Temperature and Moisture Effects on Soil Respiration in Alpine Grasslands

Xiaofeng Chang,[1,2] Xiaoxue Zhu,[1,3] Shiping Wang,[4,5] Caiyun Luo,[1] Zhenhua Zhang,[1] Jichuang Duan,[1] Ling Bai,[5] and Wenying Wang[6]

Abstract: The Tibetan Plateau, the low-latitude and high-altitude cold region, has a variety of soils rich in organic carbon (C). Climate change will have large impacts on soil carbon dioxide (CO_2) efflux in the region. These impacts will subsequently affect global-scale climate and C cycle links. However, the magnitude of this feedback is still uncertain. Here we use a laboratory incubation experiment to investigate how soil temperature and moisture affected the rate and temperature sensitivity of heterotrophic respiration of three alpine ecosystems (alpine meadow [M], alpine shrubland [SB], alpine swamp [SP]) on the Tibetan Plateau. Soil samples were incubated under three temperature (0°C, 15°C, and 30°C) and two moisture (50% and 100% water-holding capacity) conditions. The response of soil respiration to temperature and moisture varied with ecosystems. Soil respiration in SP was the most temperature sensitive, and higher moisture increased its temperature sensitivity (Q_{10}). The respiration and Q_{10} depended on total nitrogen in soils. Moreover, high moisture increased the dependence of Q_{10} on total nitrogen. Our results suggest that rising temperature in Tibetan Plateau may cause a positive feedback to the soil C cycle, particularly coupled with increasing precipitation and N addition.

Keywords: Alpine soils, climate change, incubation, temperature sensitivity, soil respiration, Tibetan Plateau.

(*Soil Sci* 2012;177: 564–570)

Soil respiration is temperature sensitive (Mikan et al., 2002; Fang and Moncrieff, 2005). Global warming will probably stimulate carbon dioxide (CO_2) release from soil, which will further exacerbate the problem (Ågren, 2010). One crucial determinant of the climate-carbon (C) cycle feedback is the effects of temperature on soil organic C (SOC) decomposition, which has been subject to much debate (Conant et al., 2011). Some studies found that increasing global temperature is likely to enhance the rate of respiration causing a significant release of CO_2 (Uchida et al., 2010; Allison and Treseder, 2011), whereas in other studies temperature increase did not stimulate respiration (Liu et al., 2009). Water availability is also a critical factor controlling microbial respiration. Respiration declines at the extreme ends of the soil-moisture spectra from laboratory studies and from theory (Davidson and Janssens, 2006). Laboratory incubation with a soil-moisture gradient revealed a constraint of temperature responses of soil respiration by low soil-moisture content (Liu et al., 2009). However, another incubation study with four type soils (typical steppe, mountain meadow, sand dune, and marshland) reported that both significant positive soil moisture and temperature affect CO_2 emissions (Wu et al., 2010). It is therefore necessary to determine which environmental factors affect soil respiration from different ecosystem soils and to predict the effect of climate change on regional/global C cycle in the alpine region.

Alpine grasslands (i.e., alpine meadow [M], shrubland [SB], swamp [SP] ecosystems) cover as much as 60% of the total area of the Tibetan Plateau and span a wide range of soil types (Zhou 2001). Recent studies have shown climate warming on the plateau (Thompson et al., 1993; 2000; Holmes et al., 2009). This strong warming signal has been accompanied by a precipitation increase in most parts of this region (Niu et al., 2004). Climate changes in the region are likely to strongly affect C cycling, thus exerting a feedback on climate (Zhao, 2009). Despite increasing observations of field CO_2 efflux in alpine ecosystems (Kato et al., 2004; Tao et al., 2007), there is a lack of studies testing soil respiration across multiple, diverse grassland soils on the Tibetan Plateau. Moreover, the effects of temperature and moisture on microbial respiration are usually confounded by variations in substrate (Pregitzer et al., 1999). Therefore, a laboratory experiment was carried out in which three alpine grassland soils representative of the region were incubated for 74 days at three temperature (0, 15, and 30°C) and two moisture (50% and 100%, water-holding capacity [WHC]) conditions. Our objectives were to (i) assess the changes in measured soil respiration arising from different temperature and moisture conditions and (ii) to investigate the temperatures sensitivity of C mineralization (Q_{10}) to different moisture conditions across the three grassland ecosystems. We hypothesized that increasing temperature will stimulate heterotrophic respiration, whereas saturated condition (e.g., 100% WHC) would constrain it, and altered soil moisture would modify its temperature sensitivity.

MATERIALS AND METHODS

Study Area

The Three-River Source Region, the source region of Yangtze River, Yellow River, and Mekong River, is located in central part of the Tibetan Plateau (Fig. 1). The Three-River

[1]Key Laboratory of Adaptation and Evolution of Plateau Biota, Haibei Alpine Meadow Ecosystem Research Station, Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining, China.
[2]Institute of Soil and Water Conservation, Northwest A & F University, Yangling, China.
[3]Graduate University, Chinese Academy of Sciences, Beijing, China.
[4]Laboratory of Alpine Ecology and Biodiversity of Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing, China.
[5]Naqu Ecological and Environmental Observation and Research Station, University of Tibet and Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Naqu, China.
[6]College of Life and Geography, Qinghai Normal University, Xining, China.
Address for correspondence: Xiaofeng Chang, PhD, Northwest Institute of Plateau Biology, 23 Xin'ning Road, Xining, Qinghai, 810008, China; E-mail: changxf12@yahoo.cn
Financial Disclosures/Conflicts of Interest: *This research was funded by the Chinese National Natural Science Foundation (41030105), the Special Program of Carbon Sequestration of the Chinese Academy of Sciences (XDA05070205), the National Basic Research Program (2010CB833502), and the Kunlun Scholarship of Qinghai Province.*
X.C. and X.Z. made an equal contribution to this article.
Financial Disclosures/Conflicts of Interest: *None reported.*
Received February 8, 2012.
Accepted for publication July 25, 2012.

ISSN: 0038-075X
DOI: 10.1097/SS.0b013e31826bdd5d

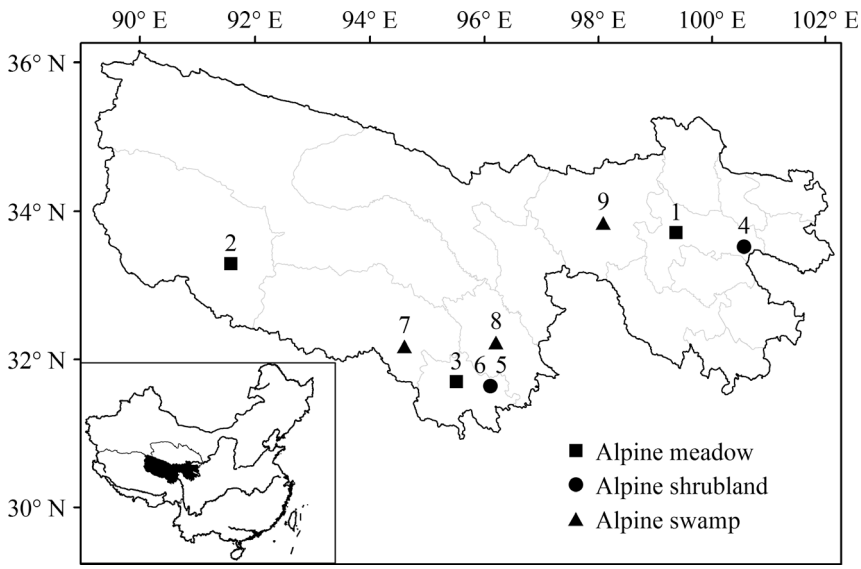

FIG. 1. Distribution of sampling sites with ecosystems.

Source Region has a typical continental plateau climate, with cold, dry, large diurnal variation of temperature, and strong radiation. The vegetation is mainly composed of M, SB, and SP. Alpine meadow is dominated by *Kobresia pygmaea* (C. B. Clarke), *Kobresia humilis* (C. A. Mey) Serg., *Kobresia tibetica* Maxim. Alpine shrubland is covered by *Salix oritrepha* var. *amnematchinensis* (L.). Alpine swamp has formed in permanently waterlogged areas or where the soil has been oversaturated and supports hardy perennial hydrophilous or hydromesophytic herbs such as *K. tibetica* (Zhou et al., 1987; Li and Zhou, 1998; Zhou, 2001). In general, soils are not well developed in this region, and soil is thin with a depth about 30 to 50 cm because of the impacts of high elevation and cold weather.

Soil Sampling

Soil samples were collected from August to September 2006 and 2008 with three replicated sites for each ecosystem. Five field replicates at each site were taken from the surface layer (0–10 cm). Collected soil samples were air-dried, passed through a 2-mm sieve, and stored at room temperature. From these samples, five sub-samples at each location were bulked and homogenized for analyses of physical and chemical properties. These composite samples were stored separately and taken back to the laboratory. The sampling locations provide a typical representation of the region. The sampling locations ranged from 32°18′ to 34°38′ N, 92°05′ to 100°43′ E, and 3,900 to 4,740 m in elevation (Fig. 1). Mean annual temperature (MAT) and mean annual precipitation (MAP) ranged from −3.6°C to 3.8°C and 312 to 526 mm, respectively. The total organic C (TOC) and total nitrogen (TN) in soils ranged from 5.14% to 21.25% and 0.44% to 1.21%, respectively (Table 1). Mean TOC and TN in soils were greatest for SP and were similar for M and SB (Table 1).

Laboratory Incubation

Soil gravimetric moisture was obtained after drying at 105°C for 24 h. A composite sample of each soil was used for determination of SOC and TN (measured with a Shimadzu 5000 SOC analyzer; Shimadzu Corporation, Kyoto, Japan). Total WHC was determined by placing 20 g of fresh soil into 10-cm funnels and soaking them in water to saturate the soil (n = 8). Soils were covered with a plastic sheet to minimize evaporation losses and left for 4 to 8 h to drain before being reweighed. This operation was repeated several times to ensure that a constant mass was reached. The soil was then oven-dried at 105°C to a constant mass. Water-holding capacity was

TABLE 1. General Description of the Research Sites

Site	Latitude	Longitude	Elevation (m a.s.l.)	MAT (°C)	MAP (mm)	TOC (%)	TN (%)	Clay (%)	Silt (%)	Sand (%)	pH	Ecosystem	Soil Type
1	34°34′ N	99°33′ E	4,330	−1.8	474.3	6.05	0.53	30.6	39.1	30.3	6.7	M	Mat-Cryic Cambisols
2	33°35′ N	92°05′ E	4,740	−3.6	311.6	8.96	0.55	32.3	43.4	24.4	7.4	M	Mat-Cryic Cambisols
3	32°19′ N	96°03′ E	4,563	2.4	507.8	13.41	0.97	31.7	40.7	27.6	5.3	M	Mat-Cryic Cambisols
4	34°25′ N	100°43′ E	3,900	−0.2	510.2	8.11	0.61	32.3	40.2	27.5	5.7	SB	Mol-Cryic Cambisols
5	32°18′ N	96°37′ E	4,215	3.8	525.6	6.80	0.44	32.4	40.3	27.3	5.7	SB	Mol-Cryic Cambisols
6	32°18′ N	96°37′ E	4,215	3.8	525.6	11.17	0.74	30.8	39.5	29.7	5.4	SB	Mol-Cryic Cambisols
7	32°44′ N	95°08′ E	4,350	0.5	514.7	12.13	0.98	32.3	42.4	25.2	6.8	SP	Organic Cryic Gleysols
8	32°54′ N	96°39′ E	4,327	2.0	485.5	21.25	1.21	32.3	42.0	25.7	6.7	SP	Organic Cryic Gleysols
9	34°38′ N	98°18′ E	4,240	−3.2	356.9	5.14	0.52	32.3	42.2	25.4	6.8	SP	Organic Cryic Gleysols

Note: Sites 5 and 6 are beneath-shrub and intershrub locations, respectively.

determined as the percentage of water retained after several h of drainage (equal to 100% WHC). Soil sub-samples of 10 g (based on dry weight at 105°C) were incubated using air-dried soil in 1,000-mL glass bottles for 74 days at three temperatures (0°C, 15°C, and 30°C) (±0.4°C) and two moisture levels (50% and 100% WHC) with six treatments in a full-factorial design with three replicates of each treatment. The aliquot samples from each site were stored and incubated separately and thus represent independent replicates. Each bottle at each temperature was randomly assigned to an incubator during the incubation experiment to eliminate the potential effect of different incubators on microbial respiration. The 0°C treatment reflected a temperature slightly higher than the mean annual soil temperature, whereas the 30°C treatment represented the extreme maximum soil temperature recorded, and 15°C approximately represents the mean soil temperature during summer in the region. Soil temperatures were not decreased below 0°C to avoid changing substrate availability due to alterations in the proportion of liquid water present (Mikan et al., 2002; Monson et al., 2006). Generally, 50% to 70% is considered to be optimum moisture content for laboratory incubations of soils (Paul et al., 2001). One hundred percent WHC sometimes happens in the region because of rainstorms especially considering climate change with increasing the frequency of extreme events. Soil moisture was monitored gravimetrically and was adjusted with distilled water on a daily basis.

Soil Respiration Measurements and Q_{10} Coefficients

Samples were incubated for 1 day before measurements were started to allow short-term equilibration after manipulating the soil. Soil respiration was measured at 12 points during the incubation periods (days 2, 4, 7, 10, 13, 16, 23, 30, 37, 44, 59, and 74, respectively). The first gas samples were taken from the headspace of the bottles using a 60-mL gas-tight syringe by drawing and plunging the syringe three times for homogeneous gas sampling when the bottles were opened to ensure exchange with free air outside each time. Then all bottles were sealed with rubber stoppers for 40 min before measurements, and gas samples were taken again. The soil respiration rates were measured as the difference between accumulated CO_2 concentrations during the 40-min incubation in the headspace of the sample glass bottles. For all samples, CO_2 concentration was measured by gas chromatography (HP Series 4890D; Hewlett Packard, Santa Clara, CA) within 24 h following gas sampling. The minimum detectable difference was less than 5×10^{-6} μg C/s for the instrument. Soil respiration rates were expressed as μg CO_2 g soil^{-1} h^{-1}.

Normally, Q_{10} expresses the temperature sensitivity of soil respiration (Davidson and Janssens, 2006). Based on the soil respiration rates at different locations and at three different soil temperatures with two soil moistures, the Q_{10} values were calculated as Q_{10}L (low; based on the soil respiration rates measured at 0°C and 15°C), Q_{10}M (medium; based on the soil respiration rates measured at 0°C and 30°C), and Q_{10}H (high; based on the soil respiration rates measured at 15°C and 30°C), with each moisture level using the average respiration rates (R) at two interval temperatures (T) (Howard and Howard, 1993; Kirschbaum, 1995):where R_1 and R_2 indicate the mean soil respiration rate at T_1 and T_2 temperature levels, respectively.

$$Q_{10} = \left(\frac{R2}{R1}\right)^{\frac{10}{T_2 - T_1}}$$

Statistical Analyses

General Linear Model–Repeated Measures Define Factors (SPSS 13.0; SPSS Inc., Chicago, IL) was used to assess the significance of the impacts of incubation temperature, moisture, ecosystem, site and incubation day, and their interactions on soil respiration, in which temperature, moisture, ecosystem, and site were treated as between-subject variables, and incubation day was treated as a within-subject variable. Multicomparisons were measured for soil respiration under different treatments for each ecosystem and at different sites for different treatments within the same ecosystem. For Q_{10} values, a four-way analysis of variance was analyzed to test differences between ecosystem, site, moisture, temperature range with initial temperature, and their interactions using a General Linear Model–Univariate procedure. Stepwise multiple linear regression analysis was performed to test the possible dependency of soil respiration and Q_{10} on soil TOC, TN, latitude, longitude, MAT, MAP, and altitude. All significances mentioned in the text were at $P < 0.05$ level.

RESULTS

Soil Respiration

There were significant effects of incubation day, temperature, moisture, ecosystem, site, and most of their interactive effects on soil respiration (Supplementary Digital Content, Table S1, http://links.lww.com/SS/A16). Soil respiration values decreased with incubation time in all soils (Supplementary Digital Content, Figs. S1–S3, http://links.lww.com/SS/A16). At the end of incubation day 74, the differences in soil respiration among treatments were not significant between M and SB soils. Generally, across all soil samples, high temperature and

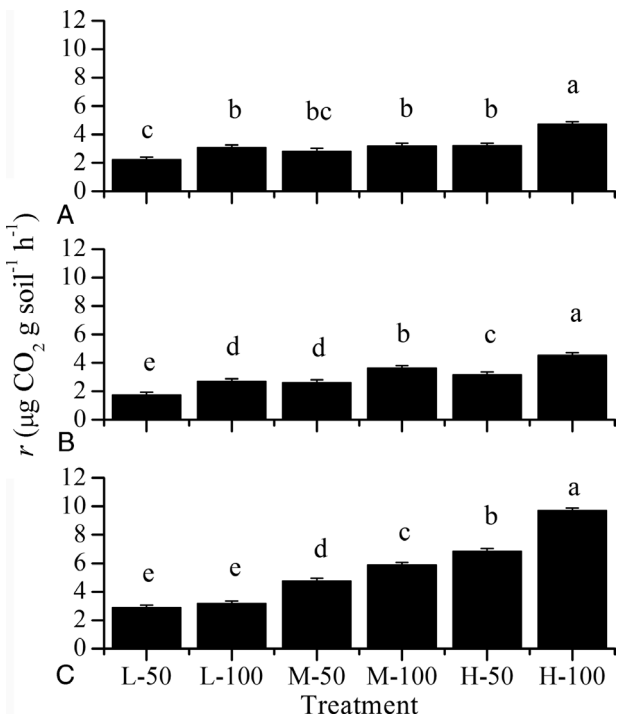

FIG. 2. Mean of respiration rates under different treatments for each ecosystem during the incubation period. M (A), SB (B), SP (C). L-50 and L-100, M-50 and M-100, and H-50 and H-100 represent treatments for 0°C, 15°C, and 30°C with 50% and 100% WHC, respectively. Error bars represent the S.E.M. Different letters between treatments indicate a significant difference at $P < 0.05$.

moisture increased average soil respiration rates (average, 2.63, 3.68, and 5.36 μg CO_2 g $soil^{-1}$ h^{-1} at 0°C, 15°C and 30°C; 3.28 and 4.50 μg CO_2 g $soil^{-1}$ h^{-1} at 50% and 100% WHC). However, this increase depended on ecosystem (Fig. 2). For example, for SB and SP soils, increasing temperature significantly increased the rates of CO_2 release from soils, whereas soil respiration from M soils significantly increased only at 30°C (Fig. 2). Soil respiration rates were higher under higher soil-moisture conditions in SB soils for all temperatures, whereas they were greater with higher soil moisture only at 0°C and 30°C and at 15°C and 30°C for M and SP soils, respectively (Fig. 2).

Stepwise regression analyses indicated that a significant positive correlation was observed only for TN in soils (Fig. 3). Furthermore, except for L-100 treatment, the TN effect on soil respiration was greater at higher temperatures and moistures (larger regression slop values) (Fig. 3; Supplementary Digital Content, Table S2, http://links.lww.com/SS/A16). When all data across treatments were pooled together, the best-fit model of the stepwise regression was as follows:where SR is mean soil respiration rate, *H* is elevation, LIM is laboratory incubation soil moisture, and LIT is laboratory incubation temperature.

$$SR = 15.680 + 4.826 \times TN - 0.445 \times MAT - 0.004H + 0.091 \times LIT + 2.460 \times LIM (R^2 = 0.70, P<0.001, n = 54)$$

Temperature Sensitivity of Microbial Respiration (Q_{10})

The effect of ecosystem on Q_{10} was significant (Supplementary Digital Content, Table S3, http://links.lww.com/SS/A16). When data across all six treatments and three sites were combined, the mean Q_{10} values for M, SB, and SP were 1.15, 1.19, and 1.40, respectively. High soil moisture increased Q_{10}. Moreover, the Q_{10} value also varied with sampling site at the same ecosystem under different soil moistures. For example, in the M soil, the Q_{10} value was smallest at sampling Site 2, and 100% WHC significantly increased the Q_{10} value compared with 50% WHC at sampling Site 3 (Fig. 4). In the SP soil, 100% WHC significantly increased Q_{10} value compared with 50% WHC at sampling Site 7 (Fig. 4). In addition, significant interactions of ecosystem, sampling site, and temperature ranges (i.e., 0°C–15°C, 15°C–30°C) affected Q_{10} (Supplementary Digital Content, Table S3, http://links.lww.com/SS/A16).

Stepwise regression analysis showed that only TN in soils was linearly and positively related to Q_{10} values, and dependency of Q_{10} on TN effect was stronger at higher soil moisture (slope value: 0.24 at 50% WHC and 0.41 at 100% WHC) (Fig. 5).

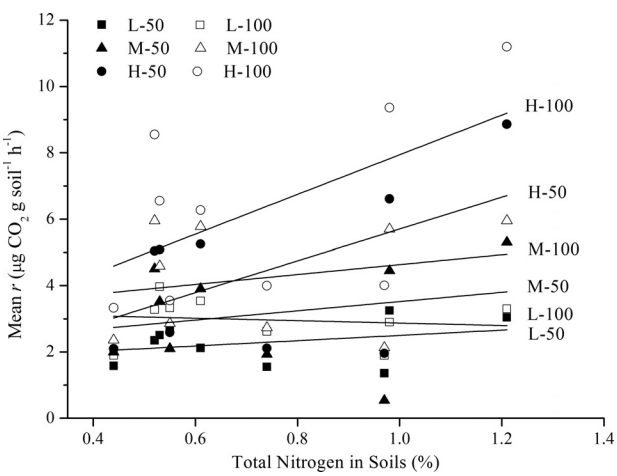

FIG. 3. Stepwise regression analysis using the mean respiration rate as the dependent variable, and using TOC concentration and TN concentration in soils and latitude, longitude, and altitude of sampling sites as variables under different treatments. Only TN concentration in soils remained. L-50 and L-100, M-50 and M-100, and H-50 and H-100 represent treatments for 0°C, 15°C, and 30°C with 50% and 100% WHC, respectively.

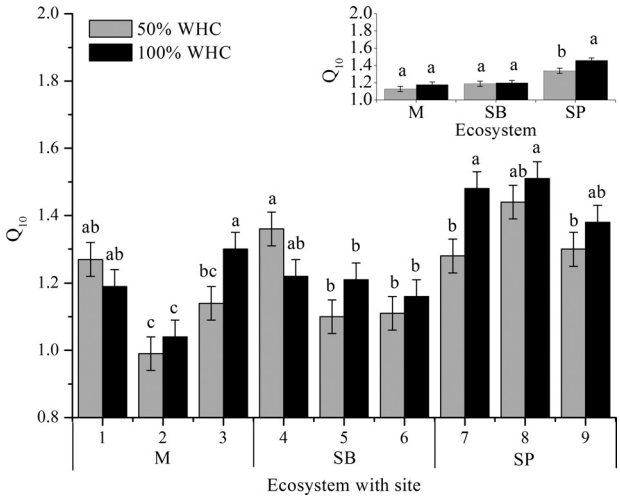

FIG. 4. Temperature sensitivity of the respiration rate (Q10) under different soil moisture for three ecosystems with different sites. Numbering of sites is the same as shown in Table 1. Comparisons were conducted just within the same ecosystem. Bars labeled with different letters within the same ecosystem differ significantly at $P < 0.05$. Error bars represent +1 S.E.

DISCUSSION

Effect of Temperature on Soil Respiration

Temperature manipulations can provide information about the direct response of microbial communities and decomposition

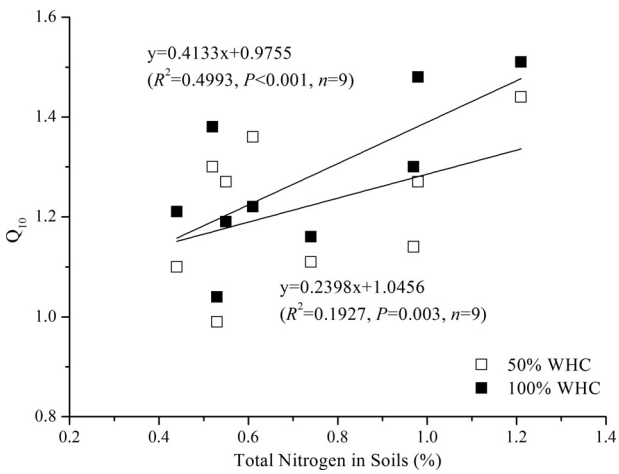

FIG. 5. Stepwise regression analysis using the mean temperature sensitivity of the respiration rate (Q10) as the dependent variable and using TOC concentration and TN concentration in soils and latitude, longitude, and elevation of sampling sites as variables under different soil moistures. Only TN concentration in soils remained.

rates to temperature in various terrestrial ecosystems (Cusack et al., 2010). However, there were inconsistencies in the results of the effects of experimental warming on microbial biomass and respiration. In contrast to our results, some researchers have found negative soil respiration response to warming (Liu et al., 2009). Variations in the environmental conditions are possible explanation. For example, exacerbated soil-water deficit leads to suppressed microbial activities and respiration in a semiarid temperate steppe (Liu et al., 2009). However, significant observed increase in soil respiration was due to elevated temperature rather than water limitation in our study. This increased respiratory process accelerated the exhaustion of available substrate at high temperatures (Dalias et al., 2001; Hamdi et al., 2010), and soil microorganisms were thus subject to higher substrate constraints at higher incubation temperatures with prolonged soil incubation (Feng and Simpson, 2009). Our study also indicated that TN significantly affected soil respiration. Soil respiration rates decreased with incubation time, also reflecting substrate limitation. Similarly, several studies have reported limited soil respiration responses to temperature alone, but there was significant response with external C supply (Song et al., 2010). These results suggest that temperature can not only directly impact the heterotrophic respiratory process, but also indirectly affect these processes via changing supply of substrate (Dalias et al., 2001; Hamdi et al., 2010). However, at the present stage, it is difficult to separate the interacting effects of incubation temperature and temperature-induced substrate constraints on soil respiration (Feng and Simpson, 2009; Uchida et al., 2010).

Effect of Soil Moisture on Soil Respiration

Many laboratory and theoretical studies showed that reduced soil respiration under very wet conditions as high water content can impede diffusion of O_2 (Linn and Doran, 1984; Davidson et al., 1998), which inhibit microbial respiration (Davidson et al., 1998). However, in the present study, high soil moisture significantly enhanced soil respiration, although the effect varied with temperature and sampling site. There are some possible explanations for this. First, according to Luo and Zhou (2006), the optimum soil-water content is usually somewhere near field WHC, whereas other authors reported that optimal soil water content for soil respiration is significantly (positively) related to soil clay content (Balogh et al., 2011). Alpine organic horizon soils with high clay content should have higher soil water content optimal for soil respiration and therefore facilitate diffusion of solutes and gases at high WHC. Second, low temperature (i.e., 0°C) may limit the diffusion of substrate in water films and microbial activity, which also inhibits the positive effect of high water content on soil respiration. On the other hand, low temperature rather than soil moisture is the main limitation of CO_2 production in the SP soil. Third, previous studies on tundra observed that the metabolism of the microbial communities of mesic sites is more adapted to anaerobic conditions. Changes in microbial community structure and decreases in the total microbial biomass were documented along with the drop in soil moisture in surface peat layers (Makiranta et al., 2009). In our study, surface dryness (although samples were watered each day) can limit decomposition rates, thus overriding the positive effect of decreasing anoxia (Makiranta et al., 2009). Fourth, it is possible that under the incubation conditions (high moisture content and temperature), some physicochemical processes produced a readily metabolizable substrate from the soil organic matter, or incubation conditions had activated microbes, which had remained inactive in the soils (Guntiñas et al., 2009). Independently of the cause of this response, the greater emissions of CO_2 under condition of high moisture content in soils will have important repercussions on the alpine regional C cycle (Guntiñas et al., 2009). If the response observed here is confirmed, alpine soil microbial respiration may have a pulsed response to rainstorm events, especially during prolonged summer drought, which is inconsistent with previous reports (Davidson et al., 1998).

Temperature Sensitivity of Soil Respiration (Q_{10})

The mean Q_{10} values for different alpine soils ranged from 1.15 to 1.40. The range of Q_{10} values was close to the range of reported temperature sensitivities (Q_{10} = 1.2 to 3.9) from different alpine soils (Dutzler-Feanz, 1981), but lower compared with values reported in the same region (Xu et al., 2005; Zhao et al., 2005; Peng et al., 2009; Zheng et al., 2009). These differences may be attributed to the following reasons. First, the Q_{10}, which was observed in previous studies, was based on changes in seasonal Q_{10} in intact plant-soil system. These results could have been caused by seasonal changes in the contribution of roots versus soil microbes to total below-ground respiration. The contribution of the more temperature-sensitive autotrophic respiration (Boone et al., 1998; Schindlbacher et al., 2008) and rhizosphere priming effect (Zhu and Cheng, 2010) could explain their apparent high Q_{10} (Grogan and Jonasson, 2005). In our study, by carrying out measurements in the absence of a rhizosphere, we avoided the possibility of microbial response being mediated through changes in plant activity (Hartley et al., 2008). Second, the low Q_{10} we observed could be related to an adaptation of microbial community to the alpine cold regions. The diurnal temperature fluctuation may reach 25°C to 40°C on the Tibetan Plateau (Ping et al., 2004). Thus, the near-surface microbes may experience strong freeze-thaw action. Waldrop and Firestone (2006) have shown that microbial communities in soil with variable soil environmental conditions are less temperature sensitive than those from more stable environment.

The temperature dependence of respiratory process may vary depending on the investigated temperature range, soil moisture, and the native climatic regime (Mikan et al., 2002; Yuste et al., 2007; Balser and Wixon, 2009; Rinnan et al., 2009; Craine and Gelderman, 2011). However, there was no significant relationship between the Q_{10} values and MAT, MAP, incubation temperature, and moisture in our study. This can be partly caused by the small range in MAT and MAP among sites of −3.6°C to 3.8°C and 312 to 526 mm, respectively. We found that the Q_{10} values were affected by the interactions of ecosystem, sampling site, and moisture /temperature ranges and were positively correlated to TN in soils. Other studies also report temperature dependence of soil organic matter decomposition to changes in soil nutrient content (Vanhala et al., 2008; Song et al., 2010). It appeared that the biological activity in alpine grasslands is likely limited by the soil TN and water availability.

CONCLUSIONS AND IMPLICATIONS

Elevated temperature and moisture enhanced soil respiration in this alpine region. This study also revealed Q_{10} values in the lower range of reported values from the literature. This relatively low temperature response may be an adaptation to a cold environment and elimination of plant activity effects. The among-site variability in the temperature response was related to TN in soils. Moreover, high moisture increased the dependence of Q_{10} on TN. The Tibetan Plateau is currently experiencing rapid changes such as warming and N deposition. Hence, under future climate change, the microbial decomposition of

SOC in alpine ecosystems will be stimulated. However, interacting effects of temperature and temperature-induced substrate constraints on soil decomposition process have not been resolved. Further work is needed to elucidate (i) the interactive effects of temperature and substrate on microbial physiology and respiration and (ii) the potential for CO_2 to be emitted from specific grassland soil due to climate change and vegetation change.

REFERENCES

Ågren, G. I. 2010. Climate change: Microbial mitigation. Nature Geoscience 3:303–304.

Allison, S. D., and K. K. Treseder. 2011. Climate change feedbacks to microbial decomposition in boreal soils. Fungal Ecol. 4:362–374.

Balogh, J., K. Pintér, S. Fóti, D. Cserhalmi, M. Papp, and Z. Nagy. 2011. Dependence of soil respiration on soil moisture, clay content, soil organic matter, and CO_2 uptake in dry grasslands. Soil Biol. Biochem. 43: 1006–1013.

Balser, T. C., and D. L. Wixon. 2009. Investigating biological control over soil carbon temperature sensitivity. Global Change Biol. 15:2935–2949.

Boone, R. D., K. J. Nadelhoffer, J. D. Canary, and J. P. Kaye. 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. Nature 396:570–572.

Conant, R. T., M. G. Ryan, G. I. Ågren, H. E. Birge, E. A. Davidson, P. E. Eliasson, S. E. Evans, S. D. Frey, C. P. Giardina, and F. M. Hopkins. 2011. Temperature and soil organic matter decomposition rates—Synthesis of current knowledge and a way forward. Global Change Biol. 17: 3392–3404.

Craine, J. M., and T. M. Gelderman. 2011. Soil moisture controls on temperature sensitivity of soil organic carbon decomposition for a mesic grassland. Soil Biol. Biochem. 43:455–457.

Cusack, D. F., M. S. Torn, W. H. Mcdowell, W. L. Silver. 2010. The response of heterotrophic activity and carbon cycling to nitrogen additions and warming in two tropical soils. Global Change Biol. 16:2555–2572.

Dalias, P., J. M. Anderson, P. Bottner, and M. M. Couteaux. 2001. Temperature responses of carbon mineralization in conifer forest soils from different regional climates incubated under standard laboratory conditions. Global Change Biol. 7:181–192.

Davidson, E. A., E. Belk, and R. D. Boone. 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. Global Change Biol. 4:217–227.

Davidson, E. A., and I. A. Janssens. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440:165–173.

Dutzler-FranzDutzler-Franz, G. 1981. Einfluss der temperature auf die mikrobielle Aktivität einiger Böden aus der temperierten und hochalpinen Klimaregion. *In* Bodenbiologische Untersuchungen in den Hohen Tauern 1974–1978, Veröffentlichungen des österreichischen MaB-Programms, bd. 4. H. Franze (ed.). Univ. Wanger, Innsbruck, pp. 263–294.

Fang, C., and J. B. Moncrieff. 2005. The variation of soil microbial respiration with depth in relation to soil carbon composition. Plant Soil 268: 243–253.

Feng, X. J., and M. J. Simpson. 2009. Temperature and substrate controls on microbial phospholipid fatty acid composition during incubation of grassland soils contrasting in organic matter quality. Soil Biol. Biochem. 41:804–812.

Grogan, P., and S. Jonasson. 2005. Temperature and substrate controls on intra-annual variation in ecosystem respiration in two subarctic vegetation types. Global Change Biol. 11:465–475.

Guntiñas, M., F. Gil-Sotres, M. Leirós, and C. Trasar-Cepeda. 2009. CO_2 emission from soils under different uses and flooding conditions. Soil Biol. Biochem. 41:2598–2601.

Hamdi, S., T. Chevallier, N., Ben Aïssa, M. Ben Hammouda, T. Gallali, J. L. Chotte, and M. Bernoux. 2010. Short-term temperature dependence of heterotrophic soil respiration after one-month of pre-incubation at different temperatures. Soil Biol. Biochem. 43:1752–1758.

Hartley, I. P., D. W. Hopkins, M. H. Garnett, M. Sommerkorn, and P. A. Wookey. 2008. Soil microbial respiration in arctic soil does not acclimate to temperature. Ecol. Lett. 11:1092–1100.

Holmes, J. A., E. R. Cook, and B. Yang. 2009. Climate change over the past 2000 years in Western China. Quaternary Int. 194:91–107.

Howard, D. M., P. J. A. Howard. 1993. Relationships between CO_2 evolution, moisture content and temperature for a range of soil types. Soil Biol. Biochem. 25(11):1537–1546.

Kato, T., Y. Tang, S. Gu, X. Cui, M. Hirota, M. Du, Y. Li, X. Zhao, and T. Oikawa. 2004. Carbon dioxide exchange between the atmosphere and an alpine meadow ecosystem on the Qinghai-Tibetan Plateau, China. Agricul. Forest Meteorol. 124:121–134.

Kirschbaum, M. U. F. 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. Soil Biol. Biochem. 27(6):753–760.

Li, W., and X. Zhou. 1998. The Ecosystem of Qinghai-Tibet Plateau and Its Optimizing Utilized Model. Guangzhou Science and Technology Press, Guangzhou, China.

Linn, D. M., and J. W. Doran. 1984. Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and untilled soils. Soil Sci. Soc. Am. J. 48(6):1267–1272.

Liu, W. X., Z. Zhang, and S. Q.Wan. 2009. Predominant role of water in regulating soil and microbial respiration and their responses to climate change in a semiarid grassland. Global Change Biol. 15:184–195.

Luo, Y., and X. Zhou. 2006. Soil Respiration and the Environment. Academic/Elsevier, San Diego, CA, pp 328.

Makiranta, P., R. Laiho, H. Fritze, J. Hytonen, J. Laine, and K. Minkkinen. 2009. Indirect regulation of heterotrophic peat soil respiration by water level via microbial community structure and temperature sensitivity. Soil Biol. Biochem. 41:695–703.

Mikan, C. J., J. P. Schimel, and A. P. Doyle. 2002. Temperature controls of microbial respiration in arctic tundra soils above and below freezing. Soil Biol. Biochem. 34:1785–1795.

Monson, R. K., D. L. Lipson, S. P. Burns, A. A. Turnipseed, A. C. Delany, M. W. Williams, S. K. Schmidt. 2006. Winter forest soil respiration controlled by climate and microbial community composition. Nature 439: 711–714.

Niu, T., L. Chen, and Z. Zhou. 2004. The characteristics of climate change over the Tibetan Plateau in the last 40 years and the detection of climatic jumps. Adv. Atmosph. Sci. 21:193–203.

Paul, E. A., S. J. Morris, and S. Bo?hm. 2001. The determination of soil C pool sizes and turnover rates: Biophysical fractionation and tracers. *In* Assessment Methods of Soil Carbon. R. Lal, J. M. Kimble, R. F. Follett, and B. A. Stewart (eds.). CRC Press, Boca Raton, pp. 193–205.

Peng, S. S., S. L. Piao, T. Wang, J. Y. Sun, and Z. H. Shen. 2009. Temperature sensitivity of soil respiration in different ecosystems in China. Soil Biol. Biochem. 41(5):1008–1014.

Ping, C. L., G. Qiu, L. Zhao. 2004. The periglacial environment of China. *In* Cryosols. Permafrost-Affected Soils. J. M. Kimble (ed.). Springer-Verlag, Berlin, Germany, pp. 275–291.

Pregitzer, K. S., D. R. Zak, N. W. Macdonald, and W. E. Holmes. 1999. Soil temperature, matric potential, and the kinetics of microbial respiration and nitrogen mineralization. Soil Sci. Soc. Am. J. 63:575–584.

Rinnan, R., J. Rousk, E. Yergeau, G. A. Kowalchuk, and E. Baath. 2009. Temperature adaptation of soil bacterial communities along an Antarctic climate gradient: Predicting responses to climate warming. Global Change Biol. 15:2615–2625.

Schindlbacher, A., S. Zechmeister-Boltenstern, B. Kitzler, and R. Jandl. 2008. Experimental forest soil warming: Response of autotrophic and heterotrophic soil respiration to a short-term 10 degrees C temperature rise. Plant Soil 303:323–330.

Song, M., J. Jiang, G. Cao, and X. Xu. 2010. Effects of temperature, glucose and inorganic nitrogen inputs on carbon mineralization in a Tibetan alpine meadow soil. Eur. J. Soil Biol. 46:375–380.

Tao, Z., C. D. Shen, Q. Z. Gao, Y. M. Sun, W. X. Yi, and Y. N. Li. 2007. Soil organic carbon storage and soil CO2 flux in the alpine meadow ecosystem. Sci. China Ser. D Earth Sci. 50:1103–1114.

Thompson, K., J. P. Grime, S. H. Hillier, A. P. Askew, D. Corker, J. P. Kielty, G. J. Masters, V. K. Brown, and I. P. Clarke. 2000. Predicting the response of limestone grassland to climate change. Aspects Appl. Biol. 58:329–336.

Thompson, L. G., E. Mosleythompson, M. Davis, P. N. Lin, T. Yao, M. Dyurgerov, and J. Dai. 1993. Rencent warming-ice core evidence from tropical ice cores with emphasis on Central-Asia. Global Planet. Change 7:145–156.

Uchida, Y., T. J. Clough, F. M. Kelliher, and R. R. Sherlock. 2010. Soil microbial respiration responses to changing temperature and substrate availability in fertile grassland. Soil Res. 48:395–403.

Vanhala, P., K. Karhu, M. Tuomi, K. Bjorklof, H. Fritze, and J. Liski. 2008. Temperature sensitivity of soil organic matter decomposition in southern and northern areas of the boreal forest zone. Soil Biol. Biochem. 40:1758–1764.

Waldrop, M. P., and M. K. Firestone. 2006. Response of microbial community composition and function to soil climate change. Microb. Ecol. 52:716–724.

Wu, X., Z. Yao, N. Brüggemann, Z. Y. Shen, B. Wolf, M. Dannenmann, X. Zheng, and K. Butterbach-Bahl. 2010. Effects of soil moisture and temperature on CO_2 and CH_4 soil-atmosphere exchange of various land use/cover types in a semi-arid grassland in Inner Mongolia, China. Soil Biol. Biochem. 42:773–787.

Xu, S. X., X. Q. Zhao, Y. L. Fu, L. Zhao, Y. N. Li, G. M. Cao, S. Gu, Q. X. Wang, and M. Y. Du. 2005. Characterizing CO_2 fluxes for growing and non-growing seasons in a shrub ecosystem on the Qinghai-Tibet Plateau. Sci China Ser D 48:133–140.

Yuste, J. C., D. D. Baldocchi, A. Gershenson, A. Goldstein, L. Misson, and S. Wong. 2007. Microbial soil respiration and its dependency on carbon inputs, soil temperature and moisture. Global Change Biol. 13:2018–2035.

Zhao, L., Y. N. Li, X. Q. Zhao, S. X. Xu, Y. H. Tang, G. R. Yu, S. Gu, M. Y. Du, and Q. X. Wang, . 2005. Comparative study of the net exchange of CO_2 in 3 types of vegetation ecosystems on the Qinghai-Tibetan Plateau. Chinese Sci Bull 50(16):1767–1774.

Zhao, X.Q. 2009. Alpine Meadow and Global Change. Science Press, Beijing, China.

Zheng, Z. M., G. R. Yu, Y. L. Fu, Y. S. Wang, X. M. Sun, and Y. H. Wang. 2009. Temperature sensitivity of soil respiration is affected by prevailing climatic conditions and soil organic carbon content: A trans-China based case study. Soil Biol. Biochem. 41(7):1531–1540.

Zhou, X. 2001. Chinese *Kobresia pygmaea* Meadow. Science Press, Beijing, China.

Zhou, X., Z. Wang, and Q. Du (eds.). 1987. The vegetation of Qinghai Province. Qinghai People Press, China.

Zhu, B., W. Cheng. 2010. Rhizosphere priming effect increases the temperature sensitivity of soil organic matter decomposition. Global Change Biol. 17:2172–2183.