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N fertilization decreases soil organic matter decomposition in the rhizosphere

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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

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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.