



# Responses of microbial biomass carbon and nitrogen to experimental warming: A meta-analysis



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## ABSTRACT

Soil microbes play important roles in regulating terrestrial carbon and nitrogen cycling and strongly influence feedbacks of ecosystems to global warming. However, the inconsistent responses of microbial biomass carbon (MBC) and nitrogen (MBN) to experimental warming have been observed, and the response ratio between MBC and MBN (MBC:MBN) has not been identified. This meta-analysis synthesized warming experiments at 58 sites globally to investigate the responses of MBC:MBN to climate warming. Our results showed that warming significantly increased MBC by  $3.61 \pm 0.80\%$  and MBN by  $5.85 \pm 0.90\%$  and thus decreased the MBC:MBN by  $3.34 \pm 0.66\%$ . MBC showed positive responses to warming but MBN exhibited negative responses to warming at low warming magnitude ( $<1\text{ }^{\circ}\text{C}$ ); however, at high warming magnitude ( $>2\text{ }^{\circ}\text{C}$ ) the results were inverted. The different effects of warming magnitude on microbial biomass resulted from the warming-induced decline in soil moisture and substrate supply. Moreover, MBC and MBN had strong positive responses to warming at the mid-term (3–4 years) or short-term (1–2 years) duration, but the responses tended to decrease at long-term ( $\geq 5$  years) warming duration. This study fills the knowledge gap on the responses of MBC:MBN to warming and may benefit the development of coupled carbon and nitrogen models.

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## 1. Introduction

Soil microbes play an important role in regulating terrestrial carbon (C) and nitrogen (N) cycling by controlling litterfall decomposition, C and N mineralization, N nitrification and denitrification (Murata et al., 1999; Liski et al., 2003). Temperature is considered as one of the most important variables for microbial activities, and therefore climate warming strongly alters microbial activities resulting in substantial changes of ecosystem C and N cycles (Zhang et al., 2005; Butenschoen et al., 2011; Xu et al., 2016). Moreover, coupled C and N cycles can influence the ecological process (Gruber and Galloway, 2008). Several modeling studies have highlighted that interactions between C and N cycles within land ecosystems are likely to impact the trajectories of atmospheric

CO<sub>2</sub> concentration and associated global climate changes (Thornton et al., 2007; Zaehle et al., 2010).

Recently, the coupled C and N models have been developed and fully incorporated into the ecosystem models, such as the CENTURY family (Parton et al., 1987, 1988, 1998; Metherell et al., 1993), CASA-CNP (Wang et al., 2010), JSBACH-CNP (Goll et al., 2012), CABLE-CNP (Exbrayat et al., 2013), ORCHIDEE-CN (Zaehle et al., 2010), CLM-CN (Thornton et al., 2007) and N14CP (Davies et al., 2016). Previous studies showed the improvements of coupled C and N models in predicting vegetation production and the responses to CO<sub>2</sub> fertilization and climate warming (Zaehle et al., 2010; Smith et al., 2014). In general, the coupled C and N models are fully prognostic with respect to all C and N state variables in the vegetation, litter, soil organic matter and microbial biomass (Zaehle et al., 2014). Plant growth is limited when the N demand, driven by C:N ratios, is not satisfied by the amounts of soil inorganic N available for plant uptake (Greaver et al., 2016). Biological gross N mineralization is coupled with C mineralization using the C:N ratio of each litter or soil organic C (SOC) compartment (Aber et al., 1997; McMurtrie et al., 2000; Verburg and Johnson, 2001). Therefore, the ratio of

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MBC and MBN links SOC, inorganic N availability and vegetation production. A thorough understanding of responses of soil MBC and MBN to temperature is urgently needed to accurately predict and understand how climate warming will alter greenhouse gas emissions (Conant et al., 2011; Frey et al., 2013).

In addition, microbial models were developed to improve the prediction accuracy of C cycling, which strongly rely on the responses of microbial to climate warming (Schimel and Weintraub, 2003; Allison et al., 2010; German et al., 2012; Wang et al., 2012). Contemporary Earth System Models (ESMs), using traditional soil C models, simulate microbial decomposition by first-order kinetics that determines turnover rates of soil C pools (Friedlingstein et al., 2006; Todd-Brown et al., 2013). However, traditional models do not incorporate microbial physiological processes that transform and stabilize soil C pools (Conant et al., 2011; Schmidt et al., 2011). In contrast, recent microbial models explicitly simulate microbial biomass, and such models simulate soil C pools that more closely match contemporary observations compared with traditional models (Wieder et al., 2013). However, the microbial models also project a much wider range of soil C over the twenty-first century largely depended on the responses of microbial to climate warming (Allison et al., 2010; McGuire and Treseder, 2010; Fang et al., 2013). If microbial growth efficiency does not change with warming, then enzyme kinetics dominate and soils lose up to 300 Pg C in year 2100 (Wieder et al., 2013). However, this effect can be completely offset if microbial growth efficiency declines with warming and global soil C losses over the twenty-first century could be negligible.

Field experiments can provide profound insights for model development of microbial activity responding to climate warming. However, previous experiments reported substantially different effects of warming on soil microbial activity across climate regions and ecosystem types (Bradford et al., 2008; Liu et al., 2009; Wang et al., 2014; Chen et al., 2015). For example, experimental warming increased soil MBC in the US Great Plains (Belay-Tedla et al., 2009), but decreased MBC in alpine meadow on the Tibetan Plateau (Fu et al., 2012). The different responses of MBC to warming between above two studies result from different mechanisms in microbial acclimation: the former was related to warming-induced increase in substrate supply from plant biomass input for microorganisms (Belay-Tedla et al., 2009) while the latter was attributed to the limit of warming-induced decline in soil water content on microbial activity (Fu et al., 2012). Moreover, both short-term and long-term warming duration had different effect on the MBC and MBN. For example, some studies with short-term warming duration ( $\leq 4$  years) showed experimental warming had a positive (Belay-Tedla et al., 2009; Shi et al., 2012) or a neutral (Zhang et al., 2005; Xu et al., 2010) effect on MBC and MBN, whereas other studies with long-term ( $\geq 5$  years) warming duration indicated that warming significantly decreased MBC and MBN (Rinnan et al., 2007, 2009). Previous meta-analyses revealed that field warming increased MBC worldwide but there have been inconsistent reports of the MBN response to warming (Bai et al., 2013; Zhang et al., 2015). However, another meta-analysis found significant increases in both MBC and MBN on the Tibetan Plateau (Zhang et al., 2015). Each of these meta-analyses only focused on MBC or MBN independently (Bai et al., 2013; Lu et al., 2013; Chen et al., 2015), or analyzed in limited-region (Zhang et al., 2015). Therefore, a worldwide meta-analysis with both MBC and MBN response to climate warming is needed to develop realistic microbial responses to warming in coupled CN models.

The changes in the MBC:MBN strongly determined the adjustment of microbial N use efficiency (NUE) and C use efficiency (CUE), which are important for resource stoichiometry balance (Mooshammer et al., 2014). At the low substrate C:N ratios (N-sufficient), strictly homeostatic organisms have low NUE but high

CUE. In contrast, at high substrate C:N ratios (N-deficiency) they are expected to lower their CUE while increasing their NUE (Mooshammer et al., 2014). Recent study showed that in soils with higher water content where available C is relatively more sufficient than available N, soil microbes prioritize the immobilization of available N. Under this conditions, microbes may decrease their CUE but increase their NUE, resulting in lower MBC:MBN (Chen et al., 2016).

In this study, global experimental warming measurements at 58 sites were synthesized to examine responses of MBC and MBN, including their coupled relationship, to experimental warming on a global scale. Specifically, we hypothesized that MBC:MBN would increase with warming. In addition, Lu et al. (2013) showed short-term warming significantly increased MBC but long-term duration decreased MBC. Therefore, we hypothesized different responses of MBN and MBC:MBN to warming duration.

## 2. Materials and methods

### 2.1. Data collection

We searched journal articles published during 1980–2016 by Web of Science. The search key words were combined with “warming”, “elevated temperature”, “microbial biomass carbon” (MBC) and “microbial biomass nitrogen” (MBN). We selected data according to the following criteria: (1) the studies reported changes in microbial variables (i.e., MBC, MBN, and MBC:MBN) in both warming and control groups; (2) the measurements were conducted over at least a full year in field experiments; and (3) the means, standard deviations of microbial variables, and sample sizes were reported or could be calculated. If standard errors (SE) were reported, the standard deviations were calculated by the equation ( $SD = SE \times \sqrt{n}$ , where  $n$  was the replicate numbers). In cases in which no standard errors were reported, we assigned standard deviations that were 1/10 of the means (Luo et al., 2006). (4) Warming variables (warming methods, warming time, warming magnitude, and warming duration) had to be clearly described in the articles. If at least two of the multiple measurements were measured in the same year, we chose the mean of the measurements. If the results were reported from different layers, we only included the results from the uppermost soil layer.

Overall, 100 published papers were selected from 58 study sites among five ecosystem types (i.e., tundra, shrubland, grassland, forest, or cropland) (Fig. S1; Table S1). For each selected paper, we recorded MBC, MBN, the MBC:MBN, soil total C (TC), soil total N (TN), the ratio of soil C to N (soil C:N), soil organic C (SOC), and soil inorganic N (i.e., soil  $\text{NH}_4\text{-N}$  and soil  $\text{NO}_3\text{-N}$ ). Relevant experimental information was also reported, including the latitude, longitude, elevation, mean annual precipitation (MAP), mean annual temperature (MAT), soil moisture, elevated soil temperature, ecosystem type (i.e., tundra, shrubland, grassland, forest, or cropland), warming methods (i.e., curtain reflecting infrared radiation (curtains), greenhouse, heating cables, infrared heaters, and open top chambers (OTC)), warming time (i.e., continued warming or night warming), warming duration (divided from the warming start of the year, i.e., short-term warming duration (1–2 years), mid-term warming duration (3–4 years), and long-term warming duration ( $\geq 5$  years)), warming magnitude (classified as low warming magnitude ( $\leq 1$  °C), medium warming magnitude (1–2 °C), and high warming magnitude ( $> 2$  °C)). The warming magnitude strongly relies on the warming method (data not shown). On average, heating cables method reached the largest warming magnitude ( $3.41 \pm 1.25$  °C), and followed by greenhouse ( $1.84 \pm 0.27$  °C), infrared heaters ( $1.74 \pm 0.72$  °C), OTC

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