Applied Soil Ecology 114 (2017) 152–160

Contents lists available at ScienceDirect

Applied Soil Ecology

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

Labile carbon and nitrogen additions affect soil organic matter decomposition more strongly than temperature

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ARTICLE INFO

Article history:
Received 7 January 2017
Accepted 16 January 2017
Available online 2 March 2017

Keywords:
Subtropical forest soil
Priming effects
Carbon availability
Nitrogen mining
Temperature sensitivity

ABSTRACT

Inputs of labile carbon (C) and nitrogen (N) affect the intensity and direction of priming effects (i.e., increase or decrease of soil organic matter (SOM) decomposition caused by labile inputs). Increased temperature is also an important factor affecting SOM decomposition. However, the effects of temperature on priming of SOM decomposition remain unclear. To investigate how temperature affects priming of SOM decomposition through changing microbial composition, we added ^{13}C-labeled glucose with or without NO_3^- or NH_4^+ to a subtropical plantation soil in southern China and incubated the soil at 15 °C and 25 °C for 10 days. Soil microbial composition was assessed by analysis of phospholipid fatty acids (PLFAs). Glucose led to positive priming (release of additional CO_2) at both temperatures. In contrast, glucose addition with NO_3^- or NH_4^+ resulted in negative priming. Temperature did not show a significant effect on SOM decomposition, while the effects of temperature on priming of SOM decomposition were dependent on labile C and N. Labile C addition induced stronger priming at 25 °C than at 15 °C, while combined C and N addition more strongly reduced priming at the high than the low temperature. Although PLFA composition was affected by temperature and labile C and N inputs, changes in PLFA composition were not correlated with priming. We conclude that temperature changes may have limited effects on SOM decomposition in this subtropical soil, while the availability of labile organics has a much stronger effect on priming under warming.

1. Introduction

Soil organic matter (SOM) contains the largest amount of carbon (C) in terrestrial ecosystems (German et al., 2011), almost four times higher than that in the atmosphere (Tarnocai et al., 2009). Even small changes in this soil C pool could significantly affect atmospheric CO_2 concentration, leading to positive feedbacks on climate change (Raich and Potter, 1995; Schlesinger and Lichter, 2001). Therefore, investigating the factors affecting SOM dynamics is a prerequisite for better understanding climate-carbon cycle feedbacks (Sun et al., 2014).

Temperature is an important factor affecting SOM dynamics. Increased temperature substantially accelerates SOM decomposition (Kirschbaum, 2006; Conant et al., 2011; Razavi et al., 2015), thus potentially contributing to global warming. Therefore, many studies have examined temperature sensitivity of SOM decomposition in the alpine, boreal, and temperate ecosystems (Lu et al., 2013), where the most dramatic increases in temperature have been predicted. Although greater understanding has been achieved, the results from various studies regarding the temperature sensitivity of SOM decomposition remain controversial (Giardina and Ryan, 2000; Fang et al., 2005; Bradford, 2013). Although a temperature increase is also expected in subtropical forests (Liski et al., 2003; Tan et al., 2012; Dai et al., 2016), few studies have explored the effects of warming on SOM decomposition (Wu et al., 2016).

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http://dx.doi.org/10.1016/j.apsoil.2017.01.009
0929-1393/

Priming effect, defined as strong short-term changes in SOM decomposition rates caused by labile additions (Kuzyakov et al., 2000), has been shown to accelerate SOM decomposition by up to 380% or to decrease SOM decomposition by up to 50% (Kuzyakov, 2002; Cheng et al., 2014). Here, accelerated SOM decomposition is referred to as a positive priming effect while decreased SOM decomposition is regarded as a negative priming effect (Kuzyakov et al., 2000). Labile C inputs have a strong potential to affect SOM decomposition through inducing positive priming (Kuzyakov, 2010; Cheng et al., 2014) and, therefore, are another critical factor affecting SOM dynamics and the C cycle. Preferential substrate utilization (Cheng, 1999), microbial community shifts (Fontaine et al., 2003), mining of N (Craine et al., 2007), C starvation (Hobbie and Hobbie, 2013), and microbial activation (Blagodatskaya et al., 2007) have been invoked to explain the occurrence of priming effects; however, the mechanisms are still not fully understood. Microbial N mining could be an important mechanism responsible for priming of SOM decomposition, as N limitation occurs in most terrestrial ecosystems (LeBauer and Treseder, 2008). However, this possibility still needs extensive experimental investigation.

Both temperature and priming effects can accelerate SOM decomposition, but their effects may have distinct pathways. Generally, increased temperature enhances the rates of enzyme reactions through decreasing activation energy (Davidson et al., 2006; Blagodatskaya et al., 2016). At the same time, temperature can directly affect microbial metabolism or change microbial composition through influencing microbial interactions. Therefore, increased temperature can produce short-term and long-term effects on microbial decomposition of SOM. In contrast to temperature, other priming effects affect SOM decomposition mainly through labile inputs, which affect microbial growth and activities. In most soils, 10–40% of microbes are potentially active. Addition of labile organics to soils could stimulate potentially active microbes and contribute to microbial activities over short-term periods (Blagodatskaya and Kuzyakov, 2013). Additionally, labile inputs can cause microbial community shifts and/or lead to preferential substrate utilization by the microbes. Overall, both temperature and added substrates can cause changes in microbial composition (Zhou et al., 2015). Further, temperature can also affect microbial utilization of labile organics (Manzoni et al., 2012) and thus influence SOM priming. These interactions have not yet been evaluated.

Soil microbes need C and N in stoichiometric ratios for their growth and functioning (Lovell and Jarvis, 1995; Bardgett et al., 2008). Thus, inorganic N addition could modify the effects of added organics on microbial decomposition and microbe responses to increased temperature. Inorganic N forms have distinct properties, e.g., NH_4^+ is reduced and positively charged, while NO_3^- is oxidized and negatively charged. Microbes can directly use NH_4^+ for protein assimilation, but they need energy to reduce NO_3^- to NH_4^+ for further utilization. This indicates that NH_4^+ and NO_3^- could produce distinct effects on microbial decomposition of SOM (Britto and Kronzucker, 2013), but these effects remain unclear.

Forests play an important role in the global and regional C cycle; the C stock of forests, including soil and vegetation, has been estimated to be approximately 1,150 Pg C (Dixon et al., 1994). Approximately 40% of the total C is stored in subtropical and tropical forests (Dixon et al., 1994). In such forest types, most tree species are broad-leaved evergreens, and root exudation and litter decomposition occur nearly throughout the year, which can induce a positive priming effect and thus affect SOM dynamics (Qiao et al., 2014, 2016). Additionally, local temperatures are predicted to increase in these regions. Understanding how temperature affects priming of SOM decomposition will provide insights into climate C cycle feedbacks in subtropical forests. To address this question, we conducted an incubation experiment using subtropical plantation soil from southern China where such plantations are widely distributed and cover an area of approximately 25 million hectares (Wang et al., 2010). As microbial responses to labile inputs and temperature are very rapid, we incubated soil amended with glucose or glucose and inorganic N for a short period (10 days) at two temperatures (15 and 25 °C). Phospholipid fatty acid (PLFA) analysis was used to evaluate changes in microbial composition. We hypothesized that: (1) SOM decomposition is modified by labile C and N additions in subtropical soils, and that labile C addition induces positive priming, while N addition reduces SOM decomposition (NH_4^+ might have a stronger inhibitory effect than NO_3^- because energy is necessary for NO_3^- reduction); (2) priming of SOM decomposition increases with temperature; and (3) priming of SOM decomposition is related to changes in microbial composition.

2. Materials and methods

2.1. Site location and description

The study site is located at Qianyanzhou Forest Experimental Station in Jiangxi Province, southern China (115°04′13″E, 26°44′48″N), at an altitude of 100 m. The site is characterized by typical subtropical monsoon climate. Meteorological records for Qianyanzhou from 1989 to 2010 showed that average annual precipitation ranges from 1,300 mm to 1,600 mm, and the mean annual temperature is 18.0 °C, with the highest and lowest temperatures recorded as 39.5 °C and −5.8 °C, respectively. The native vegetation type is broad-leaf evergreens. However, the natural vegetation was destroyed by human activities and was changed to plantations in the 1980s. These plantations are dominated by Chinese fir (*Cunninghamia lanceolata*), slash pine (*Pinus elliottii*), masson pine (*Pinus massoniana*), and mixed with *Schima superba*, *Cinnamomum camphora*, and *Liriodendron chinense*. The main soil type in this region is red earth (Wang et al., 2004; Sun et al., 2006; Yuan et al., 2015) of the orthic acrisol category (FAO, 2014). The soil is a silty clay and contains 17% sand, 68% silt, and 15% clay by weight (Wen et al., 2010).

Because Chinese fir is the most important plantation tree species in this region, we collected the soil samples (top 10 cm), from a Chinese fir plantation that was established in 1998. The plantation was dominated by Chinese fir, with a few other species also present, such as masson pine and *Liquidambar formosana*. The dominant species of the understory layer were *Adinandra millettii*, *Callicarpa*, *Dicranopteris dichotoma* and *Woodwardia japonica*. The soil organic carbon (SOC) content in the sample was 18.2 g kg^{-1} with a field water-holding capacity (WHC) of 39.8% and soil pH of 4.3.

2.2. Soil collection and preparation

Before collecting soil samples, four plots (20 m × 20 m) were randomly selected in one Chinese fir plantation ecosystem and the plots were separated by buffer zones of more than 20 m. In each plot, five points were randomly set up to collect soil samples (the distance between points was more than 5 meters). After the aboveground vegetation and litter layer were removed, soil was collected from the top 10-cm soil layer using a polyvinylchloride cylinder (4.0-cm diameter). Four soil cores were collected from each point and 20 soil cores from one plot were pooled as one sample. In total, four soil samples were collected. After removing roots and stones, each soil sample was passed through a 2-mm sieve for homogenization. The sieved soil samples were stored at 4 °C until the incubation experiment started.