22-82-0	40-22-83-0	0-0-0-0
	Synthetic	0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0	0-0-0-0
NPKCa + s + m (+s +m)	Base	120-31-116-0	40-31-116-0	80-31-116-0	50-31-116-0	0-31-116-1143
	Manure	0-0-0-0	40-22-83-50	40-22-83-50	40-22-83-50	0-0-0-0
	Synthetic	0-0-0-0	40-22-83-0	40-22-83-0	40-22-83-0	0-0-0-0

fertilization management of treatments +m and +s +m has only slightly changed between 1904 and the sampling date in 2019 (115 years), but the +s treatment and the unfertilized control strips received some manure before 1932 (Seidel et al., 2021). From 1953 to the sampling date in 2019 (66 years), the fertilization management of all treatments did not change except for a slight increase of N fertilizer application in +s and +s +m treatments on winter wheat, which occurred in the 1980s.

2.2. Soil sampling and analysis

The soil was sampled from the selected treatments cultivated with sugar beet in July 2019. Four sub-samples representing each treatment plot (4 × 4 = 16 samples in total) were randomly collected from the upper 20 cm soil layer in zipped plastic bags, immediately stored in a cooler box (with ice packs) and transported to the laboratory. Upon arrival at the laboratory, the samples were sieved through a 2 mm mesh to remove litter, debris, and rock fragments. The sieved soils were homogenized and sub-divided into different portions, i.e., ~50 g from each sample for soil C and N analysis, and ~100 and ~500 g stored at 4 °C to be used for soil microbial biomass analysis and incubation, respectively.

The total soil C and nitrogen (TN) content were analyzed in triplicated sub-samples by dry combustion at 950 °C using Elemental Analyzer (Vario EL Cube, Elementar Analysensysteme Systems GmbH, Hanau, Germany) after being oven-dried at 40 °C for three days. Since no reactions were observed after adding a few drops of 1 M HCl (no CaCO$_3$) to the soils, the total soil C content was considered equivalent to soil organic C (SOC). On the other hand, microbial biomass C (MBC) and N (MBN) were determined by the chloroform fumigation and extraction

methods (Beck et al., 1997; Brookes et al., 1985). For each subsample (16 samples in total), two 15 g fresh soil samples were weighted. The first subsample was fumigated with ethanol-free chloroform for 24 h at 25 °C in a desiccator. After fumigation, the desiccator was flushed with air eight times to allow the remaining chloroform to evaporate. The soil was extracted with 60 mL of K$_2$SO$_4$ (0.05 M) after one hour of horizontal shaking at 200 rpm and filtered through a Whatman 0.45 μm paper. The second subsample was extracted directly (unfumigated) using the above procedure. The concentration of dissolved organic C (DOC) and N (DN) in the extraction were measured with a Multi N/C 2100S Analyzer (Analytik Jena, Germany).

The MBC and MBN were determined by the difference in K$_2$SO$_4$-dissolved C or N between fumigated and non-fumigated samples and corrected using conversion factors of 0.45 and 0.54 for MBC and MBN, respectively (Brookes et al., 1985; Wu et al., 1990). The K$_2$SO$_4$-dissolved C and N content for the non-fumigated soil samples was considered as dissolved organic C (DOC) and dissolved N (DN) (Boyer and Groffman, 1996). The stoichiometric imbalances (C:N imbalance) between the resources and microbes were calculated by dividing the available resources (*DOC:DN*) by the microbial biomass C to N ratio (*MBC:MBN*) (Mooshammer et al., 2014). A high C:N imbalance corresponds to lower N availability relative to C availability and could thereafter be used as a proxy of microbial N limitation. Given that dissolved organic matter pools are much more readily available for microorganisms, the imbalance of the dissolved organic matter pool is presumably a better proxy for microbial resource stoichiometry (Mooshammer et al., 2014).

2.3. Incubation setup and CO$_2$ isotope analyzer

The experimental setup consisted of two 250 mL glass jars connected to each other with an inlet and an outlet tube representing a microcosm for continuous monitoring of soil CO$_2$ and ^{13}CO$_2$ (Fig. S2). The first glass jar containing the soil sample was connected to the inlet tube, which provided CO$_2$-free air from inflowing ambient air through a soda lime column. The soda lime column was equipped with a unidirectional valve to ensure none of the respired CO$_2$ from the sample was absorbed back by the soda lime. Another tube connected the first glass jar to the second glass jar, representing an air-drying unit (glass jar filled with 100 g orange gel) to remove water vapor associated with the CO$_2$ coming from the samples. The outlet tube from the drying unit was connected to an automated CO$_2$ isotope analyzer (CCIA-38d-EP, Los Gatos Research (LGR), USA) based on Off-Axis Integrated Cavity Output Spectroscopy (Jost et al., 2006), through a Multi-Port Inlet measurements unit. The Multi-Port measurements unit consisted of 16 inlet ports, and a digital vacuum air pump was connected to a CO$_2$ isotope analyzer (Fig. S2).

Before the experimentation, 16 reference microcosms (four replicates per treatment) were prepared from the fridge-stored samples (4 °C) with soil equivalents to 150 g of dry soil. The soil water content was adjusted to 50 % of the water holding capacity (WHC) and pre-incubated at 20 °C for seven days. After the pre-incubation, the microcosms were closed and attached to the measurement system (Fig. S2). During the incubation period, the soil water content was maintained at 60 % WHC and air temperature of 20 °C. Another set of samples (16 samples) was prepared and incubated in the same way as described for the reference microcosms but with the addition of ^{13}C-labeled glucose (D-Glucose-^{13}C6, 99 atom% ^{13}C, SIGMA-ALDRICH, Germany) to allow SOC-induced respiration and priming effect calculations. The amount of labeled glucose added to the samples was equivalent to 100 % of the average MBC from the treatments. In this case, the initial soil water content in the seven-day pre-incubation was 50 % of WHC, then adjusted to 60 % with the addition of dissolved glucose, and incubated for 33 days using the same microcosm as described for the reference soil.

2.4. Quantification of CO$_2$ source and priming effect calculations

At the beginning of the CO$_2$ measurements, each microcosm was

flushed with CO_2-free air for 30 min. Thereafter, the CO_2 concentration and its $\delta^{13}C$ were measured using the CO_2 isotope analyzer with a 20-second recording interval for 30 min. The measurements were carried out every day from day 1 to day 7 and then every second day until the end of the incubation (day 33). All the microcosm systems were kept close throughout the entire incubation with no contamination by atmospheric CO_2. The objective of the incubation was to quantify the soil respiration rate (mg C g soil^{-1} day^{-1}) and the PE induced by glucose addition by partitioning the total CO_2 efflux into SOC-derived CO_2 (SOC-CO_2) and glucose-derived CO_2 (glucose-CO_2). However, the laser-based CO_2 isotope analyzer reads the concentration of CO_2 arriving in its optical cell in ppm. To quantify the concentration of CO_2 in the soil containing microcosm (monitored profiles of CO_2 concentration by laser) and relate it to the mass of dry soil, a simple model was developed to describe the transport of CO_2 through three well-mixed compartments (Fig. S2). This model and procedure of quantifying the concentration of CO_2 in the soil containing microcosm are described in detail as supplementary material.

The isotope data ($\delta^{13}C$) were extracted as an average of time period measurements representing the accumulated CO_2 peak time in each sample. A two-step calibration was conducted to correct the concentration-dependent error and the deviations in measured $\delta^{13}C$ values due to the offset introduced by the laser spectrometer described by Joseph et al. (2019). The corrected $\delta^{13}C$ was reported in atom% and used for the calculations based on the equivalent weight of C in the CO_2. Therefore, the total C (C_{total}) was partitioned into SOC-derived C (C_{SOC}) and glucose-derived C ($C_{glucose}$) using a two-source $\delta^{13}C$ isotope ratio mixing model (Phillips and Gregg, 2001):

$$C_{glucose} = \frac{C_{total}(\delta^{13}C_{labeled} - \delta^{13}C_{unlabeled})}{(\delta^{13}C_{tracer} - \delta^{13}C_{unlabeled})} \quad (1)$$

$$C_{SOC} = C_{total} - C_{glucose} \quad (2)$$

where $\delta^{13}C_{labeled}$ and $\delta^{13}C_{unlabeled}$ are the measured $\delta^{13}C$ values of soils with and without ^{13}C-glucose addition, respectively; $\delta^{13}C_{tracer}$ is the $\delta^{13}C$ value of the added glucose tracer (99 ‰).

Finally, the priming effect (PE) induced by glucose addition was calculated:

$$PE = C_{SOC, glucose} - C_{SOC, CK} \quad (3)$$

where $C_{SOC,glu}$ is the SOC-derived CO_2 of soil with glucose addition and $C_{SOC,CK}$ is the basal CO_2 efflux of soil without glucose addition.

The cumulative CO_2 emissions and PE were calculated by linear interpolation of the measurements over the incubation period. Eventually, the metabolic quotient (qCO_2) was calculated (qCO_2 = basal CO_2/MBC), which refers to the amount of CO_2 released per unit of biomass and thus represents a critical indicator for the microbial activity and C use efficiency (Anderson and Domsch, 1990; Deng et al., 2016).

2.5. Statistical analysis

The normality of the data was approved using the Shapiro-Wilk test (P > 0.05). Soil parameters, i.e., SOC, TN, DOC, DN, MBC, MBN, final cumulative CO_2 emissions, qCO_2, and C:N ratios between the treatments, were analyzed using a linear mixed model with the fertilization treatments and soil sampling replicates considered as fixed and random effects, respectively. Since CO_2 (basal, total, SOC, and glucose-CO_2) were measured (or calculated) repeatedly, a linear mixed-effect repeated model was used to quantify the treatment effects as a fixed factor, with the microcosms (four per treatment) and measurement date as random factors. A significant threshold of P ≤ 0.05, unless otherwise specified, was used for treatment mean comparisons using Holm-Sidak methods, with the mean variations documented using standard error of the means. Overall, variable interactions were identified using the Pearson correlation coefficient. Additionally, linear regression analyses

were also applied to further explore the relationships between CO_2 emissions and PE on the one hand and the C:N imbalance on the other. The data handling, statistical analysis, and figure generation were conducted using Python (version 3.8) and SigmaPlot (Version 14.5, Systat Software Inc, Richmond, California, USA).

3. Results

3.1. Soil properties

The SOC, TN, DOC, DN, microbial biomass C (MBC, and N (MBN) differed significantly between the treatments (Fig. 1). Compared to the unfertilized soil, +m and +s +m treatments increased SOC by 45 and 65 %, respectively (Fig. 1a). Similarly, TN varied significantly and increased in the following order: unfertilized < +s < +m < +s +m (Fig. 1b). The DOC content was the highest in the +m treatments, followed by +s +m and +s, and the lowest under the unfertilized control (Fig. 1c). Interestingly, synthetic fertilization either alone (+s) or combined with manure application (+s +m) significantly increased the DN compared to +m and the unfertilized control (Fig. 1d). For example, +s and +s +m increased DN by 35 and 52 % compared to +m, respectively. The variations in MBC between the treatments followed a similar trend to SOC (Fig. 1e). While no significant difference was observed between the unfertilized soil and +s, +s +m increased MBC by 30 % compared to +m. The highest MBN (326.87 ± 32. 3 mg C kg soil^{-1}) was observed under +s +m followed by +s and +m, and the lowest (326.87 ± 32. 3 mg C kg soil^{-1}) under the unfertilized control (Fig. 1f).

In addition to soil properties, the microbial stoichiometry (Fig. 2) also varied with fertilization treatments, with a significantly higher SOC to TN ratio (SOC:TN) at the +m, followed by the unfertilized control, and lowest in +s and +s +m (Fig. 2a). The ratio of the dissolved organic pool (DOC:DN) and that of the microbial pool (MBC:MBN) followed exactly the same pattern as in the SOC:TN (Fig. 2b and c). The C:N imbalances (DOC:DN/MBC:MBN) between the dissolved organic pool and microbial biomass were significantly highest in the +m treatment (Fig. 2d), corresponding to a 30 % increase compared to +s +m and as much as 15-fold compared to the unfertilized control.

3.2. Soil CO_2 efflux

Basal CO_2 efflux (soil incubated without glucose) decreased significantly in all treatments, with the lowest CO_2 efflux recorded at the end of the incubation period (Fig. 3). The CO_2 efflux was consistently greater in the treatments including manure (i.e., +m and +s +m) than the unfertilized and +s treatments (Fig. 3a). While the CO_2 rate was constantly lower in the +s than the unfertilized control, variability was observed between the treatments that had manure, with significant variations observed from day 25 onward, where +m emitted more CO_2 than +s +m. The cumulative basal CO_2 efflux emitted during the incubation period (33 days) was significantly greater in +m and +s +m treatments than in the unfertilized control and +s treatment (Fig. 3b). The most remarkable difference in basal CO_2 efflux was observed between the +m and +s treatments, corresponding to a difference of 84 % (260 ± 15 *vs* 140 ± 8 mg C kg soil^{-1}). It is worth noting that the qCO_2 was significantly highest in +m and the lowest in +s +m, with the unfertilized control and +s treatment being intermediate (Fig. S4).

Generally, the treatments showed a sharp increase in total CO_2 efflux (CO_2 from soil incubated with glucose) from day 1 to day 3, followed by a sharp decline on day 4 for the unfertilized control, +s +m and, on day 5, for the +s treatment (Fig. 4a). The total CO_2 efflux from the +m treatment also declined after day 3; however, the decline was less steep and continued until day 17. During this time (from days 3 to 17), the +m treatment had the greatest total CO_2 efflux of all the treatments. After day 17, the +s +m treatment was consistently higher than the unfertilized control and +s treatments. The +m treatment induced the greatest final cumulative total CO_2 efflux of 1792 ± 34 mg C kg soil^{-1},
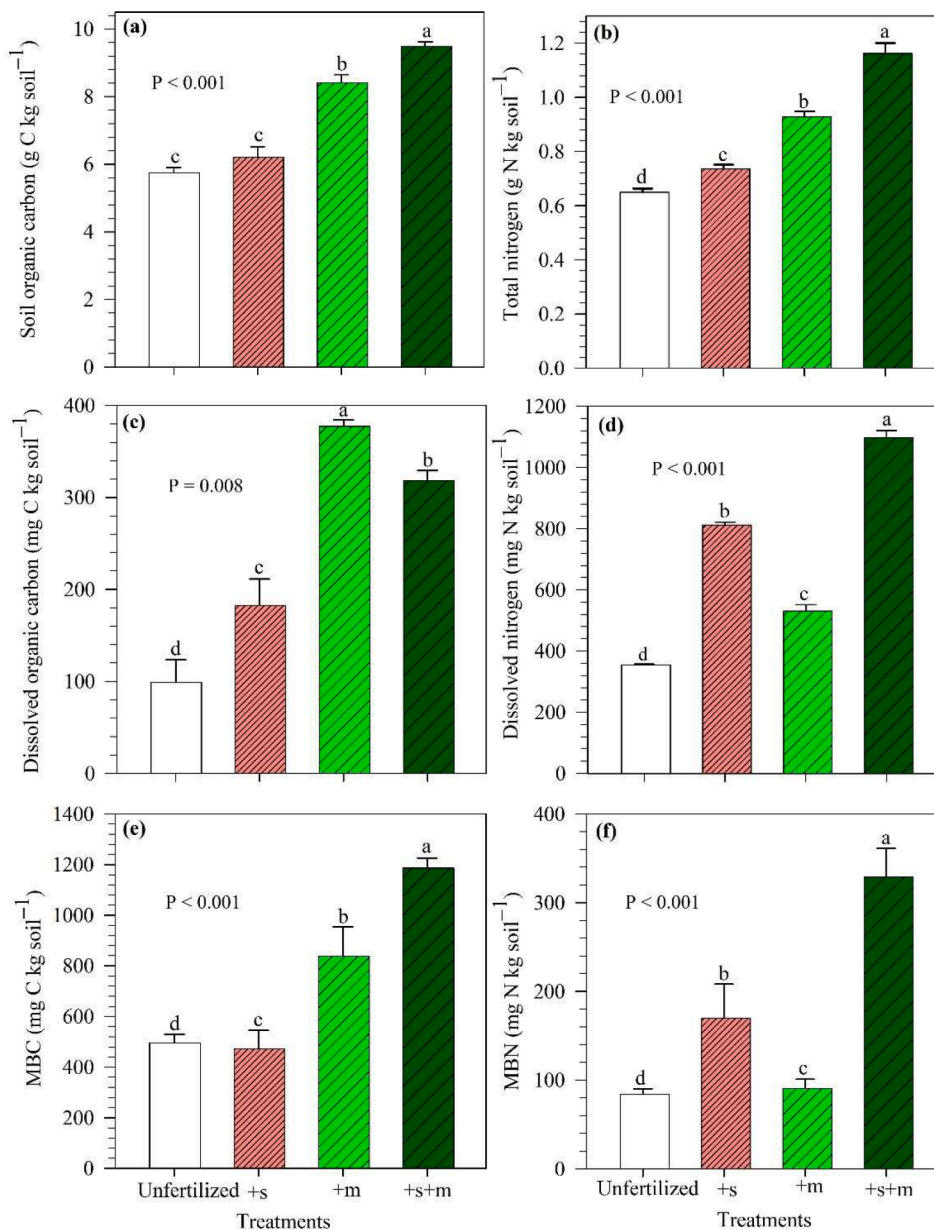
Fig. 1. Mean ± standard error of soil organic carbon (a), total nitrogen (b), dissolved organic carbon (c), dissolved nitrogen (d), microbial biomass carbon (MBC, e) and microbial biomass nitrogen (MBN, f) from the fertilization treatments (unfertilized, synthetic supplemental (+s), +m; farmyard manure (+m), and synthetic base and supplemental and farmyard manure (+s +m)). Means (n = 4) followed by different letter are significantly different at P < 0.05. Error bars represent the standard errors of the means (n = 4). Means followed by different letters are significantly different at P < 0.05.

corresponding to an increase of 37, 54, and 116 % compared to +s +m, +s, and the unfertilized control, respectively (Fig. 4b).

SOC-derived CO_2 (SOC-CO_2) efflux also varied significantly among the treatments during incubation (Fig. 4c and d). High variations between the treatments in SOC-CO_2 were observed in the first three days following the glucose addition. For instance, +s +m had the greatest SOC-CO_2 on day 1 and the lowest on day 2, jointly with the unfertilized control (Fig. 4c). Starting from day 4 onwards, the unfertilized control, +s and +s +m treatments followed a slightly similar trend, with +s +m producing the highest SOC-CO_2. Interestingly, +m treatment induced the greatest SOC-CO_2 from day 2 until day 17 compared to the other treatments. The largest difference in SOC-CO_2 of +m compared to other treatments was observed on day 9, corresponding to as much as 251 % (53.3 ± 1.62 vs 15.12 ± 2.58 mg C kg soil^{-1} day^{-1}) compared to the unfertilized control. The final cumulative SOC-CO_2 decreased in the following order: +m > +s +m > +s and unfertilized control (Fig. 4d).

Glucose-derived CO_2 (glucose-CO_2) showed significant variation between the treatments from day 2 to day 13 (Fig. 4e), but this variation was less pronounced than SOC-CO_2. The greatest glucose-CO_2 from day three to day 13 of the incubation was induced by +m treatment. Unexpectedly, +s generated greater glucose-CO_2 than +s +m during this time (day 3 to day 13). The unfertilized control had the lowest glucose-CO_2 from day 4 to day 21. However, no significant difference was observed between the unfertilized control and +m on day 23, 25, and 31. The final cumulative glucose-CO_2 was greatest in +m (681.5 ± 31.3 mg C kg soil^{-1}), corresponding to an increase of 32, 50, and 110 % compared to +s, +s +m, and the unfertilized control, respectively (Fig. 4f). However, no significant difference was observed between the +s +m and +s treatments.

3.3. Priming effect

The priming effect (PE) followed a similar pattern to SOC-CO_2 in all the treatments (Fig. 5a and b). In general, PE was consistently positive throughout the incubation period, except on day 4, where the unfertilized control induced a negative PE (Fig. 5a). The +s +m treatment induced the greatest PE on the first day of the incubation, followed by the unfertilized control. In contrast, no significant difference was
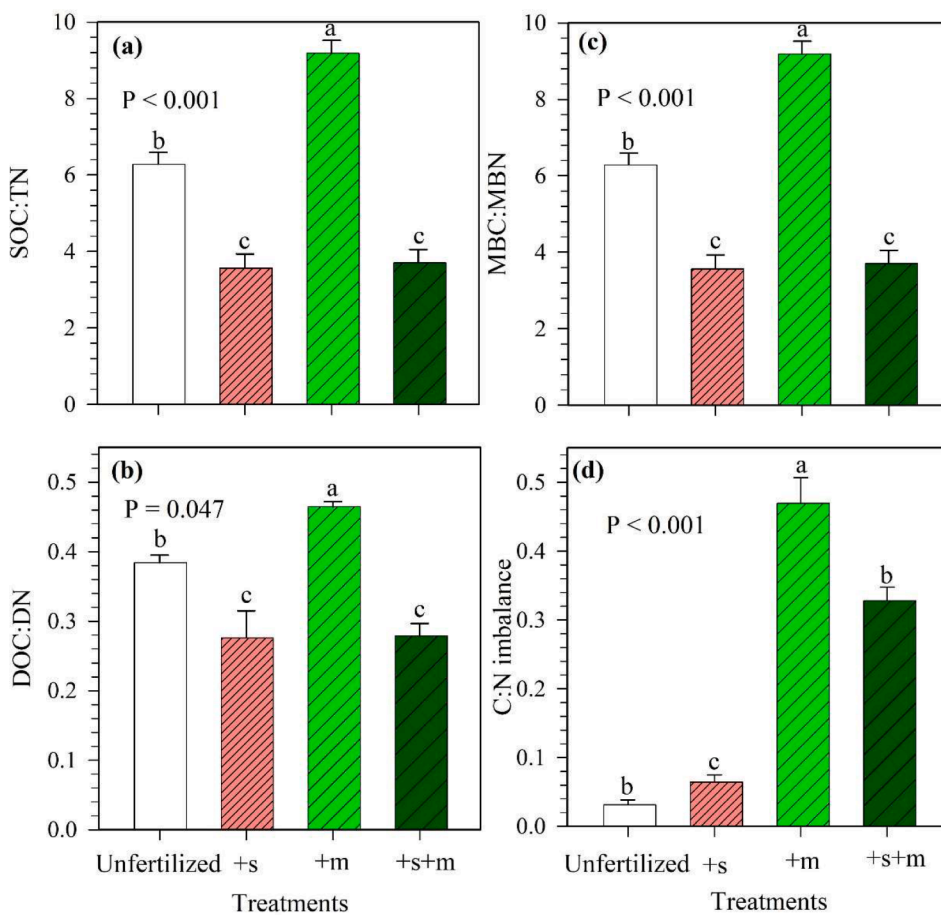
Fig. 2. Mean ± standard error of soil organic carbon: total nitrogen (a, SOC:TN), dissolve organic C: dissolved N (b, DOC:DN), microbial biomass C: microbial biomass N (c, MBC:MBN) and the C:N imbalance (d, C:N imbalance; DOC: DN/MBC:MBN) from the treatments (unfertilized, synthetic supplemental (+s), +m; farmyard manure (+m), and synthetic base and supplemental and farmyard manure (+s +m)). Error bars represent the standard errors of the means (n = 4). Means followed by different letters are significantly different at P < 0.001.
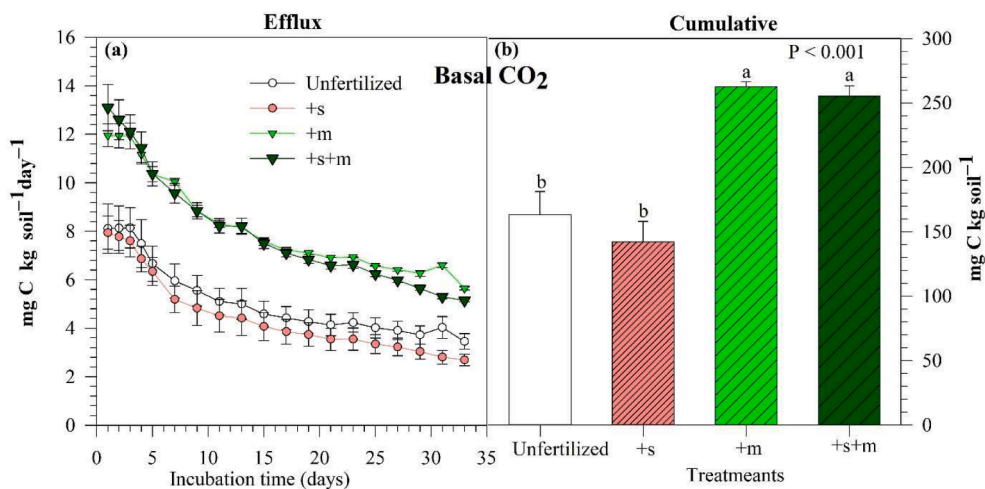
Fig. 3. Daily fluxes and cumulative (a) of basal CO_2 efflux (b) from the fertilization treatments (unfertilized, synthetic supplemental (+s), +m; farmyard manure (+m), and synthetic base and supplemental and farmyard manure (+s +m)) during the incubation period. Error bars represent the standard errors of the means (n = 4). Means followed by different letters are significantly different at P < 0.05.

observed in PE between +s and +m from day 1 to day 3; however, the +m treatment induced the greatest PE on day 4. The +m treatment continued to induce the greatest PE until day 17, with the highest variation recorded on day 9 compared to the other treatments. Compared to the unfertilized control and +s, +s +m had the highest PE and unfertilized soil induced the lowest PE from day 4 to the end of the incubation. Cumulatively, +m treatment induced the highest PE of 390 ± 21 mg C kg soil^{-1}, corresponding to a 35 % greater PE than +s and as

much as 137 % greater than the unfertilized treatment (Fig. 5b).

3.4. Relationships between C effluxes and soil parameters

Across the study data, the highest correlation coefficient value (r = 0.98) was observed between SOC-CO_2 and PE, followed by the significant positive correlation of r = 0.95 observed between SOC and TN, which corresponded to a significant difference at P ≤ 0.001 (Table 2). A
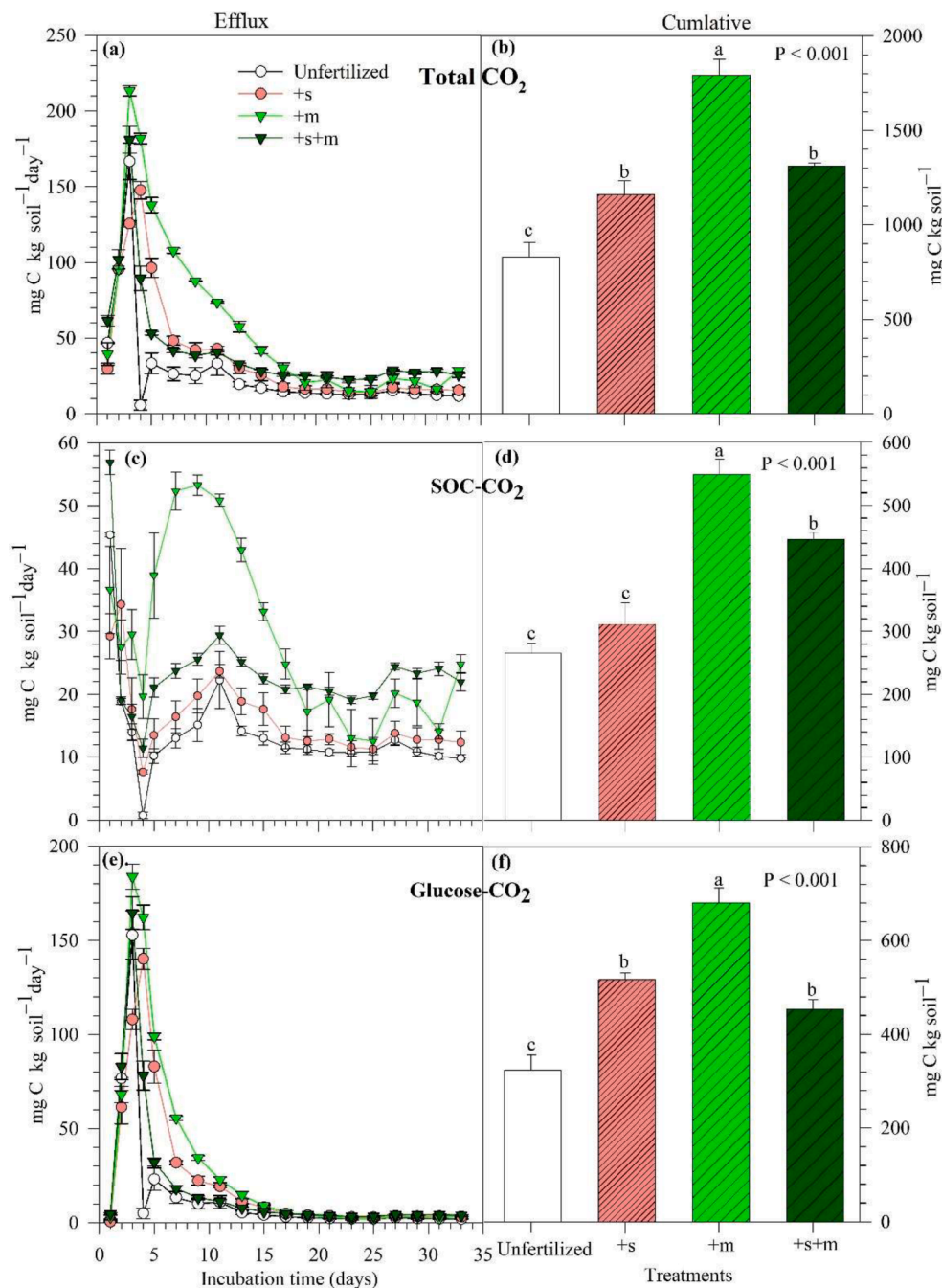
Fig. 4. Daily fluxes and final cumulative of total CO_2 (a and b, total CO_2 with glucose addition), soil organic carbon-derived CO_2 (c and d, SOC-CO_2) and glucose-derived CO_2 (c and d, glucose-CO_2) from the fertilization treatments (unfertilized, synthetic supplemental (+s), +m; farmyard manure (+m), and synthetic base and supplemental and farmyard manure (+s +m)) during the incubation period. Error bars represent the standard errors of the means (n = 4). Means followed by different letters are significantly different at P < 0.05.

highly positive correlation was also found between other variables such as SOC *vs* MBC, TN *vs* DN, and SOC *vs* DOC. Interestingly, C:N imbalance induced the highest positive correlations to basal CO_2, SOC-CO_2, and PE. Additionally, a significant positive correlation was also observed between soil pH on one hand and basal CO_2, SOC-CO_2, PE, and C:N imbalance on the other hand, with the strongest correlation, (r = 0.81) observed between pH and C:N imbalance.

To further explore the influence of C:N imbalance on SOM mineralization, a linear regression between C:N imbalance to either SOC-CO_2 (Fig. 6a) or PE (Fig. 6b) based on the fertilization treatment mean values was conducted. The linear relationship showed a significant increase (r = 0.87) in SOC-CO_2 with the increase of the C:N imbalance, among the treatments in the following order: unfertilized > +s > +s +m > +m. The correlation between the C:N imbalance and PE among the treatments was also significant (P = 0.002) (Fig. 6b).

4. Discussion

4.1. Effect of long-term continuous fertilization on soil and microbial carbon and nitrogen

Long-term yearly application of 60 tonnes ha^{-1} of farmyard manure in a five-year crop rotation either alone (+m) or combined with synthetic fertilizers (+s +m) resulted in higher topsoil SOC and TN contents (by an average of 58 %, Fig. 1a and b) compared to the unfertilized control, suggesting high benefits of organic manure in increasing SOC and TN content. These increases were greater than the impact induced by synthetic fertilizers (i.e., no effect on SOC and 13 % increase in TN), which agrees with several previous studies (e.g., Su et al., 2006; Ren et al., 2018; Liu et al., 2020). The greater impact of farmyard manure can directly be linked to the amount of additional C and N contained
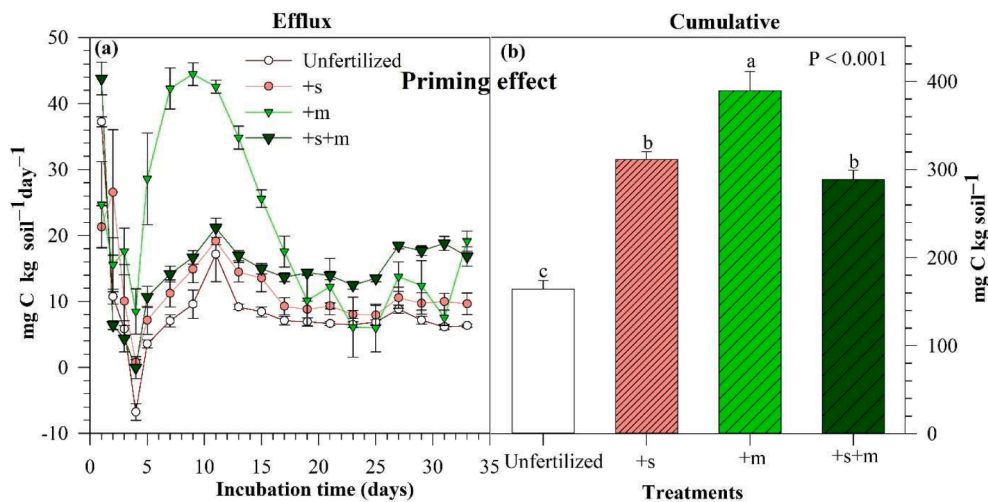
Fig. 5. Daily fluxes (a) and final cumulative (b) priming effect from the fertilization treatments (unfertilized, synthetic supplemental ($+s$), $+m$; farmyard manure ($+m$), and synthetic base and supplemental and farmyard manure ($+s +m$)) during the incubation period. Error bars represent the standard errors of the means ($n = 4$). Means followed by different letters are significantly different at $P < 0.05$.

Table 2
Coefficients of correlation (r) of between the studied soil parameters; Basal CO_2 (CO_2), glucose derived-CO_2 (glucose-CO_2), soil organic carbon-derived CO_2 (SOC-CO_2), priming effect (PE), soil organic carbon (SOC), total nitrogen (TN), dissolved organic carbon (DOC), dissolved nitrogen (DN), microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), carbon: nitrogen imbalance (C:N_{imb}) and soil pH. N = 16.

	CO_2	Glucose-CO_2	SOC-CO_2	PE	SOC	TN	DOC	DN	MBC	MBN	C:N_{imb}	pH
CO_2												
CO_{2glu}	ns											
CO_{2SOC}	0.89***	0.74**										
PE	0.78**	0.80***	0.98***	–								
TC	0.90***	ns	0.76**	0.65*	–							
TN	0.78**	ns	0.66*	0.56*	0.95***	–						
DOC	0.81***	ns	0.69**	0.60*	0.93***	0.92***	–					
DN	ns	ns	ns	0.01	ns	0.94***	0.60*	–				
MBC	0.86***	ns	0.79***	0.70**	0.94***	0.64*	0.93***	ns	–			
MBN	0.65*	ns	0.64*	0.59*	0.75**	0.76**	0.60*	ns	0.80**	–		
C:N_{imb}	0.89***	0.67**	0.91***	0.86***	0.85***	0.76**	0.81***	ns	0.86***	0.71**	–	
pH	0:68*	ns	0:67*	0.62*	0.65*	ns	ns	ns	0.58*	0.58*	0.81**	–

Correlation followed by *, **, *** are significant at $p \leq 0.05$, ≤ 0.01, and ≤ 0.001, respectively; ns, non-significant.
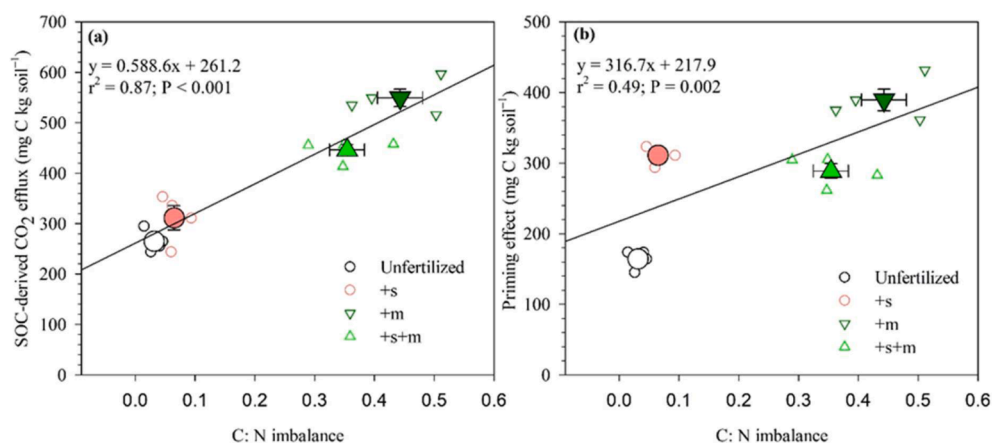

Fig. 6. Linear relationship between carbon to nitrogen imbalance (C: N imbalance: DOC:DN/MBC:MBN) and SOC-derived CO_2 (a) and priming effect rates (b) from the treatments (unfertilized, synthetic supplemental ($+s$), $+m$; farmyard manure ($+m$), and synthetic base and supplemental and farmyard manure ($+s +m$)). Each point represents the cumulative value of one replicate. Error bars represent the standard errors of the treatment means ($n = 4$).

within the farmyard manure (Islam et al., 2021; Maillard and Angers, 2014). In addition, the manure application with and without mineral fertilization has significantly increased the crop yield in the following order: unfertilized < $+s$ < $+m$ < $+s +m$, at the study site (Hadir et al., 2021; Rueda-Ayala et al., 2018), indicating more fresh C input via rhizodeposition and plant residues (Jacobs et al., 2020; Maltas et al., 2018; Stewart et al., 2007).

Moreover, the present study showed that microbial biomass C also

strongly increased under manure application compared to the unfertilized control (Fig. 1c), which was explained by the increase of available C for microbial growth as indicated by the high DOC in the manure treatment (Fig. 1b). While the DOC and DN content were higher under sole synthetic fertilization, there was no difference in both total C and microbial C contents compared to the treatments with manure additions. Unlike synthetic fertilizer, manure applications can improve soil physical and chemical properties, i.e., maintaining neutral pH, having a higher water holding capacity and lower bulk density, and favoring microbial growth and microbial-driven processes compared to synthetic fertilizers (Hadir et al., 2021; Rayne and Aula, 2020; Zhang et al., 2012). This could be supported by the present study results showing a significant increase in soil pH toward neutrality in treatments with manure application compared to the unfertilized control and the treatment with synthetic fertilizer only (Fig. S5), confirming the positive effect of manure addition on soil properties. In light of this, Xiao et al. (2021) concluded that the alleviated soil acidification induced by long-term manure amendment could increase microbial C use efficiency and decrease PE, thus facilitating soil C sequestration. This reflects that manure application could improve soil organic matter quantity and quality, and soil fertility, compared to synthetic fertilizer under long-term continual application (Bhogal et al., 2018; Singh Brar et al., 2015).

In terms of the treatments with manure fertilization, the combined manure and synthetic fertilizers led to higher SOC, TN, and microbial biomass (C and N) compared to manure alone (Fig. 1), implying a greater benefit of manure in the presence of available nutrients. The higher positive effect on SOC induced by +s +m, was possibly due to (i) the overall higher inputs of bioavailable nutrients (Table 1) resulting in higher plant (documented by Hadir et al. (2021)) and microbial biomass, or (ii) the lower respiratory C output via SOC mineralization compared to +m (Fig. 5). The current study further investigated the PE on SOM decomposition to explore the mechanisms of SOM turnover and their effects on the net SOC balance under different fertilization regimes.

4.2. Effect of long-term continuous fertilization on soil carbon turnover

Without adding a labile C source, soil basal respiration rates were increased under the manure fertilization, but not under synthetic fertilization alone (Fig. 4). These increments of basal respiration induced by manure application were significantly related to the increased SOC and TN contents after long-term continuous fertilization (Fig. 1a and b), where microbes were more abundant and active as revealed, e.g., from higher microbial biomass and a higher metabolic quotient (qCO_2) (Fig. 1e–f and Fig. S2).

The glucose addition caused a significant increase in the total and SOC-CO_2 fluxes when compared to the basal respiration, thus explaining the positive PE induced in all treatments after the labile C addition (Fig. 5). These results are in line with previous studies (Fontaine et al., 2004; Kuzyakov, 2010). This is presumably explained by the microbial activation hypothesis (Cheng and Kuzyakov, 2005), which states that low molecular weight organic substances might trigger an acceleration of microbial metabolic activities, leading to the production and release of extracellular enzymes for SOM decomposition (Mason-Jones and Kuzyakov, 2017). Glucose is often used to mimic plant-derived labile C from root exudates or decomposing plant residues (Gunina and Kuzyakov, 2015). The positive relationships between the glucose-CO_2 and SOC-CO_2 (or PE) (Table 2), indicate that the expected increase of plant-derived labile C inputs due to the increased crop production under long-term continuous fertilization will probably enhance the microbial decomposition of SOM.

Further, the study reveals that the intensity of PE is then regulated by soil C and nutrient availability, which depends on the type and quantity of long-term continuous fertilization. The synthetic supplemental fertilization led to higher PE than the unfertilized control (Fig. 5), despite being no significant difference in the SOC and SOC-CO_2 efflux, which contradicts some recent studies (Wang et al., 2019; Wu, 2019;

You et al., 2020).

The treatments with manure application (i.e., +m and +s +m) induced a greater PE than in the +s treatment or in the unfertilized soil, suggesting a crucial role of organic fertilizer application SOM mineralization via regulation of PE. The significant positive correlation between PE on the one hand and soil available nutrient (i.e., DOC and DN) content and microbial biomass on the other hand (Table 2) is strong evidence of the role of long-term fertilization in regulating PE by changing soil nutrient status, microbial biomass, and microbial activities (Blagodatskaya and Kuzyakov, 2011; Mohanty et al., 2013; Wen et al., 2020). Therefore, organic fertilization enhances microbial growth, thus altering microbial activities, resulting in accelerated SOM decomposition and thus high PE (Fang et al., 2020; Francioli et al., 2016; Marinari et al., 2000).

In terms of the treatments with manure, the manure application alone led to higher SOC-CO_2 and PE than those under the combined manure and synthetic fertilization. However, SOC, TN, and microbial biomass (C and N) showed opposite trends. There are three potential explanations for such a trend. Firstly, the greatest increase in the SOC-CO_2 and PE under +m compared to +s +m (Fig. 4c and d) could be explained by the relatively higher microbial activity under sole manure application than the combined application of organic and synthetic fertilizer. This explanation is supported by the qCO_2, which was significantly greater in the +m than in the +s +m treatment (Fig. S4) despite the lower MBC in +m (Fig. 1), thus indicating a larger portion of the active microbial biomass in +m than the +s +m, congruent with studies showing that organic fertilizer is known to increase microbial activity and diversity (Hu et al., 2011; Li et al., 2015; Zhang et al., 2012).

Secondly, the MBC:MBN ratio increased with manure application, while it decreased with synthetic fertilization (Fig. 2c). Such a response of microbial biomass C and N suggests a shift in the microbial community toward bacterial dominance under synthetic fertilization (Six et al., 2006), while the microbial community could be more dominated by fungi under manure application only. This could be due to manure/synthetic fertilization changing soil biochemical and physical properties; for example, synthetic fertilization may decrease soil pH, but manure application can adjust the soil pH to the neutral range (Hadir et al., 2021; Liu et al., 2020). In addition, the C:N ratio of resources for microbial growth (C:N ratio and DOC:DN ratio) was a determinant of the fungal to bacterial growth ratio, with lower C:N ratios of environmental resources being more beneficial to bacterial growth than to fungal growth (Grosso et al., 2016). Fungi have a higher capacity to produce the enzyme for SOM decomposition than bacterial communities (Lashermes et al., 2016; Romaní et al., 2006), thus supporting the present study results in which sole manure application led to the highest SOM decomposition and PE.

Finally, the effect of N availability on SOM mineralization and PE is obvious when the soil with farmyard manure (+m) and with a combined application of synthetic fertilizers and manure (+s +m) are compared (Fig. 4 and Fig. 5). The current findings confirm the N mining hypothesis in systems with organic fertilizer input (Craine et al., 2007; Li et al., 2017). The results of this study show that dissolved N was significantly lower (by as much as 110 %) in the soil with +m than +s +m (Fig. 1d). In addition, since microbial nutrient demands are determined by microbial biomass stoichiometry (Khan and Joergensen, 2019; Zhu et al., 2018), the higher C: N imbalance in soil with +m than +s +m indicates that microbes are more N-limited under farmyard manure only.

In N-limited conditions, i.e., +m, microbes obtain their required N for growth and activities by mining the SOM, resulting in high SOM mineralization and a positive PE (Chen et al., 2014; Li et al., 2017; Meyer et al., 2018). Conversely, in the +s +m treatment, total N in the soil (Fig. 1b) and dissolved N (Fig. 1d) were significantly greater than in +m, resulting in a lower C:N imbalance (Fig. 2d). A lower C:N imbalance indicates less N limitation, and hence the need to mine SOM for N was reduced in +s +m, resulting in reduced PE compared to the +m treatment (Fig. 5). The current study provides evidence of increasing

microbial *N*-mining in soils fertilized solely with farmyard manure, inducing a positive PE and leading to higher organic matter decomposition (Mooshammer et al., 2014). The explanation is valid for the current study, as the C:N imbalance correlated positively with SOC-CO_2 and the priming effect (Fig. 6). However, some other studies have contradicted the *N*-mining theory, suggesting that N mining is not always an explanation for the priming phenomena (Chowdhury et al., 2014; Mason-Jones et al., 2018; Tian et al., 2016). In fact, the type and amount of the organic substrate can largely determine the direction and intensity of PE (Di Lonardo et al., 2019; Mason-Jones et al., 2018; Wang et al., 2015).

Overall, these results supported the hypothesis of greater SOM mineralization following long-term continuous farmyard manure application. Despite the greater SOM mineralization in the farmyard manure treatments (+m and +s +m) compared to the other treatments, the final SOC balance was still higher in the farmyard manure treatments. Thus, the SOC gains from manure application in this study certainly exceeded the SOC losses, resulting in higher net SOC accumulation than under the sole application of synthetic fertilizer or without any fertilization. Additionally, the higher plant C allocation could compensate for the greater outputs in +s, +m, and +s +m treatments than the unfertilized soil, as mineral fertilizer can significantly enhance above- and below-ground biomass growth, resulting in high rhizodeposition of C (Hirte et al., 2018; Kätterer et al., 2011). These results emphasized the importance of organic manure application to increase SOC, regardless of the enhanced SOM mineralization resulting from the induced priming effect due to C input (Cai et al., 2016; Mahanta et al., 2013; Wu, 2019). The manure potential for SOC sequestration was remarkable when the farmyard manure was applied in combination with synthetic fertilizer (i.e., +s +m). Such findings are consistent with many previous studies (Ding et al., 2014; Iqbal et al., 2020; Wu, 2019) and highlight the importance of managing farmyard manure application to increase manure-derived C in spite of increasing SOC mineralization for optimizing C sequestration efficiency in agricultural systems.

5. Conclusions

The study aimed to assess the impacts of different fertilization regimes on soil organic carbon in soils subjected to long-term annual synthetic and/or organic fertilization. The results showed that farmyard manure addition, either alone or combined with synthetic fertilizers, largely increased basal CO_2, with a subsequent acceleration of soil organic carbon mineralization resulting in a positive priming effect. The magnitude of fertilization-induced priming effect was highest in the manure treatment followed by supplemental application of synthetic fertilizer, but lower in the treatment combining the manure with synthetic fertilizers or in the unfertilized soil, emphasizing the importance of fertilization in regulating priming effect intensity. Compared to unfertilized soil, fertilization considerably increased soil nutrient status (i.e., carbon and nitrogen) and microbial biomass, primarily due to the increased carbon inputs to the soils. The newly formed manure carbon overcompensated for the soil organic carbon losses through the priming effect, resulting in net soil carbon gain, which was greatest under the manure with synthetic fertilizer treatment. Consequently, the manure with synthetic fertilizer treatment lowered the priming effect and increased soil carbon, thus increasing overall soil carbon sequestration. Future research linking the accumulated soil carbon stocks, fertilizer types, microbial diversity, and microbial activity with the priming effect using ^{13}C-labeled forage to livestock would improve the understanding of the underlying mechanism of carbon sequestration in response to manure application.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Data availability

Data will be made available on request.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2022.116216.

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