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Microbial carbon use efficiency and priming effect regulate soil carbon storage under nitrogen deposition by slowing soil organic matter decomposition

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ABSTRACT

Microbial carbon use efficiency (CUE) strongly influences the rate of soil organic carbon (SOC) formation by mediating C loss via microbial respiration, whereas the priming effect plays a crucial role in regulating the stability of SOC. Nitrogen (N) deposition increases N availability and alters litter quality and quantity, both of which could strongly affect the CUE and priming effect. However, it remains unclear whether and how, under N deposition, the CUE and priming effect could affect soil C cycling. In this study, we conducted a consecutive 12-yr N addition experiment in a temperate steppe. We evaluated how increasing N inputs affect soil C accumulation, microbial respiration, microbial biomass and composition in the field. We also performed an incubation experiment by adding ^{13}C labeled glucose and phenol to the pre-incubated soils to test how N addition affects microbial CUE and the priming effects on stable soil C. Our field experiment showed that N addition increased soil organic C concentration and decreased soil microbial respiration, microbial total phospholipid fatty acids (PLFAs), and fungi to bacteria (F:B) ratio. Our incubation experiments indicated that N addition increased microbial CUE of glucose but decreased that of phenol. The priming effects of both glucose and phenol were suppressed by N addition. Redundancy analysis (RDA) showed the importance of fungi in regulating microbial CUE and priming effect. Specifically, multi-model averaging suggested that the decreased fungal biomass under N addition was the most important predictor for changes in CUE of glucose, while decreased fungal biomass and F:B ratio were the most important predictors for changes in the CUE and priming effects. In addition, the increased CUE of glucose best explained the decreased microbial respiration, and the reduced priming effect of glucose best explained the increased SOC under N addition. Overall, our finding suggested that N addition would alter microbial CUE and the priming effects on stable soil C. The different responses of CUE and priming effects to glucose and phenol addition imply that the decreased microbial respiration and increased C storage under N deposition could be more attributed to labile C inputs rather than recalcitrant C inputs.

1. Introduction

Soil C storage is largely controlled by the balance between aboveground C inputs and belowground microbial-mediated decomposition (Riggs et al., 2015). It is well-known that N deposition generally stimulates aboveground productivity (Liu and Greaver, 2010; Frey et al., 2014), but whether and how N deposition can affect soil C storage and stability is less understood. A growing body of evidence reveals that N deposition could suppress microbial respiration, which has been explained by intensified soil acidification (Bowman et al., 2008; Treseder, 2008; Liu et al., 2014), decreased microbial biomass (Riggs and Hobbie, 2016), or inhibited oxidative enzyme (Boot et al., 2016). However, plant substrate quality and microbial composition could also affect microbial respiration by altering the efficiency of the microbial community in producing and maintaining microbial biomass (Schimel and Weintraub, 2003). Furthermore, changes in plant C inputs under N deposition could affect the microbial capacity to decompose stable soil C thus regulate long-term soil C storage (Dijkstra et al., 2013). Therefore, a better understanding of the metabolic responses of microbes is needed to distinguish the underlying mechanisms driving the response

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of soil C storage to N deposition.

Soil microbial C use efficiency (CUE) is defined as the efficiency of production of soil microbial biomass from plant detrital C (Cotrufo et al., 2013; Sinsabaugh et al., 2013). Thus, a portion of plant detrital C is incorporated into microbial biomass, while other portions are used to maintain microbial metabolism and released to the atmosphere as microbial respiration. Microbial CUE is affected by N availability, since microbes need energy and N to balance anabolic and catabolic reactions (Sinsabaugh et al., 2013). Theoretical models predict that N limitation results in higher C allocation to N acquisition, which subsequently decreases microbial CUE and inhibits microbial growth (Agren et al., 2001; Schimel and Weintraub, 2003; Manzoni et al., 2012). Accordingly, as N availability increases, soil microbes would allocate less energy to the acquisition of N, and less C would be respired (Spohn et al., 2016).

In addition, different microbial species differ in their substrate preference and thus their CUE (Morrissey et al., 2017). Because microbial community often has higher CUE when utilize substrates with lower C:N ratio (Devêvre and Horwáth, 2000), N deposition could promote microbial CUE via decreasing C:N ratio of substrates (Craine et al., 2007; Manzoni et al., 2012; Finn et al., 2015). Moreover, N deposition could shift soil microbial community toward copiotrophic microbial community with greater bacterial abundance (Fierer et al., 2012), and consequently facilitates CUE since bacterial CUE tends to increase with increasing N availability (Keiblinger et al., 2010). Although microbial community composition has been investigated under N addition (Leffa et al., 2015), it is unclear how N deposition affects microbial CUE and consequent microbial respiration by changes in microbial communities.

The priming effect is defined as changes in the decomposition rate of soil organic matter in response to fresh C input and, consequently, influences soil C stability and storage (Kuzyakov, 2010; Dijkstra et al., 2013). The strength of the priming effect is closely related to N availability (Fontaine et al., 2011; Chen et al., 2014). The priming effect is higher under lower N availability because microbes have to mine organic carbon to meet their N requirements (Craine et al., 2007; Fontaine et al., 2011). Conversely, N enrichment can alter plant chemistry by reducing the C:N ratio (Li et al., 2015; Sardans et al., 2017). The priming effect tends to decrease when substrates with low C:N ratio are supplied, because microbes do not need to decompose SOM to acquire N (Dijkstra et al., 2013). A better understanding on how the priming effect responds to intensified atmospheric N deposition will facilitate the simulation and prediction of soil C stability and storage in the future.

Grassland ecosystems contain more soil C per unit area than the global average and play a central role in the global C cycle (Riggs and Hobbie, 2016). In this study, we examined how increasing N inputs affect a range of soil and microbial properties, including soil carbon concentration, microbial respiration, microbial biomass and composition in a temperate grassland in the Mongolian Plateau. Ambient N deposition is about 1.6 g N m^{-2} and is expected to continually increase in this area (Zhang et al., 2008). We also pre-incubated soils to deplete active C pool and amended those soils with ^{13}C labeled glucose and phenol to evaluate how N inputs influence microbial CUE and priming effect on the stable C pool. We aimed to test three hypotheses: (1) N addition stimulates microbial CUE and thus decrease microbial respiration per unit of soil organic C; (2) increased N availability decreases the priming effect on stable soil C; (3) the changes in microbial CUE and priming effect are partially driven by the changes in microbial community composition under N addition.

2. Materials and methods

2.1. Field experiment and field measurements

The experimental site is located in a semiarid steppe (42.02′ N, 116.17′E and 1324 m a.s.l) in Duolun County, Inner Mongolia, Northern China. Mean annual temperature and precipitation are 2.1 °C and 382.3 mm, respectively. The soil type is classified as Haplic Calcisols (FAO classification), with 69.21 ± 0.06% sand, 15.60 ± 0.02% silt and 15.19 ± 0.02% clay. Soil organic C and total N contents are 16.94 ± 2.34 and 1.65 ± 0.27 g kg^{-1}. Soil pH is approximately 6.84 ± 0.02. The plant community at our experiment site is dominated by *Stipa krylovii* Roshev., *Agropyron cristatum* (L.), *Artemisia frigida* Willd, and *Cleistogenes squarrosa* (Trin.).

Sixty-four plots were arranged in 8 rows and 8 columns. Starting in 2003, each of the 8 plots in each row was randomly assigned with one of the 8 levels of N fertilization treatments (0, 1, 2, 4, 8, 16, 32 and 64 g N m^{-2} y^{-1}). The N addition rates were comparable to other N addition experiments in grassland ecosystems (Bai et al., 2010; Dickson and Foster, 2011). Once a year since 2003, N fertilization was conducted in July in the form of urea. Since 2005, four rows (one in each two rows) were clipped once a year. The plot size was 10 × 15 m with 5-m buffer zones between adjacent plots.

Root exclusion with trenched plot techniques was used to partition soil respiration (R_s) into autotrophic (R_a) and heterotrophic (R_h) components (Kuzyakov, 2006). PVC collars with 20 cm diameter were inserted 30 cm into soil to isolate plant roots and exclude Ra in September 2013. Two PVC collars with 11 cm diameters were subsequently inserted 2–3 cm into soil inside the large PVC collars (R_h without roots as root exclusion collars) and outside (R_s with roots as control collars) to measure respiration. The EGM-4 infrared gas analyzer system equipped with the SRC-2 soil respiration chamber (PP systems, Hitchin, UK) was used to measure soil CO_2 flux (on both root exclusion collars and control collars) in situ four times per month during the growing season from 29 May to 15 September in 2014. At the time of measuring soil respiration, soil moisture and soil temperature at 10 cm depth were also be measured concurrently.

Soil temperature and soil moisture were higher inside of the collars compared to outside because of the root exclusion tubes. Heterotrophic respiration could be overestimated when measuring respiration inside of the collars (root exclusion collars). To correct the R_h measured for any soil temperature and moisture differences induced by collar trenching, an exponential quadratic function adapted from Saiz et al. (2007) was used to calibrate R_h as the following,

$$R_h = a*\exp(b*ST)*(c*SM + d*SM^2)*\exp(e*R_s).$$

In the function, R_h, ST, SM were heterotrophic respiration, soil temperature, and soil moisture inside of the collars, respectively; a, b, c, d, and e were coefficients determined in the equation fitting. Then, we used the coefficients, soil temperature, and soil moisture outside of the collars to correct the R_h. To validate the equation, we calculated R_h using the coefficients, soil temperature, and soil moisture inside of the collars, and obtained the relationships between calibrated R_h and measured R_h (Fig. S1).

2.2. Soil sampling and chemical analysis

On August 21, 2013, fresh soil samples were collected from the unclipped plots with the exception for the 64 g N m^{-2} y^{-1} treatment. At each plot, four 0–15 cm cores (5 cm in diameter) were randomly taken and composited to obtain a fresh sample. After removing stones and sieving at 2 mm, the sieved fresh soil samples were stored in iceboxes, and transferred to the laboratory for microbial analysis and laboratory incubation. Hence, we obtained 28 soil samples in total. Subsamples for each soil sample were separated and air-dried to analyze soil organic C content.

2.3. Plant biomass, soil chemical properties and microbial measurements

Aboveground plant biomass (AGB) was estimated by clipping live biomass on August 20, 2014. All living plant tissues were harvested