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A meta-analysis of the effects of experimental warming on soil carbon and nitrogen dynamics on the Tibetan Plateau

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ABSTRACT

Alpine ecosystems at high altitudes and latitudes are notably sensitive to climatic warming and the Tibetan Plateau is a widely distributed alpine ecosystem. The magnitude of climatic warming on the Tibetan Plateau is expected to be considerably greater than the global average. However, a synthesis of the experimental warming soil carbon and nitrogen data is still lacking and whether forest soils are more sensitive to warming than grassland soils remains unclear. In this study, we used a meta-analysis approach to synthesise 196 observations from 25 published studies on the Tibetan Plateau. Warming significantly increased microbial biomass carbon (MBC) by 14.3% (95% CI: 2.9–24.6%), microbial biomass nitrogen (MBN) by 20.1% (95% CI: 2.0–45.1%), net nitrogen mineralization by 49.2% (95% CI: 38.1–62.3%) and net nitrification by 56.0% (95% CI: 51.4–66.1%), but did not significantly affect soil carbon (95% CI: −13.9 to 2.7%) or nitrogen (95% CI: −12.4 to 2.6%). The mean annual air temperature was negatively correlated with the warming effects on MBC and MBN. Grasslands exhibited significant MBC and MBN responses to warming. Specifically, soil microbial biomass was more responsive to warming in colder environments. Moreover, forest soils are not always more sensitive to warming than grassland soils as previous studies have suggested. These findings indicate that clarifying the effect of warming on alpine soils need consider ecosystem types and their local climate.

1. Introduction

Alpine ecosystems at high altitudes and latitudes are notably sensitive to climatic change, although there are many uncertainties in how these systems will respond to climatic change (IPCC, 2007; Shen et al., 2014). The Tibetan Plateau, a widely distributed alpine ecosystem, is one of the most sensitive regions to global climatic change worldwide (Chen et al., 2013; Fu et al. in press; Miehe et al., 2011; Zhang et al., 2000). The magnitude of warming in alpine regions is predicted to be much greater than the global average (IPCC, 2007). The warming amplitude increases with increasing altitude on this Plateau (Liu and Chen 2000; Yao et al., 2000). Field experiments have analysed the potential effects of warming on the alpine soils on the Tibetan Plateau (Fu et al., 2012; Li et al., 2011; Rui et al., 2011; Xu et al., 2010a; Yu et al., 2014). However, a synthesis of the experimental warming data is still unavailable and thus, the general tendency of the warming effects remains unclear for alpine soils across this Plateau.

The microbial biomass of carbon (MBC) and nitrogen (MBN) in soil are important components in terrestrial ecosystem carbon and nitrogen cycling and serve as sources (mineralization) or sinks (immobilisation) of labile carbon and nitrogen pools (Bai et al., 2013; Lu et al., 2013a). The microbial biomass in soil responds quickly to changes in the soil temperature (Alvarez et al., 1995). MBC is likely to be more responsive to warming than MBN across all terrestrial ecosystems (Bai et al., 2013; Lu et al., 2013a). The non-significant response of MBN to warming may result from the limited availability of carbon sources (Bai et al., 2013), while warming significantly increases the dissolved organic carbon (DOC), an important carbon source for soil microorganisms (Lu et al., 2013a). Therefore, the underlying mechanism causing the non-significant effect that warming has on MBN remains unclear.

Both the increase in soil respiration (R_s) (Lin et al., 2011b; Lu et al., 2013b; Shi et al., 2012; Xiong et al., 2010; Xu et al., 2010b) and the decline in litter quantity (Li et al., 2011; Lin et al., 2011a; Luo et al., 2009) contribute to the decrease in the soil carbon and nitrogen pools on the Tibetan Plateau. The increase in MBC caused

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by warming also implies that warming may accelerate organic matter decomposition in soil (Wang et al., 2011), while inconsistent responses of MBC and MBN to warming have been reported on this Plateau (Chen et al., 2010; Fu et al., 2012; Wang et al., 2011). Warming-induced increases in the net nitrogen mineralization and nitrification rates increased the nitrogen availability in soil (Bai et al., 2013; Rustad et al., 2001), which in turn increased plant biomass accumulation (Fu et al., in press; Rustad et al., 2001) and soil microbial biomass (Yin et al., 2012; Yu et al., 2014). Furthermore, a warming-induced increase in plant biomass may more or less counterbalance the warming-induced increases in R_s and decreases in litter quantity (Lu et al., 2013a). However, the effects of warming on plant biomass were negative (Klein et al., 2007; Yang et al., 2013), positive (Li et al., 2011; Wang et al., 2012) or neutral (Fu et al., 2013) in alpine ecosystems. The variability between these two factors may result in the inconsistent response of soil carbon and nitrogen to warming on the Tibetan Plateau (Chen et al., 2010; Shi et al., 2012; Wang et al., 2011).

Forests show stronger responses to warming than grasslands in terms of soil respiration and soil nitrogen availability (Bai et al., 2013; Lu et al., 2013a; Rustad et al., 2001), which may be related to the fact that most observations in forests were conducted in more temperature-limited areas (Bai et al., 2013). However, grasslands may generally have lower air temperatures than forests in alpine regions on the Tibetan Plateau (Luo et al., 2010; Shen et al., 2014; Yin et al., 2013). Therefore, it remains unclear whether forests are always more sensitive to warming than grasslands in alpine regions.

In this study, we compiled data from 25 published experimental warming studies across the Tibetan Plateau. The goal was (1) to identify quantitatively the general tendencies caused by warming effects on 18 variables related to the soil carbon and nitrogen pools

Table 1
Site characteristics and response variables from a meta-analysis of 25 studies on the Tibetan Plateau.

Site	Latitude	Longitude	Altitude (m)	MAT (°C)	MAP (mm)	Response variables	References
Damxung grassland station	30.50	91.07	4300	1.3	476.8	MBC, MBN	Fu et al., 2012
Eastern slope of Mount Gongga	29.83	101.88	3000	3.8	1940	Plant biomass, root length	Yang et al., 2013
Ebao, Qilian County	37.97	100.92	3512	1	409	Soil C and N, MBC, MBN	Heng, 2011
Fenghuoshan region	34.73	93.07	4600–4800	−5.3	269.7	Soil C and N, MBC, MBN	Li et al., 2010
						Soil C and N, MBC, MBN, catalase, urease, protease	Li et al., 2011
Haibei alpine meadow ecosystem research station	37.62	101.20	3200	−2	500	Soil respiration	Lin et al., 2011b
						Soil N, MBC, MBN, DOC, DON, NH_4^+-N and NO_3^--N	Rui et al., 2011
						Net N mineralization	Wang et al., 2012
Hongyuan alpine ecosystem research station	32.45	102.37	3561	1.1	752.4	Polyphenol oxidase, urease	Liu et al., 2011a
						MBC, MBN	Wang et al., 2011
Kakagou, Songpan County	32.85	103.55	3400	2.8	718	Soil N, MBC, MBN, net N mineralization, NH_4^+-N and NO_3^--N, soil respiration	Shi et al., 2012
						Plant biomass	Shi et al., 2010
Maoxian ecological station	31.68	103.88	1820	8.9	920	Soil C and N, MBC, MBN, NH_4^+-N and NO_3^--N	Chen et al., 2010
						Soil C and N, MBC, MBN, NH_4^+-N and NO_3^--N, root length	Liu et al., 2011b
						MBC, MBN, NH_4^+-N and NO_3^--N, soil respiration	Xiong et al., 2010
						Soil C and N, MBC, MBN, net N mineralization and nitrification, NH_4^+-N and NO_3^--N, root length	Yin et al., 2012
						Net N mineralization, polyphenol oxidase, urease, plant biomass	Yin et al., 2013
Miyaluo experimental forest of Lixian County	31.58	102.58	3150	8	600–1100	Soil C and N, polyphenol oxidase, catalase, invertase, urease, protease	Pan et al., 2008
						Plant biomass	Han et al., 2009
						MBC, MBN, DOC, DON, net nitrification, NH_4^+-N and NO_3^--N, polyphenol oxidase, catalase, invertase, urease	Xu et al., 2010a
						Soil C and N, soil respiration	Xu et al., 2010b
						Net N mineralization, plant biomass	Xu et al., 2012
						Plant biomass	Yin et al., 2008a
						Plant biomass	Yin et al., 2008b
Xainza alpine steppe and wetland ecosystem observation and experiment station	30.95	88.7	4675	0	300	Soil respiration	Lu et al., 2013b

MBC: soil microbial biomass carbon; MBN: soil microbial biomass nitrogen; DOC: dissolved organic carbon; DON: dissolved organic nitrogen.

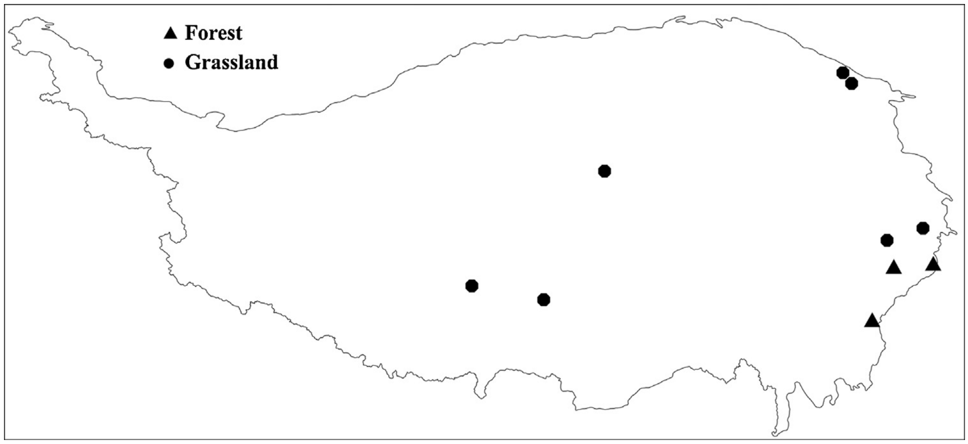

Fig. 1. Study sites and vegetation types from a meta-analysis of 25 studies on the Tibetan Plateau.

in the “Earth’s Third Pole” and (2) to determine whether forests are not always more sensitive to warming than grasslands.

2. Materials and methods

2.1. Data compilation

We sought papers and theses published prior to September, 2013 using the Web of Science and the China National Knowledge Infrastructure (Table S1). The compiled database included biomass parameters [plant biomass (PB) and root length], soil carbon pools (soil carbon, MBC, and DOC), soil nitrogen pools [soil nitrogen, MBN, dissolved organic N (DON), ammonium nitrogen (NH_4^+-N) and nitrate nitrogen (NO_3^--N)], R_s, net nitrogen mineralization and nitrification rates, and soil enzymes (polyphenol oxidase, catalase, invertase, urease and protease) (Table 1).

Our criteria were as follows: only studies conducted on the Tibetan Plateau were included; at least one of the variables considered here was measured; studies with laboratory incubation, temperature gradients and growth chambers were excluded and only field warming experimental studies were included; only data from control and warming treatments were used for multifactor experiments; only the latest results were used for multiple observations at different times from the same study site because the observations should be independent in the meta-analysis (Hedges et al., 1999; Rosenberg et al., 2000); means, standard deviations (or standard errors), and sample sizes were directly provided or could be calculated from the studies; multiple soil depths, warming magnitudes or ecosystem types were treated as independent variables (Bai et al., 2013; Lu et al., 2013a).

The warming duration was calculated in months. The data were extracted using GetData software if the studies provided the data in figures (Fu et al., in press). We grouped all of the studies into those analysing forests and grasslands at the ecosystem level and into those analysing trees and grasses at the species level (Fig. 1).

2.2. Statistical analyses

The METAWIN 2.1 software (Sinauer Associates Inc., Sunderland, MA, USA) (Rosenberg et al., 2000) was used to perform meta-analysis in this study. The natural logarithm of the response ratio (R) was used as the effect size (Hedges et al., 1999), see Eq. (1):

$$\mathrm{Log_e}R = \mathrm{Log_e}\left(\frac{\overline{X_t}}{\overline{X_c}}\right) = \mathrm{Log_e}(\overline{X_t}) - \mathrm{Log_e}(\overline{X_c}) \quad (1)$$

where $\overline{X_c}$ and $\overline{X_t}$ are the mean values in the control and warming treatments, respectively.

For each study, the inverse of the pooled variance ($1/\nu$) was used as the weighting factor (w) in Eq. (2):

$$\nu = \frac{S_t^2}{n_t X_t^2} + \frac{S_c^2}{n_c X_c^2} \quad (2)$$

where S_c^2 and S_t^2 are the standard deviations in the control and warming treatments, respectively; n_c and n_t are the sample sizes in the control and warming treatments, respectively.

Therefore, the mean effect size ($\overline{\mathrm{Log_e}R}$) for all observations were obtained, see Eq. (3):

$$\overline{\mathrm{Log_e}R} = \frac{\sum_{i=1}^{m} w_i \mathrm{Log_e}R_i}{\sum_{i=1}^{m} w_i} \quad (3)$$

where w_i and $\mathrm{Log_e}R_i$ are w and $\mathrm{Log_e}R$ of the ith observation, respectively.

We used a fixed effects model, which is the simplest data structure model for meta analyses, to test whether warming had a significant effect on a specific variable across forests and grasslands (Rosenberg et al., 2000). The mean effect size and 95% bootstrap confidence intervals (CI) were generated. For each variable, the warming effect on this variable is statistically significant if the 95% bootstrap CI did not bracket zero (Wan et al., 2001).

A fixed effects model with a grouping variable was used to compare responses between forests and grasslands and between some related variables (i.e., MBC vs. MBN, NH_4^+-N vs. NO_3^--N, and net nitrogen mineralization rate vs. net nitrification rate), which is analogous to ANOVA (Rosenberg et al., 2000). In the grouping models, the mean effect size of a specific group can be calculated using only the observations of that group (Rosenberg et al., 2000). Similarly, the warming effect is statistically significant if the 95% bootstrap CI did not cover zero for each group (Rosenberg et al., 2000).

A random effects model with a continuous variable (>15 observations) was used to examine the relationships between the mean effect size of warming and the warming duration, increased soil temperature and mean annual air temperature (Rosenberg et al., 2000). A weighted least squares regression was used to determine the relationship between the effect sizes and the independent

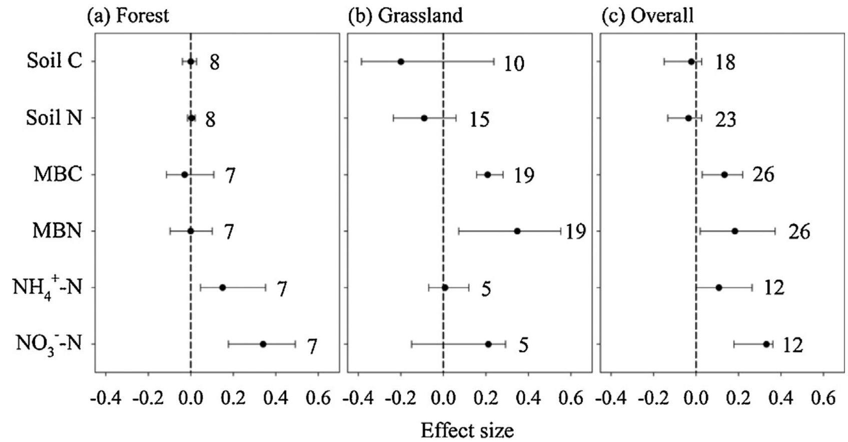

Fig. 2. Effect sizes of the experimental warming on soil carbon, soil nitrogen, soil microbial biomass carbon (MBC) and nitrogen (MBN), ammonium nitrogen (NH_4^+-N) and nitrate nitrogen (NO_3^--N) for alpine forests (a), grasslands (b) and forests + grasslands (c) from a meta-analysis of 25 studies on the Tibetan Plateau. The error bars indicate effect sizes and 95% bootstrap confidence intervals. The warming effect was statistically significant if the 95% CI did not bracket zero. The dashed lines are drawn at effect size = 0. The sample size for each variable is shown next to the bar.

variables for a continuous model (Rosenberg et al., 2000). A significant regression coefficient (i.e., slope) indicates that a significant amount of the variation between the effect sizes can be explained by an independent variable (Rosenberg et al., 2000).

For grouping and continuous models, the total heterogeneity (Q_T) of the effect sizes can be partitioned into the variation among the effect sizes, which is explained by the model (Q_M) and not explained by the model (Q_E) (Rosenberg et al., 2000). For a grouping model, a significant Q_M indicates that significant differences in the mean effect sizes are found among the groups, while a significant Q_M indicates that a significant part of the variation among effect sizes can be explained by an independent variable in a continuous model (Rosenberg et al., 2000).

All statistical significance was examined at $P < 0.05$.

3. Results

Experimental warming did not affect the soil carbon in forests (mean effect size = −0.0001; 95% CI: −0.039 to 0.027) or grasslands (mean effect size = −0.1995; 95% CI: −0.385 to 0.237) (Fig. 2a and b). Similarly, forests (mean effect size = 0.004; 95% CI: −0.015 to 0.021) and grasslands (mean effect size = −0.09; 95% CI: −0.235 to 0.060) did not experience a significant effect from experimental warming on the soil nitrogen (Fig. 2a and b). Forests and grasslands had significantly different responses of MBC (Q_M = 91.4, $P < 0.001$), MBN (Q_M = 68.8, $P < 0.001$), NH_4^+-N (Q_M = 12.7, $P < 0.001$) and NO_3^--N (Q_M = 4.5, $P < 0.05$) due to experimental warming (Fig. 2a and b). In detail, the MBC and MBN increased by 23.1% (95% CI: 16.9–32.4%) and 41.5% (95% CI: 7.5–73.7%), respectively, in grasslands. In contrast, forests had no responses (95% CI: −0.114 to 0.108 for MBC; 95% CI: −0.098 to 0.101 for MBN). The soil NH_4^+-N and NO_3^--N increased by 16.2% (95% CI: 4.7–42.2%) and 40.5% (95% CI: 19.4–63.5%), respectively, in forests due to the effects of warming, while grasslands had no responses (95% CI: −0.069 to 0.119 for NH_4^+-N; 95% CI: −0.149 to 0.292 for NO_3^--N).

In both forests and grasslands, the experimental warming had no effects on the NH_4^+-N (mean effect size = 0.108; 95% CI: −0.002 to 0.264), soil carbon (mean effect size = −0.02; 95% CI:

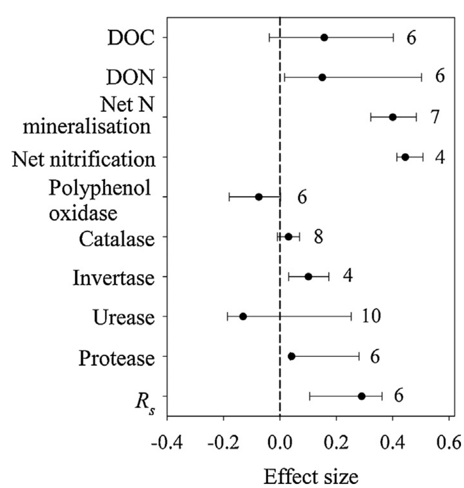

Fig. 3. Sizes of the effects of the experimental warming on dissolved organic carbon (DOC) and nitrogen (DON) in soil, net nitrogen mineralization, net nitrification, polyphenol oxidase, catalase, invertase, urease, protease and soil respiration (R_s) from a meta-analysis of 25 studies on the Tibetan Plateau. The error bars indicate the effect sizes and the 95% bootstrap confidence intervals. The warming effect was statistically significant if the 95% CI did not bracket zero. The dash lines are drawn at effect size = 0. The sample size for each variable is shown next to the bar.

Table 2
Relationships between the sizes of the effect of the experimental warming on the carbon and nitrogen pools in soil, soil microbial biomass carbon and nitrogen, warming duration, increased soil temperature and mean annual air temperature based on a random effects model with a continuous variable meta-analysis on the Tibetan Plateau.

Variables	Q_M	Q_E	Q_T	Slope	P	n
Warming duration						
Soil C	0.05	25.60	25.65	0.02	0.824	18
Soil N	0.01	16.34	16.35	0.01	0.905	23
Soil microbial biomass C	0.46	23.54	24.01	0.03	0.496	26
Soil microbial biomass N	0.24	25.99	26.23	-0.04	0.627	26
Raised soil temperature						
Soil N	0.20	10.77	10.96	0.01	0.658	19
Soil microbial biomass C	0.81	17.23	18.04	−0.03	0.369	22
Soil microbial biomass N	3.10	23.00	26.10	−0.09	0.079	22
Mean annual air temperature						
Soil C	0.004	37.94	37.94	−0.0003	0.949	18
Soil N	0.43	18.67	19.10	0.003	0.511	23
Soil microbial biomass C	11.62	26.15	37.78	−0.02	0.001	26
Soil microbial biomass N	9.53	28.54	38.07	−0.04	0.002	26

Q_T: total heterogeneity of the sizes of the effects among studies; Q_E: the residual error or the variation is not explained by the continuous randomised-effects model; Q_M: the variation is explained by the continuous randomised-effects model; Slope: regression coefficients; P: the statistical probability; n: the number of the observations used in the meta-analysis. A significant Q_M and slope shows that a significant part of the variation among effect sizes can be explained by an independent variable. The relationships were significant when $P < 0.05$.

−0.15 to 0.03) and nitrogen (mean effect size = −0.04; 95% CI: −0.13 to 0.03) (Fig. 2c). In contrast, experimental warming increased MBC (+14.3%; 95% CI: 2.9–24.6%), MBN (+20.1%; 95% CI: 2.0–45.1%) and NO_3^--N (+39.2%; 95% CI: 19.6–43.5%) (Fig. 2c). A significant difference in the warming effect was observed between MBC and MBN (Q_M = 4.21, P < 0.05) and between NH_4^+-N and NO_3^--N (Q_M = 84.87, P < 0.001).

The experimental warming did not change the DOC (mean effect size = 0.16; 95% CI: −0.04 to 0.40) but increased the net nitrogen mineralization rate by 49.2% (95% CI: 38.1–62.3%), the net nitrification rate by 56.0% (95% CI: 51.4–66.1%) and the DON by 39.2% (95% CI: 19.6–43.5%) (Fig. 3). There was a no difference in the response of the net nitrogen mineralization and net nitrification rates to warming (Q_M = 0.46, P > 0.05).

The experimental warming had positive effects on soil invertase (+10.6%; 95% CI: 3.1–18.9%) and protease (+4.2%; 95% CI: 3.8–32.4%) (Fig. 3). In contrast, soil catalase (mean effect size = 0.30; 95% CI: −0.01 to 0.07), urease (mean effect size = −0.13; 95% CI: −0.19 to 0.25) and polyphenol oxidase (mean effect size = −0.075; 95% CI: −0.180 to 0.002) did not change due to experimental warming (Fig. 3). In addition, the experimental warming increased the soil respiration by 33.6% (95% CI: 11.1–43.6%) (Fig. 3).

The warming duration did not correlate with the effects of warming on the soil carbon and nitrogen pools, MBC and MBN (Table 2). Similarly, the increased soil temperature had no correlations with the effects of warming on the soil nitrogen, MBC and MBN (Table 2). Although mean annual air temperature did not correlate with the effect of warming on soil carbon and nitrogen pools, it had a significant, negative relationship with the effect of warming on the soil MBC (P = 0.001) and MBN (P = 0.002) (Table 2).

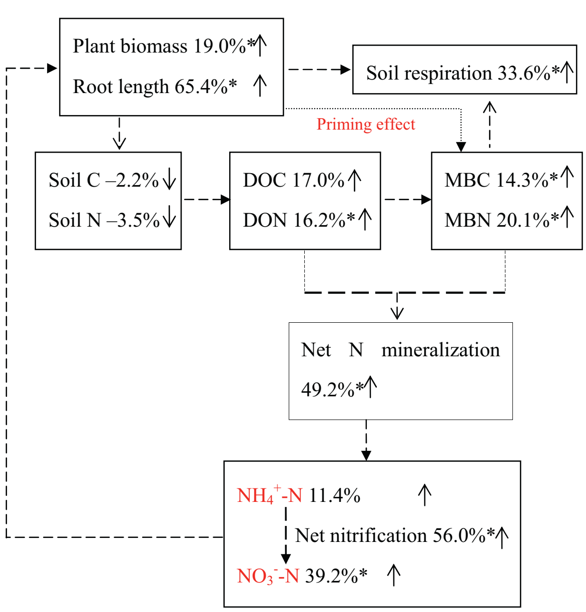

Fig. 4. Response of the soil carbon and nitrogen pools and their related biogeochemical processes to experimental warming from a meta-analysis of 25 studies on the Tibetan Plateau. ↑ and ↓ are positive and negative responses to warming, respectively. The numbers indicate the mean effect size. * P < 0.05. MBC: soil microbial biomass carbon; MBN: soil microbial biomass nitrogen; DOC: dissolved organic carbon; DON: dissolved organic nitrogen; NH_4^+-N: ammonium nitrogen; NO_3^--N: nitrate nitrogen.

4. Discussion

4.1. Soil C and N pools

The warming significantly increased the net nitrogen mineralization by 49.2% (Fig. 4), which was close to the magnitudes reported by previous meta-analyses (Bai et al., 2013; Lu et al., 2013a; Rustad et al., 2001). The warming-induced increase in the net nitrification (56.0%, Fig. 4) appeared to be larger than a previous meta-analysis (32.2%) (Bai et al., 2013), which was most likely because the forests had a greater net nitrification response to warming than the grassland/prairie and shrubland/heathland (Bai et al., 2013). In detail, all of the observations of net nitrification were derived from forests in our analysis, while those of Bai et al. (2013) were derived from all of the biomes mentioned above. The warming-induced increases in the net nitrogen mineralization and nitrification may increase plant biomass because the nitrogen availability in soil was generally one of the most vital limiting factors for plant growth in alpine regions (Lin et al., 2010). The ratio of MBC to MBN partially reflects the composition of soil microorganisms (Xiong et al., 2010), and the increased magnitude of MBN was much greater than that of MBC (Q_M = 4.21, P < 0.05). Therefore, we speculated that warming would change the composition of the soil microbial community.

We found a significant positive effect of warming on the microbial biomass in soil (Fig. 4) and a significant negative relationship between the effect size of the warming on the microbial biomass in soil and the mean annual air temperature (Table 2), indicating that the positive warming effects on soil microbial biomass in colder environments were generally greater than in warmer environments on the Tibetan Plateau. Bai et al. (2013) demonstrated that warming-induced reduction in labile carbon may result in the non-significant response of MBN to warming. However, warming did not affect DOC (Fig. 4), which is an important labile carbon pool (Lu et al., 2013a). These findings implied that DOC may not be the main limiting factors determining the increase of soil microbial biomass under warming condition on the Tibetan Plateau. Increases in plant biomass accumulation and root growth facilitated the growth of the soil microbial population and eventually the accumulation of soil microbial biomass (Barbhuiya et al., 2004; Dinakaran et al., 2011; Liu et al., 2011b Lu et al., 2013a).

The increase in the magnitude of R_s (+33.6%) due to warming in our meta-analysis was greater than that reported by previous meta-analyses (+9% to +22.5%) (Lu et al., 2013a; Rustad et al., 2001; Sun et al., 2011; Wu et al., 2011). The increases in the plant root respiration and soil microbial respiration likely resulted in the increase in the R_s, whereas the increase in the soil microbial respiration likely caused a decrease in the organic matter in soil (Lu et al., 2013a; Yan et al., 2011). In addition, decreases in soil carbon and nitrogen storage may also result from an increase in soil enzyme activity and a decrease in litter quantity due to climatic warming (Liu et al., 2011a; Pan et al., 2008; Xu et al., 2010a). However, neither the soil carbon nor nitrogen pools were significantly affected by the warming (Fig. 4), which was consistent with the previous meta-analyses (Bai et al., 2013; Lu et al., 2013a). This finding likely resulted from the fact that the increases in plant biomass and root growth (Fig. S1) may roughly offset the increase in soil microbial respiration.

4.2. Different responses between forests and grasslands

Previous meta-analyses indicated that forests were more sensitive to warming than grasslands in terms of R_s (Lu et al., 2013a; Rustad et al., 2001), net nitrogen mineralization and nitrification rates (Bai et al., 2013). The stronger response of these variables to warming in forests than in grasslands was attributed to the following causes: the effect of warming on the net nitrification was dependent on the soil moisture in the grasslands (Bai et al., 2013), and the negative response of soil moisture to warming in grasslands was greater than that in forests (Bai et al., 2013; Lu et al., 2013a). Soil respiration was positively correlated with soil moisture and soil drying can reduce the effect of warming on soil respiration (Liu et al., 2009; Shi et al., 2012). Thus, the experimental warming caused soil drying, which may offset the increased temperature effects in grasslands. In addition, Bai et al. (2013) attributed the stronger response of forests to the fact that most observations in forests were conducted in more temperature-limited areas.

In contrast, MBC and MBN showed a significant positive response to warming only in the grasslands (Fig. 2). MBC and MBN respond quickly to changes in soil temperature and moisture (Alvarez et al., 1995; Skopp et al., 1990), implying that the experimental warming caused changes in the soil temperature and moisture that affect the microbial activity and change the microbial biomass in the soil. First, the positive effects of warming on the soil microbial biomass decreased with increasing mean annual air temperature (Table 2) and grasslands had a lower mean annual air temperature than forests in our meta-analysis (most <3 °C vs. >3 °C). Second, soil drying may roughly offset the effect of warming on the microbial biomass in soil (Fu et al., 2012) and the negative effects of warming on the soil moisture in grasslands was greater than in forests (Bai et al., 2013; Lu et al., 2013a). Third, the effects of warming on the microbial biomass in soil did not change with the warming magnitude or warming duration (Table 2). Therefore, the different responses of the microbial biomass communities in the forests and grasslands may be attributed to the different mean annual air temperatures.

In addition, these results indicated that forests did not always show a stronger response to warming than grasslands. This finding was in line with recent meta-analyses which indicated that terrestrial ecosystems did not always have greater sensitivity in colder environments (Lu et al., 2013a; Wu et al., 2011).

4.3. Influences of warming duration and raised soil temperature

We did not find significant relationships between the warming duration and the sizes of the effects of the warming (Table 2), which may be observed because the soil carbon availability did not change, and the soil nitrogen availability increased in our meta-analysis. Our findings suggested that the effects of warming on gross and net primary production, net ecosystem exchange, ecosystem respiration, plant biomass, soil carbon and nitrogen, soil microbial biomass, net nitrogen mineralization and nitrification did not change with the warming duration (Bai et al., 2013; Lin et al., 2010; Lu et al., 2013a; Rustad et al., 2001; Wu et al., 2011) due to the significant, warming-induced increases in the labile carbon and nitrogen availability in the soil (Bai et al., 2013; Lu et al., 2013a; Rustad et al., 2001). In contrast, many studies indicated that the warming duration had a significant negative relationship between the warming effects and plant nitrogen uptake and R_s (Atkin et al., 2000; Bai et al., 2013; Melillo et al., 2002), which could be caused by the loss of labile carbon and nitrogen in soils (Luo et al., 2001; Melillo et al., 2002; Wu et al., 2011). Therefore, whether the effects of warming on carbon and nitrogen were correlated with the warming duration was likely dependent on the conditions of the labile carbon and nitrogen.

We did not find significant relationships between the warming magnitude and the sizes of the effects of warming on soil nitrogen, MBC or MBN (Table 2). This finding was in line with previous meta-analyses, which found that increased temperature was not significantly correlated with the effects of warming on R_s and soil carbon (Lu et al., 2013a), soil nitrogen and MBN (Bai et al., 2013).

5. Conclusions

Our meta-analysis indicated that both MBC and MBN exhibited stronger positive responses to warming in colder environments. Global warming may affect grasslands to a greater extent than forests in terms of MBC and MBN. However, warming did not affect soil carbon and nitrogen pools. Our findings should be useful for understanding the underlying mechanisms of the response of alpine soils to global warming.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.apsoil.2014.11.012.

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