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

Wenfang Xu a, b, Wenping Yuan a, c, * 

a State Key Laboratory of Cryospheric Sciences, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Lanzhou, Gansu 730000, China 
b University of Chinese Academy of Sciences, Beijing 100049, China 
c School of Atmospheric Sciences, Sun Yat-Sen University, Guangzhou, Guangdong 519082, China

A R T I C L E I N F O

Article history:
Received 2 May 2017
Received in revised form 26 August 2017
Accepted 29 August 2017

Keywords:
Microbial biomass carbon
Microbial biomass nitrogen
Climate warming
Temperature sensitivity
Meta-analysis

A B S T R A C T

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 ± 0.80% and MBN by 5.85 ± 0.90% and thus decreased the MBC:MBN by 3.34 ± 0.66%. MBC showed positive responses to warming but MBN exhibited negative responses to warming at low warming magnitude (< 1/2°C); however, at high warming magnitude (>2 °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 (>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.

© 2017 Published by Elsevier Ltd.

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 CO₂ 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 CO₂ 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...
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., 2012). 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 (<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 (>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 NH$_4$-N and soil NO$_3$-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 (>5 years)), warming magnitude (classified as low warming magnitude (<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 ± 1.25°C), and followed by greenhouse (1.84 ± 0.27°C), infrared heaters (1.74 ± 0.72°C), OTC
(1.38 ± 1.05 °C) and curtains (0.74 ± 0.30 °C). If data were presented graphically, we used WinDig 2.0 software to digitize the data.

2.2. Data analysis

For a given variable, the response ratio (RR) is used as an index of the magnitude of experimental warming effects (Hedges et al., 1999). RR is defined as the ratio of the mean value of a given variable in the treatment group (Xt) to that in the control group (Xc) (Hedges et al., 1999). The lnRR is the natural logarithm of RR. If the lnRR value is above 0, it indicates a positive effect of experimental warming on microbial biomass with increased temperature. The lnRR was calculated as:

\[
\ln RR = \ln \left( \frac{X_t}{X_c} \right) = \ln (X_t) - \ln (X_c),
\]

where \( X_t \) and \( X_c \) are the mean values of the warming and control groups, respectively.

The variance (\( \nu \)) was estimated by:

\[
y = \frac{S_t^2}{n_t X_t^2} + \frac{S_c^2}{n_c X_c^2}
\]

where \( n_t \) and \( n_c \) are the sample sizes for the warming and control treatments, respectively, and \( S_t \) and \( S_c \) are the standard deviations for the warming and control groups, respectively.

The weighted response ratio (\( RR^+ \)) is calculated from the lnRR of individual pair comparisons between warming and control groups, and the standard errors (\( S \)) and weighting factor (\( w_{ij} \)) are calculated by:

\[
RR^+ = \frac{\sum_{i=1}^{m} \sum_{j=1}^{k_i} W_{ij} \ln RR_{ij}}{\sum_{i=1}^{m} \sum_{j=1}^{k_i} W_{ij}} \quad \text{(3)}
\]

\[
S(\ln RR^+) = \sqrt{\frac{1}{\sum_{i=1}^{m} \sum_{j=1}^{k_i} W_{ij}}}
\]

\[
w_{ij} = \frac{1}{\nu}
\]

If the 95% confidence interval (95%CI = \( RR^+ ± 1.96S(\ln RR^+) \)) value of \( RR^+ \), for a variable does not cover zero, then the responses of the variable to experimental warming differ significantly between the warming and control treatments in given categories (i.e., ecosystem type, warming methods, warming time, warming magnitude, and warming duration). The frequency distributions of lnRR were assumed to follow normal distributions and fitted by a Gaussian function (i.e., normal distribution).

\[
y = a \times \exp \left[ -\frac{(x - \mu)^2}{2\sigma^2} \right]
\]

where \( x \) is lnRR, \( y \) is the frequency (i.e., number of lnRR values), \( a \) is a coefficient showing the expected number of lnRR values at \( x = \mu \), and \( \mu \) and \( \sigma \) are the mean and variance of the frequency distributions of lnRR, respectively. We used a \( t \)-test to examine whether the response ratio in the warming treatment was significantly different from that in control. The percentage change of a variable was calculated by the formula (Xu et al., 2013):

\[
\left( e^{RR^+} - 1 \right) \times 100%.
\]

### 3. Results

This study showed that experimental warming significantly increased MBC and MBN by 3.61% and 5.85%, respectively, while warming significantly decreased the MBC:MBN by 3.34% (Fig. 1; Table 1; and Tables S3–S5). Within ecosystem type, MBC and MBN were significantly increased in grassland by 3.34% and 3.87%, and in forest by 4.81% and 19.55%, respectively (Fig. 1; Table S3; and Table S4). Regarding warming methods, warming by infrared heaters significantly increased MBN by 14.49%, while warming by curtains decreased it by 42.60%. However, the effects of warming methods on MBC were insignificant in most methods except for warming by OTC, with an increase of 4.76%. When grouped by warming time, continued warming and night warming significantly enhanced MBN by 4.61% and 8.62%, while they decreased MBC:MBN by 3.38% and 3.17%, respectively (Fig. 1; Tables S4–S5). The continued warming significantly increased MBC by 5.22%, but the night warming had no effect on MBC (Fig. 1; Table S3). With reference to warming magnitude, in low warming magnitude (≤1 °C), MBC showed an increase while MBN display a decrease. In contrast, MBC exhibited a decrease above 2 °C with 13.17% in response to warming, but MBN showed an increase above 2 °C with 13.55% (Fig. 1a and b).

Warming duration did not significantly affect the responses of MBC or MBN to experimental warming in the long-term warming duration, but it had a positive effect on MBC at mid-term warming duration and a positive effect on MBN at short-term warming duration (Fig. 1a and b). The MBC:MBN showed a significantly negative response in most warming categories (i.e., ecosystem type, warming methods, warming time, warming magnitude, and warming duration), with a decrease of 2.21%–19.80% (Fig. 1c). Moreover, warming-induced changes in microbial variables showed large variability among the studies, ranging from a minimum lnRR of −0.53 to a maximum of 0.60 in MBC, from −0.89 to 1.10 in MBN, and from −0.91 to 0.58 in MBC:MBN.

There was a significant quadratic relationship between the lnRR of MBN and warming magnitude (\( p < 0.05; \) Fig. 2b). However, there was no relationship between the lnRR of MBC and latitude, longitude, elevation, MAT, MAP, warming duration, and warming magnitude (Fig. 3; Fig. S3). No relationship between the MBC:MBN and environmental variables were also found (Fig. 2a, c; Table S2). Even when grouped by different warming magnitudes, apart from the significant positive relationship between the lnRR of MBC (or lnRR of MBN) and MAT and the significant negative relationship between the lnRR of MBC (or lnRR of MBN) and elevation for the high warming magnitudes, no other significant relationships were found between the RR of MBC (or lnRR of MBN) and environmental variables (Fig. 3; Fig. S2). In addition, no relationship between warming magnitude and MAT was detected, except for MBC in high warming magnitude (Fig. S3).

We also analyzed the responses of soil total C (TC), soil organic C (SOC), soil total N (TN), and the ratio of soil C to soil N (soil C:N) to experimental warming. The warming have no effect on TC, SOC, TN, and soil C:N (Fig. 4; Table 1). Responses of soil C and N variables (i.e., TC, TN, SOC, and soil C:N) were not dependent on the methods of curtains, greenhouse, and heating cables (\( P > 0.1; \) Fig. 4). However, the indirect warming by OTC method significantly reduced TN and warming by infrared heaters significantly increased SOC (Fig. 4b and c). Warming magnitude significantly affected the responses of SOC and TN to experimental warming. For example, low warming magnitudes significantly increased SOC but high warming magnitude decreased SOC (\( P < 0.05; \) Fig. 4c). In contrast, an increase in warming magnitude from low (≤1 °C) to high temperature (≥2 °C) resulted in greater increases in TN (\( P < 0.05; \) Fig. 4b). In addition, the warming duration did not influence the changes in TC, SOC, and
soil C:N in the warming experiments. The TN showed positive responses in short-term warming duration while exhibiting negative responses in the mid-term and long-term warming duration. The responses of soil inorganic N (i.e., soil NH$_4^+$-N and soil NO$_3^-$-N) to experimental warming were significantly positive, with an increase of 10.62% (RR$^+ _{+ +} = 0.1010; 95\%$ CI: 0.0829$- 0.1190; p < 0.05) in soil ammonium N (soil NH$_4^+$-N), and 8.20% (RR$^+ _{+ +} = 0.0789; 95\%$ CI: 0.0702$- 0.0875; p < 0.05) in soil nitrate N (soil NO$_3^-$-N) across all studies (Fig. 5; Table 1). However, a significant negative response of soil nitrate N to warming was also found in the forest ecosystem (a decrease of 11.75%), in night warming time (a decrease of 11.76%), and in high warming magnitude (a decrease of 5.27%). Both soil ammonium N and soil nitrate N tended to increase more in the long-term warming duration (>5 years) than in the short-term warming duration (1–2 years). Similarly, they towered greater in the low warming magnitude (≤1 °C) than in the high warming magnitude (>2 °C).

### 4. Discussion

In this study, experimental warming significantly increased MBC and MBN, while significantly decreased MBC:MBN. These results contradicted our first hypothesis, and which assumed an increased MBC and an unchanged MBN under warming condition would result in an increase in MBC:MBN. Besides, MBC and MBN showed increased responses to mid-term (3–4 years) or short-term (1–2 years) warming duration, but weaker responses to long-term (>5 years) warming duration. This gradual diminishing responses were observed in MBC, MBN, and MBC:MBN, which was consistent with our second hypothesis that response of MBN to experiment warming would change with warming duration.

#### 4.1. Responses of MBC:MBN to experiment warming

The MBC and MBN in soil are important components of terrestrial ecosystem C and N cycling with a turnover time from days to years (Parton et al., 1987), and serve as sources (mineralization) or sinks (immobilization) of labile C and N pools. This study showed the different responses of MBC and MBN to experimental warming, and larger increases of MBN than MBC under warming conditions (Fig. 1). This is first study, by our knowledge, to address the responses of both MBC and MBN to experimental warming while previous studies only focused on each independently (Bai et al., 2013; Lu et al., 2013). Microbes play important roles in regulating N mineralization, nitrification and denitrification processes, and the former strongly influence C cycling by determining inorganic N availability (Bardgett et al., 2008). Considering that the N cycling could be accelerated in experiment warming, it would result in higher N availability as well as larger N$_2$O emissions (Abdalla et al., 2010; Yin et al., 2012).

In addition, the responses of MBC:MBN to warming enhanced the understanding of couple relationship in MBC and MBN, which

---

**Table 1** Percentage changes of microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), the ratio of MBC to MBN (MBC:MBN), soil total carbon (TC), soil total nitrogen (TN), soil C:N, soil ammonium nitrogen (soil NH$_4^+$-N), and soil nitrate nitrogen (soil NO$_3^-$-N) in response to experimental warming.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Percentage change</th>
<th>Sample size (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>MBC</td>
<td>3.61 ± 0.80</td>
<td>124</td>
</tr>
<tr>
<td>MBN</td>
<td>5.85 ± 0.90</td>
<td>97</td>
</tr>
<tr>
<td>MBC:MBN</td>
<td>–3.34 ± 0.66</td>
<td>92</td>
</tr>
<tr>
<td>TC</td>
<td>–0.52 ± 0.74</td>
<td>32</td>
</tr>
<tr>
<td>TN</td>
<td>–0.35 ± 0.32</td>
<td>94</td>
</tr>
<tr>
<td>SOC</td>
<td>0.23 ± 0.33</td>
<td>75</td>
</tr>
<tr>
<td>C:N</td>
<td>0.24 ± 0.54</td>
<td>71</td>
</tr>
<tr>
<td>NH$_4^+$-N</td>
<td>10.62 ± 0.92</td>
<td>81</td>
</tr>
<tr>
<td>NO$_3^-$-N</td>
<td>8.20 ± 0.44</td>
<td>59</td>
</tr>
</tbody>
</table>

Note: Percentage change was calculated as $(\text{RR}^+ _{+ +} - 1) \times 100\%$; values are means ± SD.
Fig. 2. Relationships between the natural logarithm of the response ratio (lnRR) of the microbial biomass carbon (MBC, a), microbial biomass nitrogen (MBN, b), their ratios (MBC:MBN, c) and elevated temperature. The different color indicates various warming duration (i.e., short-term warming duration (1–2 years), mid-term warming duration (3–4 years), and long-term warming duration (≥ 5 years)). The dotted lines are drawn at ln RR = 0. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Fig. 3. Relationship between mean annual temperature (MAT), mean annual precipitation (MAP), warming duration and the natural logarithm of the response ratio (lnRR) of microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), and the ratio of MBC to MBN (MBC:MBN). Different color indicate different warming magnitude: L (blue), low warming magnitude (≤ 1 °C); M (green), medium warming magnitude (1–2 °C); H (red), high warming magnitude (>2 °C). The red solid line shows the relationship between the MAT and RR of microbial biomass to warming in high warming magnitude. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
may benefit development of coupled C and N models. The current coupled C and N models assumed a fixed ratio of MBC and MBN, and simulated N mineralization coupled with C mineralization based on a single rate (Manzoni and Porporato, 2009; Achat et al., 2016). However, our results showed the warming will decrease MBC:MBN due to different responses of MBC and MBN to warming. In addition, microbial models have been developed and incorporated into the ecosystem models for simulating C cycle by considering the changes of microbial biomass physiological activities (Hararuk et al., 2015; Ri and Prentice, 2017). It is expected to improve simulations of N cycle by integrating microbial N biomass into the ecosystem models.

4.2. Responses of MBC and MBN to warming magnitude

Our results showed a significant positive effect of experimental warming on MBC in low warming magnitude (<1 °C) and this effect shifted to negative in high warming magnitude (>2 °C) (Fig. 1a; Table S3). Other lines of studies supported our conclusion that temperature sensitivity of microbes may decline at high temperatures (Luo et al., 2001). Warming-induced increases in air and soil temperature and a fresh C supply from the plants’ above- and below-ground parts might have enhanced microbial growth and been activated in low and medium warming magnitudes (Liu et al., 2011), resulting in an increase in MBC. However, water losses due to rising temperatures may inhibit microbial growth and activities in high warming magnitude (Allison and Treseder, 2008), which eventually decreases the microbial biomass C. We also found a reduction in soil moisture with the elevated soil temperature (Fig. 6) (Xu et al., 2013). Moreover, the changes in MBC among different warming magnitudes were consistent with the changes in SOC with various warming magnitudes (Fig. 1a; Fig. 4c), indicating substrate supply regulated the effects of warming on MBC (Frey et al., 2013). This temperature sensitivity of MBC suggested that climate warming would have non-uniform effects on microbial associated ecosystem functions, and this information should be incorporated into ESMs (Zhou et al., 2012; Wieder et al., 2013; Hararuk et al., 2015). Several ecosystem models have incorporated temperature sensitivities of microbial to warming, and reproduce much better soil C pools compared with traditional
models (Wieder et al., 2013, 2015; Sulman et al., 2014; Hararuk et al., 2015).

The results obtained in this synthesis show that experimental warming significantly decreased MBN in the low warming magnitude, while the warming increased MBN in medium and high warming magnitudes (Fig. 1b; Table S4). These responses are in agreement with the response of TN to experimental warming. A prior study indicated that greater N availability in soil could increase MBN (Yin et al., 2012). The increase in net N mineralization and nitrification are reflected as an increase in soil inorganic N (Bai et al., 2013) and an increase in soil inorganic N (i.e., soil NH4+-N and soil NO3−-N) was observed in our analysis. The warming-induced increases in the inorganic N may increase plant biomass because the N availability in soil was generally one of the most vital limiting factors for plant growth in most ecosystems (Gruber and Galloway, 2008).

The negative weighted responses of the MBC:MBN were contributed to the increased magnitude of MBN was much greater than that of MBC (Table 1; Fig. 1). Previous study indicated that the MBC:MBN has been used to indicate the relative abundance of fungi versus bacteria at a coarse level (Zhao et al., 2010). The microbial community in the warming condition was more fungi-abundant compared to the natural condition, resulting from soil fungi are more tolerant to higher soil temperature and drying than bacteria (Holland and Coleman, 1987; Manzoni et al., 2012). Therefore, we speculated that warming would change the composition of the soil microbial community. The shifting of microbial community composition most likely led to the reduced temperature sensitivity of heterotrophic soil respiration (Bradford et al., 2008), which could have decreased C loss by about 95 g C m−2 yr−1 (Zhou et al., 2012).

4.3. Responses of MBC and MBN to warming duration

Larger positive responses of MBC or MBN to experimental warming at mid-term or short-term warming duration than long-term warming duration were observed (Fig. 1). Whether positive response ratio or negative response ratio, the response ratios tended to zero with warming duration (Fig. 3g–i), which implied the impacts of climate warming on MBC and MBN will diminishing with warming duration. The gradual decrease in responses of microbes under warming could result from the soil drying reducing microbial activity (Peterjohn et al., 1994; Allison and Treseder, 2008). Warming-induced soil drying may limit the physiological performance of microbes and the diffusion of nutrients to microbes (Robertson et al., 1997), leading to reducing microbial activity (Peterjohn et al., 1994; Allison and Treseder, 2008; Bradford, 2013). For example, Bradford (2013) showed that experiment warming dried the soil and decreased diffusion rates, reducing substrate availability to microbes.

Moreover, long-term increasing temperature facilitated labile substrate fast depleting (Bradford et al., 2008; Frey et al., 2008; Curiel Yuste et al., 2010) and permitted the microbes to use more chemically recalcitrant substrate, which require great energy investment to breakdown, reducing net energy gain and hence leaving less energy available for growth (Fierer et al., 2005; Davidson and Janssens, 2006; Craine et al., 2010). At the same
time, maintenance energy costs were higher as temperature rises (Manzoni et al., 2012), which reduce the proportion of energy acquired that is available to growth. Above two maintenance activities requiring most energy suggest a decline in C use efficiency that would result in a decline in microbial biomass production over the long-term, which in turn would lead to a reduced extracellular enzyme production (soil microbes catalyze the breakdown of SOM using extracellular enzyme), thus ultimately suppressing SOM decomposition and respiration loss from the system (Allison et al., 2010; Frey et al., 2013). Recent study indicated that energy deficiency may strongly affect the balance between soil C and soil N availability as well as MBC and MBN demand, which eventually limiting net N mineralization (Wild et al., 2015).

In addition, substrate limitation might shift enzyme expression toward higher affinity enzymes (Steinweg et al., 2008; Bradford, 2013), where the trade-off is a reduction in maximum catalytic rates. Such a shift in enzyme expression would favor a lower growing microbial biomass (Steinweg et al., 2008; Bradford, 2013). Microbes actively down-regulate their metabolism under sustained warming and this physiological acclimation of microbes contribute to the diminishing effect over time of experimental warming on microbial biomass.

Microbial growth efficiency (i.e., C use efficiency) is a key parameter in most ecosystem models used to simulate SOC dynamics. However, numerical traditional models demonstrate that physiological acclimation of microbes does not need to be invoked to explain the ephemeral augmentation of soil respiration in response to a fixed and sustained increase in temperature above ambient (Allison and Martiny, 2008; Eliasson et al., 2005; Knorr et al., 2005; Allison et al., 2010); hence microbial growth efficiency is a fixed constant in traditional ESMs (Allison et al., 2010). Yet the projections for soil C stocks under warming contrast markedly between the traditional and microbial models (Allison et al., 2010; Wieder et al., 2013). For example, a recent study showed that increased temperatures accelerate enzyme kinetics in microbial models, which generally lead to soil C loss; this effect can be completely offset if microbial growth efficiency declines with warming duration and reduces the microbial biomass that controls decomposition. However, if the microbial growth efficiency does not change with warming in traditional models, the enzyme kinetics dominate and soils lose up to 300 Pg C (Wieder et al., 2013). Our meta-analysis showed gradual diminishing in the response of microbial biomass to warming duration. Therefore, the microbial biomass responds to warming duration should not be negligible. And an important ongoing endeavor in current global change ecology and biology should incorporating microbial responses into ESMs as recent studies (Zhou et al., 2012; Hararuk et al., 2015; Wieder et al., 2015).

4.4. Responses of MBC and MBN to warming over the ecosystem types and geographic areas

The responses of MBC and MBN to warming may differ considerably among ecosystem types. MBC and MBN showed a significant positive response to warming in grassland and forest (Fig. 1). MBC and MBN respond quickly to changes in soil temperature (Alvarez et al., 1995; Fang et al., 2005) and moisture (Skopp et al., 1990), implying that the experimental warming caused changes in soil temperature and moisture that affected the microbial activity and changed the microbial biomass in the soil. Soil drying may roughly offset the effect of warming on the microbial biomass in water-limited ecosystem (i.e., grassland) because this system became drier and more water-limited under warming (Bai et al., 2013). Besides, previous meta-analysis indicated that forests were more sensitive to warming than grasslands in terms of soil respiration (Rustad et al., 2001; Lu et al., 2013) and soil N availability (Bai et al., 2013), which was attributed to most observations in forests were conducted in more temperature-limited areas (Bai et al., 2013). Therefore, the forest showed a stronger response to warming than the grassland in MBC and MBN. It should be noted that the tropical forests were not included in this analysis due to no warming experiments were conducted in tropical forests. The feedback processes in tropical forests were also needed in future research.

A significant increased MBC but decreased MBN were found in shrubland ecosystems (Fig. 1). Previous study showed an increase in MBC in shrubland ecosystem may attributed to the increases in substrate use (Sowerby et al., 2005). However, the increase in microbial growth and plant growth due to warming might lead to a progressive limitation of N in nutrient poor ecosystems (such as shrubland ecosystem) (Beier et al., 2008), which may result in decreasing of MBN. Compared with more sensitive to warming in C, the N mineralization was relatively insensitive to the temperature increase (Beier et al., 2008). This lag between temperature and N mineralization suggests that changes in N cycle appear to occur more slowly than C cycle.

In general, tundra ecosystems are located at high latitude regions with permafrost thaw. Warming may increase soil moisture by permafrost melting (Xu et al., 2013; Sistla et al., 2013). Soil water availability affects the rate at which enzymes, substrates and products of degradation diffuse between microbes and their immediate environment (Davidson et al., 2012; Manzoni et al., 2012), which indirectly alter soil microbial composition structure (Deslippe et al., 2012) and N availability. In our study, no significant changes in MBC and MBN respond to warming were found in tundra. These findings were in line with recent meta-analyses which indicated that terrestrial ecosystems did not always have greater sensitivity in colder environments (Lu et al., 2013; Zhang et al., 2015).

No significant relationship between the MAT and the effects of warming on MBC or MBN were observed across all data, apart from a significant positive relationship between the InRR of MBC (or InRR of MBN) and MAT for the high warming magnitudes (Fig. 3a–b). These results contrast previous studies that positive warming effects on soil microbial biomass in colder regions were generally greater than in warmer regions due to higher substrate availability in low MAT could be particular vulnerable to climate warming (Chen et al., 2015; Zhang et al., 2015). This difference between two meta-analyses could result from warming magnitude may affect the relationship between the InRR of microbial biomass and MAT in this study (Fig. S3). Negative relationships were found in both between InRR of MBC and warming magnitude \((R^2 = 0.11, p = 0.11)\) and between warming magnitude and MAT \((R^2 = 0.16, p < 0.05)\) in high warming magnitude, which may result in a positive relationship between the InRR of MBC and MAT for the high warming magnitudes (Fig. S3).

5. Conclusion

Our meta-analysis indicated that both MBC and MBN exhibited positive responses to experimental warming, while the MBC:MBN showed negative responses to experimental warming. The microbial biomass (MBC and MBN) showed different responses to various warming magnitudes, which were consist with the responses of substrate supply (i.e., SOC and TN) to experimental warming. Besides, stronger positive responses of MBC and MBN to mid-term or short-term warming duration but a weaker response in long-term warming duration was observed. These findings indicated that microbial responses to climate change are nonlinear and temperature sensitive. Models should take the temperature sensitivity of
microbes into consideration when they are used to project future climate-carbon cycle feedback.

Acknowledgements

This study was supported by General Program of National Natural Science Foundation of China (31570468), Key Project of Chinese Academy of Sciences (CAS) (KJZD-EW-G03-04), One Hundred Person Project of CAS (Y329K71002), the CAS Interdisciplinary Innovation Team of the Chinese Academy of Sciences, Youth Changjiang Scholars Programme of China (Q2016161), and National Youth Top-notch Talent Support Program.

Author contributions

Wenping Yuan and Wenfang Xu planned and designed the study. Wenfang Xu wrote the first draft of the manuscript, and Wenping Yuan contributed to the revisions.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2017.08.033.

References


