Applied Soil Ecology 108 (2016) 47–53

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

N fertilization decreases soil organic matter decomposition in the rhizosphere

Huadong Zang[a,*], Jinyang Wang[b], Yakov Kuzyakov[a,c]

[a] Department of Agricultural Soil Science, University of Göttingen, Büsgenweg 2, 37077 Göttingen, Germany
[b] State Key Laboratory of Soil and Sustainable Agriculture, Institute of Soil Science, Chinese Academy of Sciences, 210008 Nanjing, China
[c] Department of Soil Science and Temperate Ecosystems, University of Göttingen, Büsgenweg 2, 37077 Göttingen, Germany

ARTICLE INFO

Article history:
Received 26 March 2016
Received in revised form 11 July 2016
Accepted 31 July 2016
Available online xxx

Keywords:
Priming effect
SOM decomposition
Nutrient availability
Microbes
N mineralization

ABSTRACT

Agricultural soils have experienced large anthropogenic nitrogen (N) inputs in recent decades. Our mechanistic understanding of the effects of added N on the carbon (C) cycle in agricultural soils, especially in the rhizosphere (C excess and N limitation), remains incomplete. The effects of increasing N fertilization on soil CO_2 emissions and microbial biomass in a wheat rhizosphere were investigated in a 56-day incubation experiment. The rhizosphere soil was amended with increasing NH_4^+ rates of 0 (Control), 52 (Low N), 104 (Medium N), and 208 $\mu g\,N\,g^{-1}$ soil (High N). N fertilization exponentially decreased soil CO_2 emissions by 27–42% compared to the control. Microbial biomass was decreased by N fertilization, but depended on the amount of added N and the timing of measurements. N additions caused pronounced negative priming effects ranging from −72 to −113 $\mu g\,C\,g^{-1}$ over 56 days, corresponding to a decrease in basal respiration of 27%, 35% and 42% for Low, Medium and High N, respectively. The CO_2 fluxes per unit of microbial biomass decreased exponentially with N addition ($R^2 = 0.84$), indicating increased microbial carbon use efficiency under higher N availability. A literature review and own results showed that negative PEs occurred in the most cases and getting more negative exponentially with increasing N fertilization ($n = 158$, $P < 0.001$). In conclusion, increasing N fertilization facilitates C sequestration in soil not only by higher root biomass production, but also by reducing the SOM decomposition in the rhizosphere because of decreased N limitation.

1. Introduction

Globally, most ecosystems are experiencing increased inputs of anthropogenically derived nitrogen (N), which are about 30–50% greater than that from natural sources and tenfold greater than 100 years ago (Galloway et al., 2008; Schlesinger, 2009; Canfield et al., 2010). The N increase mainly originates from chemical N fertilizers, legume cropping and atmospheric N deposition (Liu et al., 2013; Tilman et al., 2001). The nutrient requirements of microorganisms are a major controller of net C sequestration and of loss through respiration in the soil (Richardson et al., 2014). Understanding how these additional N inputs impact terrestrial ecosystems is becoming increasingly important within the context of the carbon (C) budget, especially in agricultural ecosystems (Liu and Greaver, 2010).

Because N is a limiting nutrient to plants in most natural ecosystems (except steppes and prairies), N enrichment have strong effects on aboveground primary productivity and plant community composition (Bobbink et al., 2010). Nonetheless, the responses of belowground processes and microorganisms to elevated N inputs are less well understood (Treseder, 2008). One suggestion is that the rhizosphere priming effect (PE) due to N addition may be affected by nutrient availability in plant-soil systems (Dijkstra et al., 2013). In soils with low nutrient availability, N inputs will stimulate microbial activity to mine for nutrients (i.e. C) from soil organic matter (SOM). This will accelerate SOM decomposition – a positive PE. Conversely, in soils with abundant nutrients, microorganisms will switch from decomposing SOM (old C) to utilize newly deposited C and external added N, thereby causing a negative PE (Dijkstra et al., 2013; Cheng et al., 2014). These two mechanisms have frequently been termed SOM mining and preferential microbial substrate utilization, respectively (Dijkstra et al., 2013; Cheng and Kuzyakov, 2005). Therefore, in plant-soil systems, N fertilization has divergent effects on CO_2 emissions, including increased (Cleveland

* Corresponding author.
E-mail address: zanghuadong@gmail.com (H. Zang).

http://dx.doi.org/10.1016/j.apsoil.2016.07.021
0929-1393/

and Townsend, 2006; Waldrop and Zak, 2006), decreased (Bowden et al., 2004; Burton et al., 2004), or unchanged SOM decomposition rates (Blagodatskaya et al., 2007). In incubation experiments, Ramirez et al. (2012) found that N addition decreased soil respiration in 28 soils across North America (i.e. wetland, forest, grassland and desert). This suggested that N addition causes a negative PE in the bulk soil without plant C inputs. Importantly, in field studies it is difficult to determine whether SOM decomposition changes are a direct result of N addition or an indirect result of plant C inputs to soil.

The rhizosphere receives greater inputs of labile C (e.g. root exudates) and other less decomposable rhizodeposits relative to the bulk soil (Kuzyakov and Blagodatskaya, 2015). The main C inputs are composed primarily of low molecular weight organic compounds, which microorganisms readily use for growth and respiration (Kuzyakov et al., 2007). Total microbial biomass in the rhizosphere was 14–31% higher (Blagodatskaya et al., 2014), and the activity and abundance of the microbial community can be an order of magnitude higher than those in bulk soil (Jones et al., 2004; Kuzyakov and Xu, 2013). In contrast to C, continuous N uptake by roots leads to strong nutrient depletion zones in the rhizosphere (Jungk, 2001). Combined, all these factors alter the chemistry and biology of the rhizosphere, leading to a greater response by the rhizosphere versus bulk soil to N fertilization.

Our mechanistic understanding of the effects of increasing N fertilization on CO_2 emissions in agricultural soils, especially in rhizosphere, is limited (Blagodatskaya et al., 2007; Chen et al., 2014). This calls for evaluating the effects of N fertilization on PE in the rhizosphere because of the sufficient C supply and strong N limitation (Jones et al., 2004 Kuzyakov and Blagodatskaya, 2015). We used the soil from a wheat rhizosphere to examine the effects of increasing N levels on CO_2 emissions and microbial biomass over a 56-day incubation. We hypothesized that mineral N fertilization will reduce soil CO_2 emissions in the rhizosphere and that the reduction will be stronger with increasing N levels.

2. Materials and methods

2.1. Soil sampling and preparation

Soil samples were collected from the upper layer (0–10 cm) of the Ap horizon of a wheat field in northwest Göttingen, Germany (51°33′36.8″N, 9°53′46.9″E). The soil is a haplic Luvisol with pH (H_2O) 6.6; organic C, total N, NO_3^- and available P was 11.7 g C kg^{-1}, 1.2 g N kg^{-1}, 0.083 mg N g^{-1} and 0.160 mg P g^{-1}, respectively (Schmitt et al., 2013). The soil was air-dried, homogenized and sieved (<2 mm). Fine roots and other plant residues were carefully removed manually.

The soil was placed into pots and kept at a depth of about 5 cm. The wheat seeds were germinated on a wet filter paper in Petri dishes for three days and then sufficient seedlings were transferred to each pot. The plants were grown in a greenhouse at room temperature. During plant growth, artificial lighting was used and maintained at 100 μmol m^{-2} s^{-1} for 14 h day^{-1}; relative humidity was kept at 50–60% of the available field capacity. After four weeks, all plants and fine roots were carefully removed from the soil and then mixed soil thoroughly. Because the wheat roots occupied the whole pots, the whole soil was regarded as the wheat rhizosphere and used for the following incubation.

2.2. Experimental design and incubation

Thirty grams (oven-dried weight) of the wheat rhizosphere soil were weighed into a 100-ml jar. The soil was adjusted to 50% of the water holding capacity (WHC) and pre-incubated for three days at 20 °C. After pre-incubation, the increasing levels of NH_4Cl solution (Low N: 52; Medium N: 104; High N: 208 μg N g^{-1} soil) and distilled water (Control) was applied in 2 ml total volume using a syringe to reach a final soil moisture content of 60% of WHC. Medium N input to the soil was equivalent to 150 kg NH_4^+-N ha^{-1}, which is the conventional amount of mineral N fertilizer application in northern Germany. Then the jars were incubated in the dark at 20 °C for 56 days. During the incubation, the CO_2 evolved from the soils was trapped by 3 ml of 1.0 M NaOH solution in small tubes that were exchanged at 1, 3, 5, 7 days and then weekly. In addition, three jars for each treatment were destructively sampled at 1, 3, 7, 21, 40 and 56 days to measure microbial biomass, dissolved organic carbon (DOC), and mineral N content.

2.3. CO_2 emission, microbial biomass and DOC

Carbon dioxide trapped in the NaOH solution was measured by titration of 0.5 ml with 0.1 M HCl against phenolphthalein after addition of 0.5 M $BaCl_2$. Microbial biomass was determined by the chloroform fumigation method (Vance et al., 1987; Wu et al., 1990). After destructive sampling, the soil was carefully mixed and five grams of soil were directly extracted using 20 ml of 0.05 M K_2SO_4. Another five grams of soil were fumigated with chloroform for 24 h and then extracted in the same manner. The extracts were frozen until analysis for the total C concentration using a 2100 TOC/TIC analyzer (Analytik Jena, Germany). The non-fumigated samples were used to measure NH_4^+, NO_3^- and DOC. The total amount of microbial biomass was calculated based on the difference of K_2SO_4-extracable C between fumigated and non-fumigated soil samples using the k_{ec} factor 0.45 (Joergensen and Mueller, 1996). The soil water content was determined in another five grams of soil that was dried at 105 °C.

2.4. Data collection

The synthesis was performed on published data of N effect on soil CO_2 emission using *ISI* Web of Science and Google Scholar. The criteria were applied to select appropriate studies as follows. (1) We restricted the data collection to studies that the amount of applied N-fertilizer less than 60% of total N in the studied soils; (2) if one study presented the results of different duration from the same experiment, the data from longest duration were selected; and (3) The analysis was focused on N fertilization, thus studies including the effects of N addition under low temperature, dry condition or glucose addition were excluded. In total, 158 observations were extracted from 13 studies.

2.5. Calculations and statistical analysis

Priming effects were calculated according to the following equation:

$$PE = [CO_2]_{\text{treatment}} - [CO_2]_{\text{control}} \quad (2)$$

$$\text{Relative PE} = ([CO_2]_{\text{treatment}} - [CO_2]_{\text{control}})/[CO_2]_{\text{control}} \quad (3)$$

where, $[CO_2]_{\text{treatment}}$ and $[CO_2]_{\text{control}}$ represent CO_2 emissions in the N amended and control treatments, respectively.

The metabolic quotient (qCO_2) was calculated as the ratio of the CO_2 emission rate to microbial biomass (Anderson and Domsch, 1993). Net N mineralization was calculated as the difference of the sum of NH_4^+ and NO_3^- concentrations between two sampling times. Net nitrification was calculated as the difference of NO_3^- concentrations between two times (Owen et al., 2003). The net C/N ratio of mineralized SOM was calculated as the ratio of cumulative CO_2 emission to net N mineralization.

The significant differences of CO_2 rate, cumulative CO_2, priming effect, qCO_2 and microbial biomass under N fertilization is shown as LSD (5%) estimated by one-way ANOVA. We used linear mixed effects model (LME) to analysis the time-series data (CO_2 emission rate). The LME model included N fertilization as fixed effects whereas sampling dates and replicates were included as random effects. Fixed effects were considered significant based on the analysis of variance at $P \leq 0.05$, and differences between N fertilization were assessed using Fisher's LSD test. The experiment was done with 4 replications. Data are presented as means ± standard error (±SE).

3. Results

3.1. CO_2 emission and priming effects

The CO_2 emission rates decreased from day 1 to 24 and then remained nearly constant until the end of the experiment—56 days (Fig. 1a). N fertilization significantly decreased CO_2 emission rate across the incubation period ($P < 0.05$). The dynamics were similar for the qCO_2 (Fig. 1d). N fertilization decreased CO_2 emissions by 27–42% compared to the control (273 μg C g^{-1}; $P < 0.05$; Fig. 1b). The cumulative CO_2 over 56 days decreased exponentially with increasing N fertilization ($R^2 = 0.99$, $P < 0.001$; Fig. 2a). The cumulative PEs after 56 days were −72.4, −94.5 and −113.0 μg C g^{-1} for the low, medium, and high N levels, respectively. The PE was always negative and decreased with increasing N fertilization ($P < 0.05$; Fig. 1c). Similarly, the average qCO_2 decreased exponentially with increasing N fertilization ($R^2 = 0.84$, $P < 0.001$; Fig. 2b). In conclusion, N fertilization decreased the intensity of most C-related processes: CO_2 release, qCO_2, and priming effects of SOM decomposition.

3.2. Microbial biomass and mineral N

N addition decreased microbial biomass on day 21 and 56, depending on the amount of added N and the timing of measurements ($P < 0.05$; Fig. 3). The highest microbial biomass occurred on day 21 and was 206, 112, 114 and 163 μg C g^{-1} soil for the control, low, medium, and high N additions, respectively. Net N mineralization decreased with increasing N fertilization. Low and medium N fertilization rates had only minor effects, but high N fertilization strongly (for 20–59%) decreased net N mineralization ($R^2 = 0.44$, $P = 0.019$; Fig. 2c). Based on the ratio of released CO_2 and mineralized N, we calculated the net C/N ratio of mineralized SOM (Fig. 4). The net C/N ratios of mineralized SOM pools without N fertilization were similar to the ratio of SOM, and the net C/N ratio decreased with increasing N fertilization (Fig. 4). The added NH_4^+ was quickly oxidized to NO_3^- within 21 days (Fig. S1). In conclusion, N fertilization decreased microbial biomass and the rates of N turnover in the soil.

4. Discussion

N fertilization strongly decreased CO_2 emissions and induced pronounced negative PE in the rhizosphere soil: CO_2 values dropped by 27–42% compared with the control (no N addition) (Fig. 1b, c). These findings correspond with results from field studies, where soil CO_2 emissions dropped 8–15% after N fertilization (Janssens et al., 2010; Liu and Greaver, 2010). The

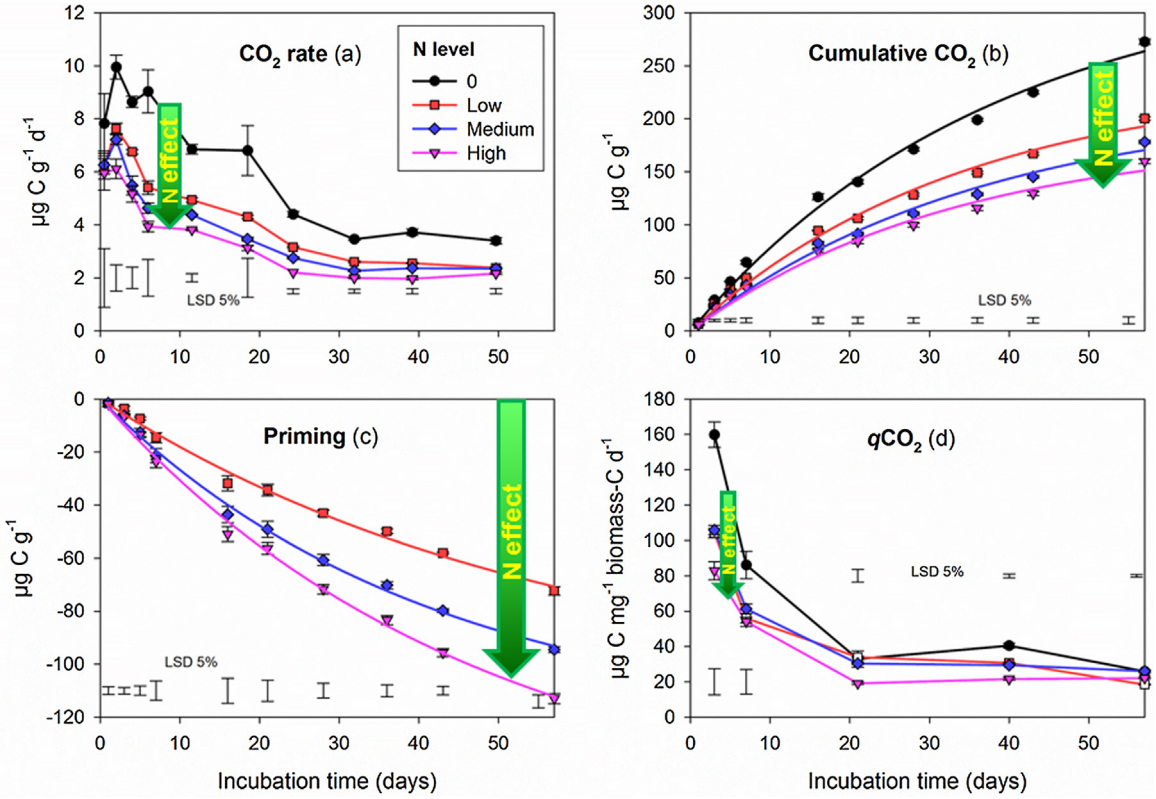

Fig. 1. CO_2 emission rates (a), cumulative CO_2 emissions (b), cumulative priming effect (c) and qCO_2 (d) over the 56-day incubation of the soil from the wheat rhizosphere after N fertilization (0, 52, 104, and 208 μg N g^{-1}). Values are means ± standard error (n = 4). The significant difference between N fertilization for each time is shown as LSD (5%). The green arrows show the N effect on CO_2 rate, cumulative CO_2, priming effect and qCO_2. Cumulative CO_2 emission and the priming effect were fitted with a one-pool decay model: CO_2 (t) = $P^*(1\text{-}\exp(-k^*t))$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

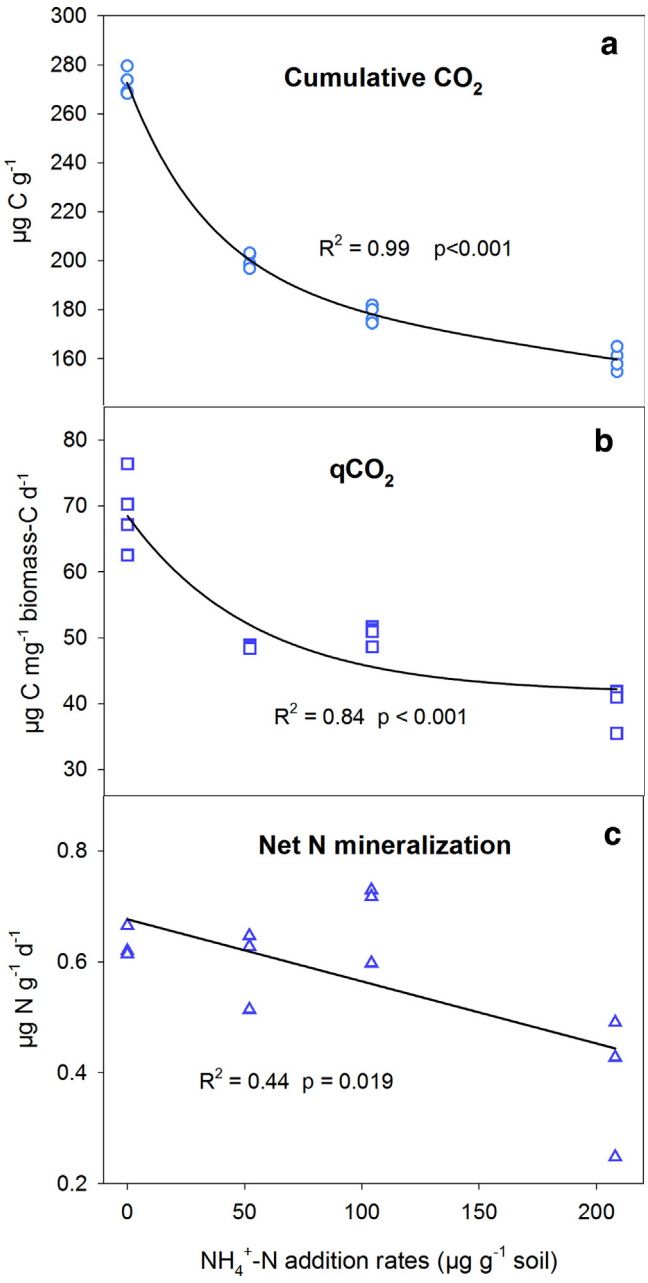

Fig. 2. Relationships of cumulative CO_2 emissions (a), qCO_2 (b) and net N mineralization (c) with N fertilization rates (0, 52, 104, and 208 μg N g^{-1}).
The qCO_2 here was calculated as average qCO_2 based on the CO_2 emission and microbial biomass in the whole incubation periods.

modeling based on exoenzyme-catalyzed SOM decomposition also indicated that adding N decreases soil CO_2 emission (Schimel and Weintraub, 2003). A meta-analysis, however, showed that N fertilization decreased CO_2 emissions only by 1.44% in forests and increased them by 7.84% and 12.4% in grasslands and croplands, respectively (Zhou et al., 2014). N additions to soil in previous field-based studies have divergent effects on SOM mineralization among terrestrial ecosystems (Janssens et al., 2010; Zhou et al., 2014; Waldrop and Zak, 2006). On one hand, N fertilization increased root growth and thus led to higher root biomass and consequently higher CO_2 release by root respiration in croplands and grasslands (Zhou et al., 2014). On the other hand, previous studies under field (Bowden et al., 2004; Mo et al., 2008) and controlled conditions (Kuzyakov et al., 2002) explained the reduced soil CO_2 emission because both root biomass and rhizodeposition dropped after increasing N availability. N fertilization generally changed root biomass and exudates and, therefore, field studies cannot fully separate the direct effect of N on SOM decomposition from the indirect effect – root-derived CO_2. In contrast, our soils did not receive any C inputs during the incubation, so that only the direct response of SOM to increased N was evaluated.

To generalize these results and partial discrepancies, we analyzed N fertilization effect on PEs from 13 studies with 158 observations in various land use and soil types (Fig. 6). PEs were negative in most of the studies and their intensity decreased exponentially with N addition ($P < 0.001$, n = 158). We found similar PE response between NH_4^+ and NO_3^-, which shows N fertilization inhibits soil microbial respiration regardless of nitrogen form. Most of the positive PEs was recorded in experiments where N addition was less than 10% of total soil N (Fig. 6). Small amounts of N, however, can stimulate microbial activity and affect the community structure; this may increase SOM mining, thereby causing positive PE (Dijkstra et al., 2013). N fertilization triggered lower extracellular enzyme activities and a shift to the preferential decomposition of more labile C pools (Ramirez et al., 2012). Because the rhizosphere experiences greater inputs of labile C than bulk soil, microorganisms will shift from mining SOM to utilizing nutrients under high nutrient availability (e.g. with high N input) (Blagodatskaya et al., 2007; Dijkstra et al., 2013; Kirkby et al., 2014). We therefore expected the decreased SOM mineralization (increased negative PE) with rising N amounts in the rhizosphere (Fig. 1c).

The decreased SOM mineralization under N fertilization may also be supported by the depressed net N mineralization after NH_4^+ addition (Fig. 2c). In contrast, N fertilization may accelerate SOM decomposition and thereby cause a positive PE (Cleveland and Townsend, 2006; Waldrop and Zak, 2006). Such positive PE is usually observed in severely N-limited soils and under elevated CO_2 (Janssens et al., 2010).

Soil microbial biomass is a sensitive indicator of environmental and land use changes (Pabst et al., 2013; Guillaume et al., 2016). The meta-analysis showed that mineral N addition reduced microbial biomass by 15–20%, thereby decreasing soil CO_2 emissions (Liu and Greaver, 2010; Treseder, 2008). N fertilization has indirect effects on microbial biomass by reducing fine root production and rhizodeposition (Treseder, 2008; Kuzyakov et al., 2002). Moreover, N addition stimulated enzymes that degrade labile C and inhibited those needed for the decomposition of recalcitrant C, thereby reducing overall microbial activity (Hobbie et al., 2012; Riggs et al., 2015; Mganga et al., 2015). Similarly, microorganisms reduced mining of recalcitrant SOM (lower N requirements) and shifted towards labile C under N addition (Moorhead and Sinsabaugh, 2006; Chen et al., 2014). The labile C pool, however, is scarce for microbial growth in most bulk soils (Blagodatsky et al., 1998; Schimel and Weintraub 2003) and, therefore, microbial biomass will decrease under N addition (Ramirez et al., 2012). In contrast to root-free soil, the rhizosphere receives greater inputs of labile C exudates, which are readily used by microorganisms (Kuzyakov et al., 2007). Thus, the microbial biomass was decreased on day 21 and 56 under N addition in the rhizosphere ($P < 0.05$; Fig. 3), but this decrease strongly depended on the amount of added N and the timing of measurements. Thus, the decreased CO_2 emission in our case was not only because of altered microbial biomass content. Moreover, the short-term incubation (56 days) was insufficient for microbial biomass to use up labile C in the rhizosphere. In a lengthier experiment, microbial biomass would probably have continuously decreased trend, as in bulk soil.

The efficiency of microbial metabolism depends strongly on nitrogen (N) availability (Blagodatskaya et al., 2014). N fertilization

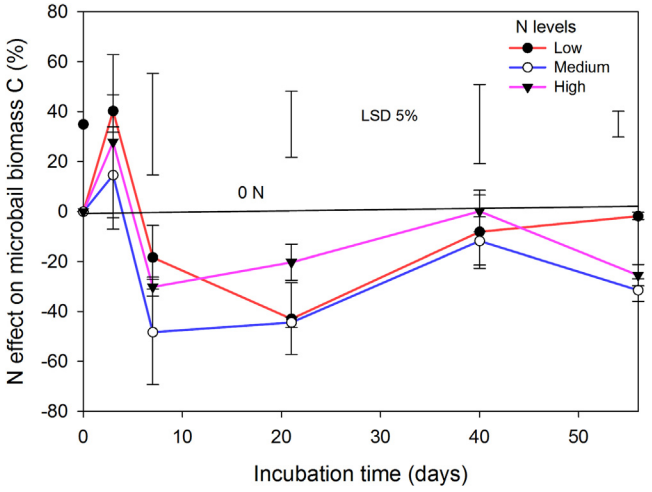

Fig. 3. Microbial biomass C changes (as% of the control) over the 56-day incubation after N fertilization (52, 104, and 208 μg N g^{-1}). Values are means ± standard error (n = 3). The significant difference between N fertilization for each time is shown as LSD (5%).

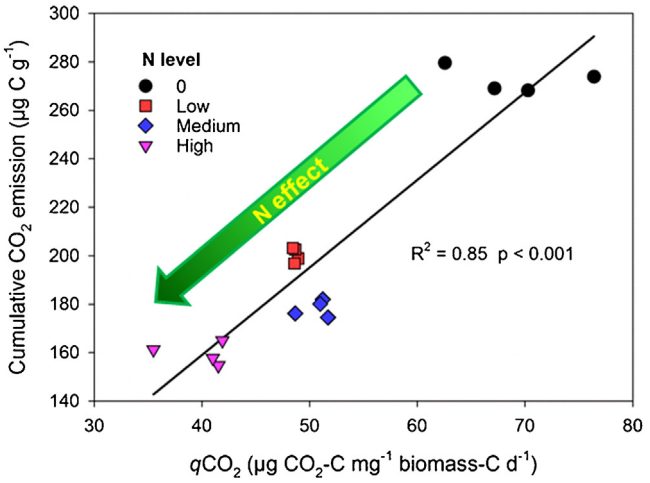

Fig. 5. Relationships of cumulative CO_2 emissions with qCO_2 over the 56-day incubation for the wheat rhizosphere under N fertilization rates (0, 52, 104, and 208 μg N g^{-1}). The green arrows show the N effect on cumulative CO_2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

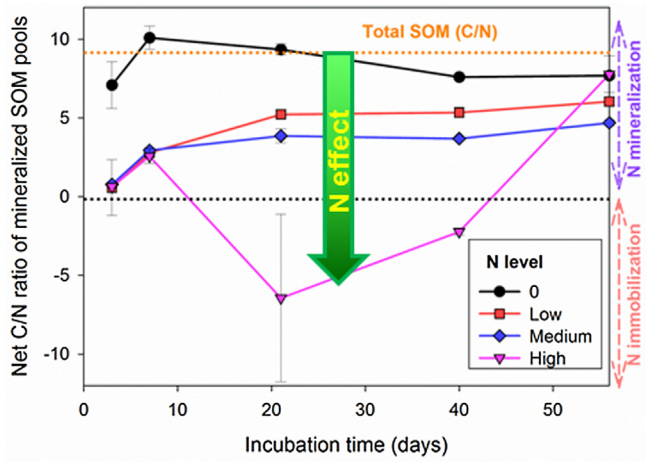

Fig. 4. Net C/N ratio of mineralized SOM pools over the 56-day incubation for the wheat rhizosphere depending on N fertilization (0, 52, 104, and 208 μg N g^{-1}). Values are means ± standard error (n = 4). The green arrows show the N effect on net C/N ratio of mineralized SOM pools. The net C/N ratio of mineralized SOM was calculated as the ratio of cumulative CO_2 emission to net N mineralization. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

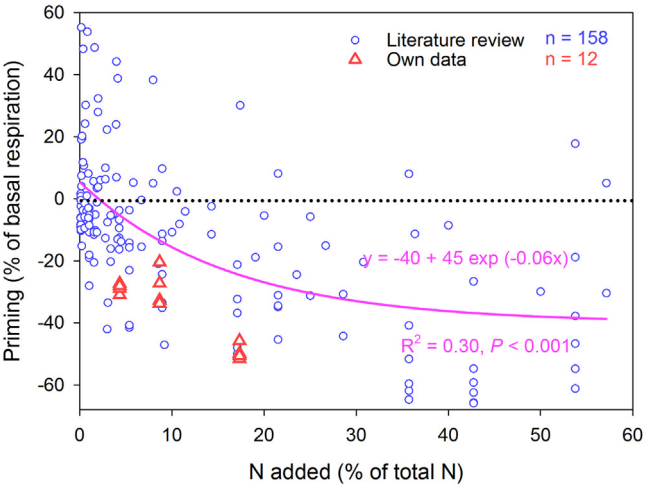

Fig. 6. Priming effect with increasing N fertilization. This figure is based on our study and the results of other studies (Ramirez et al., 2012, 2010; Waldrop and Zak, 2006; Basiliko et al., 2009; Priess and Fölster, 2001; Schaeffer et al., 2003; Mo et al., 2007; Mo et al., 2008; Lee and Jose, 2003; Ambus and Robertson, 2006; Hasselquist et al., 2012; Gao et al., 2014; Yang et al., 2014; Peng et al., 2011). The details for data selection can be found in the text.

reduces the cumulative CO_2 emission from soil with glucose. This was due to the higher efficiency of microbial C reutilization as compared with N-limited conditions (Blagodatsky et al., 1998). The negative linear relationship between qCO_2 and N addition rates confirm that the negative PE in rhizosphere is mainly driven by the increasing carbon use efficiency (CUE) with N fertilization (Figs. 1c and 5). N limitation stimulates the competitive abilities of K-strategists (Fontaine et al., 2011; Chen et al., 2014), decreases soil CO_2 emission and maintains CUE similar to in the values found in high N conditions in bulk soil (Blagodatskaya et al., 2014). In contrast, microorganisms, which show an r-strategy, increased CO_2 emission under N limitation in the rhizosphere. The result was higher specific respiration (maintenance) and thus lower CUE (Blagodatskaya et al., 2014). Overall, N fertilization reduces N limitation and increased CUE in the rhizosphere, thereby decreasing CO_2 emissions (Figs. 1b, 3 and 7).

5. Conclusions

Fertilization with NH_4^+ reduced SOM mineralization and qCO_2, but increased net N nitrification. These effects become stronger with increasing N levels. NH_4^+ fertilization decreased microbial biomass ($P < 0.05$), but depended on the amount of added N and the timing of measurements. The increased N availability in the rhizosphere (high C availability) caused a negative priming effect, presumably due to decreased microbial biomass and a higher C use efficiency, which was confirmed by the decreased qCO_2. A literature review showed that negative PEs were recorded in most (> 70%) of the studies and that values decreased exponentially with N addition ($P < 0.001$, n = 158). Even a small amount of N fertilization (< 10% total N) may cause a positive PE in about 35% of the cases. We conclude that N fertilization facilitates C sequestration in agricultural soils not only by increasing biomass

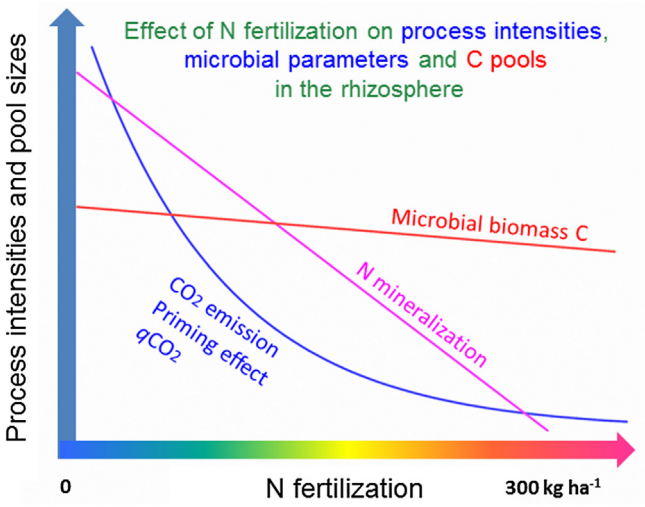

Fig. 7. Effect of N fertilization on process intensities, microbial parameters and C pools in the rhizosphere.

production and root amounts, but also by decreasing SOM decomposition.

Acknowledgements

We thank the China Scholarship Council for providing fund to Huadong Zang to pursue his study in Germany. The study was supported by German Research Foundation (DFG) within the project "Carbon input and turnover in subsoil biopores" (KU 1184/29-1). The authors also would like to thank Karin Schmidt and Anita Kriegel for laboratory assistancex.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.apsoil.2016.07.021.

References

Ambus, P., Robertson, G.P., 2006. The effect of increased N deposition on nitrous oxide, methane and carbon dioxide fluxes from unmanaged forest and grassland communities in Michigan. Biogeochemistry 79, 315–337.
Anderson, T.H., Domsch, K.H., 1993. The metabolic quotient for CO_2 (qCO_2) as a specific activity parameter to assess the effects of environmental conditions, such as pH, on the microbial biomass of forest soils. Soil Biol. Biochem. 25, 393–395.
Basiliko, N., Khan, A., Prescott, C.E., Roy, R., Grayston, S.J., 2009. Soil greenhouse gas and nutrient dynamics in fertilized western Canadian plantation forests. Can. J. Forest Res. 39, 1220–1235.
Blagodatskaya, E.V., Blagodatsky, S.A., Anderson, T.H., Kuzyakov, Y., 2007. Priming effects in Chernozem induced by glucose and N in relation to microbial growth strategies. Appl. Soil Ecol. 37, 95–105.
Blagodatskaya, E.V., Blagodatsky, S.A., Anderson, T.H., Kuzyakov, Y., 2014. Microbial growth and carbon use efficiency in the rhizosphere and root-free soil. PLoS One 9, e93282.
Blagodatsky, S.A., Yevdokimov, I.V., Larionova, A.A., Richter, J., 1998. Microbial growth in soil and nitrogen turnover: model calibration with laboratory data. Soil Biol. Biochem. 30, 1757–1764.
Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Emmett, B., 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. Ecol. Appl. 20, 30–59.
Bowden, R.D., Davidson, E., Savage, K., Arabia, C., Steudler, P., 2004. Chronic nitrogen additions reduce total soil respiration and microbial respiration in temperate forest soils at the Harvard Forest. Forest Ecol. Manag. 196, 43–56.
Burton, A.J., Pregitzer, K.S., Crawford, J.N., Zogg, G.P., Zak, D.R., 2004. Simulated chronic NO_3^- deposition reduces soil respiration in northern hardwood forests. Glob. Change Biol. 10, 1080–1091.
Canfield, D.E., Glazer, A.N., Falkowski, P.G., 2010. The evolution and future of Earth's nitrogen cycle. Science 330, 192–196.
Chen, R., Senbayram, M., Blagodatsky, S., Myachina, O., Dittert, K., Lin, X., Kuzyakov, Y., 2014. Soil C and N availability determine the priming effect: microbial N mining and stoichiometric decomposition theories. Glob. Change Biol. 20, 2356–2367.
Cheng, W., Kuzyakov, Y., 2005. Root effects on soil organic matter decomposition. Agronomy 48, 119–144.
Cheng, W., Parton, W.J., Gonzalez-Meler, M.A., 2014. Synthesis and modeling perspectives of rhizosphere priming. New Phytol. 201, 31–44.
Cleveland, C.C., Townsend, A.R., 2006. Nutrient additions to a tropical rain forest drive substantial soil carbon dioxide losses to the atmosphere. Proc. Natl. Acad. Sci. 103, 10316–10321.
Dijkstra, F.A., Carrillo, Y., Pendall, E., Morgan, J.A., 2013. Rhizosphere priming: a nutrient perspective. Front. Microbiol. 4, 183–190.
Fontaine, S., Henault, C., Aamor, A., Bdioui, N., Bloor, J.M.G., Maire, V., Mary, B., Revaillot, S., Maron, P.A., 2011. Fungi mediate long term sequestration of carbon and nitrogen in soil through their priming effect. Soil Biol. Biochem. 43, 86–96.
Galloway, J.N., Townsend, A.R., Erisman, J.W., Bekunda, M., Cai, Z., Freney, J.R., Sutton, M.A., 2008. Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. Science 320, 889–892.
Gao, Q., Hasselquist, N.J., Palmroth, S., Zheng, Z., You, W., 2014. Short-term response of soil respiration to nitrogen fertilization in a subtropical evergreen forest. Soil Biol. Biochem. 76, 297–300.
Guillaume, T., Maranguit, D., Murtilaksono, K., Kuzyakov, Y., 2016. New approach for sensitivity of soil fertility indicators to land use changes: theory and examples from conversion of Indonesian rainforest to plantations. Ecol. Indic. doi:http://dx.doi.org/10.1016/j.ecolind.2016.02.039.
Hasselquist, N.J., Metcalfe, D.B., Högberg, P., 2012. Contrasting effects of low and high nitrogen additions on soil CO_2 flux components and ectomycorrhizal fungal sporocarp production in a boreal forest. Glob. Change Biol. 18, 3596–3605.
Hobbie, S.E., Eddy, W.C., Buyarski, C.R., Adair, E.C., Ogdahl, M.L., Weisenhorn, P., 2012. Response of decomposing litter and its microbial community to multiple forms of nitrogen enrichment. Ecol. Monogr. 82, 389–405.
Janssens, I.A., Dieleman, W., Luyssaert, S., Subke, J.A., Reichstein, M., Ceulemans, R., Law, B.E., 2010. Reduction of forest soil respiration in response to nitrogen deposition. Nat. Geosci. 3, 315–322.
Joergensen, R.G., Mueller, T., 1996. The fumigation-extraction method to estimate soil microbial biomass: calibration of the k_{EN} value. Soil Biol. Biochem. 28, 33–37.
Jones, D.L., Hodge, A., Kuzyakov, Y., 2004. Plant and mycorrhizal regulation of rhizodeposition. New Phytol. 163, 459–480.
Jungk, A., 2001. Root hairs and the acquisition of plant nutrients from soil. J. Plant Nutr. Soil Sci. 164, 121–129.
Kirkby, C.A., Richardson, A.E., Wade, L.J., Passioura, J.B., Batten, G.D., Blanchard, C., Kirkegaard, J.A., 2014. Nutrient availability limits carbon sequestration in arable soils. Soil Biol. Biochem. 68, 402–409.
Kuzyakov, Y., Blagodatskaya, E., 2015. Microbial hotspots and hot moments in soil: concep & review. Soil Biol. Biochem. 83, 184–199.
Kuzyakov, Y., Xu, X., 2013. Competition between roots and microorganisms for nitrogen: mechanisms and ecological relevance. New Phytol. 198, 656–669.
Kuzyakov, Y., Siniakina, S.V., Ruehlmann, J., Domanski, G., Stahr, K., 2002. Effect of nitrogen fertilisation on below-ground carbon allocation in lettuce. J. Sci. Food Agric. 82, 1432–1441.
Kuzyakov, Y., Hill, P.W., Jones, D.L., 2007. Root exudate components change litter decomposition in a simulated rhizosphere depending on temperature. Plant Soil 290, 293–305.
Lee, K.H., Jose, S., 2003. Soil respiration, fine root production, and microbial biomass in cottonwood and loblolly pine plantations along a nitrogen fertilization gradient. Forest Ecol. Manag. 185, 263–273.
Liu, L., Greaver, T.L., 2010. A global perspective on belowground carbon dynamics under nitrogen enrichment. Ecol. Lett. 13, 819–828.
Liu, X., Zhang, Y., Han, W., Tang, A., Shen, J., Cui, Z., Zhang, F., 2013. Enhanced nitrogen deposition over China. Nature 494, 459–462.
Mganga, K.Z., Razavi, B.S., Kuzyakov, Y., 2015. Microbial and enzymatic response to nutrient additions in soils of Mt. Kilimanjaro region depending on land use. Eur. J. Soil Biol. 69, 33–40.
Mo, J., Zhang, W., Zhu, W., Gundersen, P., Fang, Y., Li, D., Wang, H., 2008. Nitrogen addition reduces soil respiration in a mature tropical forest in southern China. Glob. Change Biol. 14, 403–412.
Moorhead, D.L., Sinsabaugh, R.L., 2006. A theoretical model of litter decay and microbial interaction. Ecol. Monogr. 76, 151–174.
Owen, J.S., Wang, M.K., Wang, C.H., King, H.B., Sun, H.L., 2003. Net N mineralization and nitrification rates in a forested ecosystem in northeastern Taiwan. Forest Ecol. Manag. 176, 519–530.
Pabst, H., Kühnel, A., Kuzyakov, Y., 2013. Effect of land-use and elevation on microbial biomass and water extractable carbon in soils of Mt. Kilimanjaro ecosystems. Appl. Soil Ecol. 67, 10–19.
Peng, Q., Dong, Y., Qi, Y., Xiao, S., He, Y., Ma, T., 2011. Effects of nitrogen fertilization on soil respiration in temperate grassland in Inner Mongolia, China. Environ. Earth Sci. 62, 1163–1171.
Priess, J.A., Fölster, H., 2001. Microbial properties and soil respiration in submontane forests of Venezuelian Guyana: characteristics and response to fertilizer treatments. Soil Biol. Biochem. 33, 503–509.
Ramirez, K.S., Craine, J.M., Fierer, N., 2010. Nitrogen fertilization inhibits soil microbial respiration regardless of the form of nitrogen applied. Soil Biol. Biochem. 42, 2336–2338.

Ramirez, K.S., Craine, J.M., Fierer, N., 2012. Consistent effects of nitrogen amendments on soil microbial communities and processes across biomes. Glob. Change Biol. 18, 1918–1927.
Richardson, A.E., Kirkby, C.A., Banerjee, S., Kirkegaard, J.A., 2014. The inorganic nutrient cost of building soil carbon. Carbon Manag. 5, 265–268.
Riggs, C.E., Hobbie, S.E., Bach, E.M., Hofmockel, K.S., Kazanski, C.E., 2015. Nitrogen addition changes grassland soil organic matter decomposition. Biogeochemistry 125, 203–219.
Schaeffer, S.M., Billings, S.A., Evans, R.D., 2003. Responses of soil nitrogen dynamics in a Mojave Desert ecosystem to manipulations in soil carbon and nitrogen availability. Oecologia 134, 547–553.
Schimel, J.P., Weintraub, M.N., 2003. The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model. Soil Biol. Biochem. 35, 549–563.
Schlesinger, W.H., 2009. On the fate of anthropogenic nitrogen. Proc. Natl. Acad. Sci. 106, 203–208.
Schmitt, A., Pausch, J., Kuzyakov, Y., 2013. C and N allocation in soil under ryegrass and alfalfa estimated by ^{13}C and ^{15}N labelling. Plant Soil 368, 581–590.
Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Swackhamer, D., 2001. Forecasting agriculturally driven global environmental change. Science 292, 281–284.
Treseder, K.K., 2008. Nitrogen additions and microbial biomass: a meta-analysis of ecosystem studies. Ecol. Lett. 11, 1111–1120.
Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass C. Soil Biol. Biochem. 19, 703–707.
Waldrop, M.P., Zak, D.R., 2006. Response of oxidative enzyme activities to nitrogen deposition affects soil concentrations of dissolved organic carbon. Ecosystems 9, 921–933.
Wu, J., Joergensen, R.G., Pommering, B., Chaussod, R., Brookes, P.C., 1990. Measurement of soil microbial biomass C by fumigation – extraction – an automated procedure. Soil Biol. Biochem. 22, 1167–1169.
Yang, K., Zhu, J., Xu, S., 2014. Influences of various forms of nitrogen additions on carbon mineralization in natural secondary forests and adjacent larch plantations in Northeast China. Can. J. Forest Res. 44, 441–448.
Zhou, L., Zhou, X., Zhang, B., Lu, M., Luo, Y., Liu, L., Li, B., 2014. Different responses of soil respiration and its components to nitrogen addition among biomes: a meta-analysis. Glob. Change Biol. 20, 2332–2343.