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ORIGINAL PAPER

Responses of SOM decomposition to changing temperature in Zoige alpine wetland, China

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Abstract Alpine wetlands are considered to be very sensitive to future climate warming. Understanding changes in decomposition rates (*Rs*) of soil organic matter (SOM) and temperature sensitivity (Q_{10}) in alpine wetlands, under the scenarios of a warming climate and decreasing soil moisture, is important for predicting their carbon (C) budget. Here, we established three sampling transects from wetland edge to meadow in the Zoige alpine wetlands in China, which represented the gradients of decreasing soil moisture. We conducted an incubation experiment (5–25 °C) to explore changes in Q_{10} with the degradation process from alpine wetland to alpine meadow. The results showed that temperature significantly influenced *Rs* in all locations. *Rs* first increased from site I to site IV and then decreased from site IV to site V. However, Q_{10} and activation energy (E_a) showed no apparent trends with soil coming from sites along a moisture gradient. Overall, the Q_{10} values in the wetland (sites 1.50) were significantly lower than that of the meadow (1.83); similar trends were observed for E_a. In addition, E_a exhibited a negative logarithmic relationship with C quality indices in all locations, which suggested that the C quality-temperature hypothesis is applicable to both alpine wetlands and meadows. These findings provide a theoretical foundation for predicting the potential influences of warming climate on soil C turnover and storage in alpine wetlands.

Keywords Activation energy · Alpine wetland · Carbon quality-temperature hypothesis · Soil organic carbon · Temperature sensitivity · Soil moisture

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Introduction

It is estimated that wetlands store approximately 20–30 % of terrestrial soil organic carbon (SOC), although they occupy only 5–8 % of the land surface (Mitsch and Gosselink 2007). Wetland degradation, especially decreasing area and soil water content, has been widely observed in association with warming climate (Froend 1999; Jin et al. 2007), which is accompanied by the reduction of productivity, biodiversity (Hart and Lovvorn 2000), and soil nutrients (Gilbert et al. 2004). Gillespie et al. (2014) pointed out that under warming climate, higher decomposition of soil organic matter (SOM) and a lower water table would occur in subarctic wetlands and result in increased CO_2 release in this region. Therefore, the degradation of wetlands has an immediate impact on their C budget, and it is necessary to take effective measures to restore them (Limpens et al. 2008).

Few studies have investigated the effect of and lowered water table on SOM decomposition in alpine wetlands. Theoretically, changes in soil moisture play important roles in regulating SOM decomposition. Soil water films may promote diffusion of extracellular enzymes and soluble organic carbon (C) substrates and may increase substrate availability in micro-sites when water content is moderate (Davidson and Janssens 2006; Toberman et al. 2008). Gao et al. (2008) demonstrated that soil moisture strongly influences microbial activity and SOM decomposition in wetlands. Numerous researchers have found that the content and quality of SOM may influence SOM decomposition to large extent in alpine wetlands where temperature and moisture are not limiting (de Bruijn and Butterbach-Bahl 2010; Huo et al. 2013; Kirschbaum 2006).

Temperature is a key factor influencing the decomposition rates (*Rs*) of SOM decomposition (Jones et al. 2003; Lenton and Huntingford 2003). The temperature sensitivity (Q_{10}) has been widely used to depict the response of SOM decomposition to changing temperature (Bauer et al. 2008; He et al. 2013; Kirschbaum 2000). Some studies have demonstrated that Q_{10} is important for predicting the C budget in terrestrial ecosystems under warming scenarios, and some experimental studies have explored the spatiotemporal patterns of the Q_{10} values in terrestrial ecosystems (Davidson and Janssens 2006; Fang et al. 2005; Fierer et al. 2006; Gillabel et al. 2010). However, the response of Q_{10} values to the degradation in alpine wetlands have not been investigated to date. Furthermore, on basis of the principles of thermodynamics and enzyme kinetics, the C quality-temperature hypothesis (CQT) has been proposed to explain the mechanisms of SOM decomposition and substrate quality (Conant et al. 2008; Davidson and Janssens 2006; Xiang and Freeman 2009). This hypothesis assumes that molecular complexity of the substrate is associated with the quality of organic matter, and lower-quality substrates have recalcitrant molecular structure and higher activation energy (E_a) and thus a greater Q_{10} value. As the temperature increases, more molecules reach or exceed their E_a; however, there is a decline in the relative increase in the fraction of molecules with sufficient energy to react, indicating that Q_{10} decreases with increasing temperature (Davidson and Janssens 2006). The CQT hypothesis has been validated by some studies using different approaches (Bosatta and Agren 1999; Craine et al. 2010a, b; Mikan et al. 2002; Xu et al. 2012). However, whether or not the CQT hypothesis could be applicable to alpine wetlands has not been verified.

The Zoige alpine wetland is located at the eastern edge of the Qinghai-Tibet Plateau and is the largest alpine wetland in China (Fei et al. 2006). SOM decomposition in alpine wetlands is expected to increase to some extent under climatic warming scenarios accompanied by decreasing wetland area and water table. In this study, we established three transects from wetland edge to meadow along the gradients of decreasing soil moisture, and conducted an incubation experiment to explore the changes in *Rs* and Q_{10}. Our main objectives were to (1) investigate the changing trends of *Rs* with the degradation of the alpine wetland, (2) explore the changes in Q_{10} and E_a with the alpine wetland degradation, and (3) verify the applicability of the CQT hypothesis in the alpine wetland and meadow.

Materials and methods

Study area

The Zoige Wetlands (32°56′–34°19′N, 102°08′–103°39′E) is located at the eastern edge of the Qinghai-Tibet Plateau in China and is the largest alpine wetland in China. The altitude of the study area is approximately 3,400–3,800 m a.s.l. This region has a typical humid and semi-humid continental monsoon climate of plateau cold temperate zone. The mean annual temperature is approximately 0.7 °C, and the mean annual precipitation is 600–800 mm (Bai et al. 2013). The coldest month is January (−10.6 °C) and the warmest month is July (10.8 °C). The major vegetation types are marsh-meadow and meadow. The marsh-meadow is dominated by *Carex muliensis*, *C. lasiocarpa*, and *C. meyeriana*, whereas the meadow is dominated by *Poaceae* grasses such as *Elymus dahuricus*, and *Poa pratensis* (Huo et al. 2013).

Soil samples were collected in July 2013 in Huahu Lake, Zoige, Sichuan Province. Huahu Lake is the highest alpine lake in Zoige and has typical water-table gradients from alpine wetland to alpine meadow (Chen et al. 2011). A decline in wetland area and water table has been observed in past decades in this region (Tan et al. 2012; Tang et al. 2012; Zhang et al. 2011).

Sampling and pretreatment

We first established three transects from the edge of Huahu Lake to the alpine meadow, with five sampling locations (I, II, III, IV, and V) in each transect to represent the gradients of decreasing soil moisture. Sampling sites I–IV were in the alpine wetland region, and site V was in the alpine meadow region (Fig. 1). All sampling sites had been subjected to long-term free grazing by yak, according to local grazing tradition. Plant community composition and above-ground productivity, and coverage showed that vegetation was in good condition in locations I–IV, whereas V was slightly degraded as a result of higher grazing intensity (Table 1).

We measured soil water content, plant species composition, and aboveground biomass in six quadrats (50 × 50 cm) at random locations in each sampling site. We recorded plant coverage, density, height, and frequency in three quadrats per sampling location; aboveground biomass was clipped at ground level in all quadrats. Three soil samples were taken at each sampling location in the 0–10 and 10–30 cm soil layers using an auger (7 cm diameter). Soil samples were sieved (<2 mm), and visible roots and organic debris were removed by hand. Approximately 100 g of soil for each sample was air-dried for analysis of soil properties (C, nitrogen (N), and pH). The remaining soil samples were stored at 4 °C.

Chemical analysis and incubation experiment

Soil water holding capacity (WHC, %) and gravimetric water content (%) were measured in the laboratory. The concentrations of soil total C and total N were measured using a Vario Max CN elemental analyzer (Vario Max CN, Elementar Company, Germany). Soil pH was measured in a soil–water slurry (1:2.5, w/w) with an Ultrameter-2 pH meter (Myron L. Company, California, USA).

To prevent the thermal adaptation of soil microorganisms (Sierra et al. 2010), the 56-d laboratory incubation was conducted at five temperatures (8, 13, 18, 23, and 28 °C in the daytime; 5, 10, 15, 20, and 25 °C at night). A total of 225 soil samples (3 transects × 5 sampling sites × 3 temperatures × 3

Fig. 1 Sampling locations in the Zoige wetland, China

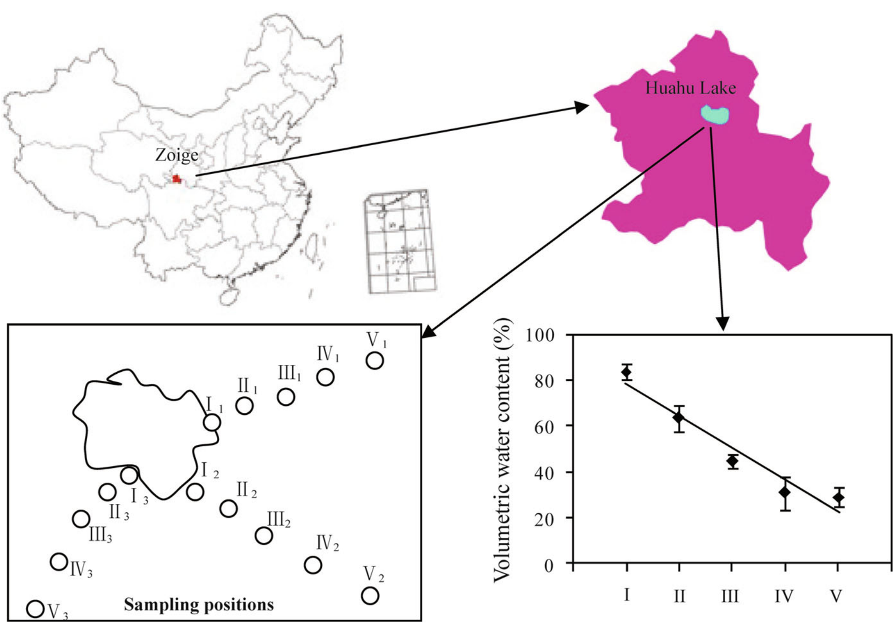

Table 1 Soil and vegetation properties at different sampling locations in the Zoige alpine wetland

Sampling location	Vegetation types	Dominant species	Volumetric water content (v/v)	Soil total carbon (%)	Soil total nitrogen (%)	Soil pH	Conductivity	Land-use condition
I[†]	Alpine wetland	*Hippuris vulgaris*, *Carex muliensis*	83.59 ± 3.56^{a}[§]	11.86 ± 6.07^{ab}	0.80 ± 0.38^{ab}	7.94 ± 0.17^{a}	231.43 ± 110.93^{ab}	Free-grazing,good condition
II	Alpine wetland	*C. muliensis*, *C. meyeriana*, *Kobresia tibetica*	63.41 ± 5.49^{b}	15.52 ± 6.74^{ab}	1.18 ± 0.51^{ab}	7.95 ± 0.03^{a}	383.10 ± 145.83^{ab}	Free-grazing,good condition
III	Alpine wetland	*C. muliensis*, *C. meyeriana*, *K. tibetica*	44.60 ± 3.32^{c}	14.84 ± 4.92^{ab}	1.12 ± 0.39^{ab}	7.85 ± 0.16^{a}	312.93 ± 111.57^{ab}	Free-grazing,good condition
IV	Alpine wetland	*C. muliensis*, *C. meyeriana*, *K. tibetica*	30.80 ± 7.21^{d}	22.05 ± 2.62^{a}	1.71 ± 0.18^{a}	7.86 ± 0.19^{a}	439.50 ± 203.56^{b}	Free-grazing,good condition
V	Alpine meadow	*Elymus dahuricus*, *Poa pratensis*, *Polygonaceae*	29.00 ± 4.15^{d}	6.71 ± 0.62^{b}	0.58 ± 0.05^{b}	7.75 ± 0.35^{a}	149.87 ± 37.64^{a}	Free-grazing, degeneration
F value			196.233	1.376	1.546	0.451	2.267	
P value			<0.001	0.310	0.262	0.770	0.134	

[†] See Fig. 1 for the relative positions of I, II, III, IV, and V

[§] Data represent mean ± SE ($n = 3$). Data with the same superscript letters within same column indicate no significant difference at $P < 0.05$

replicates) were used in the incubation experiment. In brief, 40 g of fresh soil, adjusted to 55 % WHC, was placed into incubation bottles (5 cm diameter, 10 cm tall) and mixed with 10 g quartz sand. The samples were pre-incubated at 20 °C and constant humidity (80 %) for 1 week followed by the incubation temperature for 8 weeks to measure *Rs*. During the 56-d experiment, *Rs* were measured 10 times, on days 0, 1, 3, 5, 7, 14, 21, 28, 42, and 56. Soil moisture was adjusted at 3–4 day intervals on a weight basis.

An automatic system has been developed to measure *Rs* (He et al. 2013). In practice, *Rs* (μg C g^{-1} h^{-1}) was calculated from the slope of CO_2 concentration and conversion factors as follows:

$$Rs = \frac{C \times V \times \alpha \times \beta}{m} \tag{1}$$

where C is the slope of the change in CO_2 concentration, V is the volume of the incubation bottle and gas tube, m is the soil weight (g), α is the conversion coefficient for CO_2 mass, and β is a conversion coefficient of time.

Calculation of E_a and Q_{10}

The Q_{10} values were calculated using the following exponential equations (Fierer et al. 2003):

$$Rs = Q \times e^{bT} \tag{2}$$

$$Q_{10} = e^{10b} \tag{3}$$

where T is temperature (°C); Q is C quality index of SOM (the exponential constant or activity at 0 °C); and b is the exponential fit parameter for the slope of the line describing the temperature–respiration relationship. The E_a values were calculated using the Arrhenius equations as follows (Hamdi et al. 2013):

$$Rs = A \times e^{\frac{-Ea}{RT}} \tag{4}$$

$$Ea = R \times (\ln Q_{10}) \Big/ \left(\frac{1}{T_1} - \frac{1}{T_2}\right) \tag{5}$$

where A is a pre-exponential parameter; R is the gas constant (8.314 J mol^{-1}); and T_1 and T_2 indicate temperature (K) and indicate the 10 °C temperature range for the corresponding Q_{10} (i.e., $T_1 + 10 = T_2$). In calculating E_a, Q_{10} represented the range T_{-5} to T_{+5}, where T was the average incubation temperature.

Statistical analysis

One-way analysis of variance (ANOVA) was used to compare soil water content, total C and N, pH, and conductivity among different locations. Univariate analysis was used to examine the effects of sampling location, temperature, incubation duration, and their interactions on *R*s. Differences in Q_{10} between alpine wetland and meadow were examined using independent-sample *t*-tests. Regression analyses were used to evaluate the relationships between C quality index and E_a. Significant differences were defined as $P = 0.05$. All statistical analyses were conducted using SPSS 13.0 (SPSS Inc., Chicago, IL, USA).

Results

Changes in soil and vegetation

Soil water content decreased gradually and significantly (84–29 %) from locations I to V (Fig. 1; $F = 196.233$, $P < 0.001$). Soil C and N content increased initially and then decreased from locations I to V, and they were lowest in the alpine meadow (V). Soil C content was significantly higher in wetlands than in meadow sites ($F = 10.194$, $P = 0.004$), but no significant differences were observed among different wetland locations (Table 1).

Effects of temperature and sampling location on *Rs*

Sampling location, incubation temperature, and incubation duration significantly influenced the accumulation of SOM decomposition, and there was a significant interactive effect ($P < 0.001$; Table 2). Similarly, these variables significantly affected *Rs*, and there was a significant interactive effect for sample position and temperature ($P < 0.001$; Table 2). *Rs* increased significantly with increasing incubation temperature at all sampling locations ($F = 80.880$, $P < 0.001$, Table 2), which can be well depicted by exponential equations (Fig. 2). As expected, *Rs* increased gradually from location I to IV and then decreased drastically at location V, regardless of incubation duration (Fig. 3). Furthermore, *Rs* differed significantly in relation to soil moisture ($F = 139.305$, $P < 0.001$; Fig. 3, Table 2), and showed a general trend of IV > III > II > I > V.

Changes in Q_{10} and E_a with soil moisture gradient

The Q_{10} values ranged from 1.49 to 1.83 from locations I to V, and were highest in the alpine meadow. Unexpectedly, Q_{10} did not differ significantly from location I to IV, which represented a degradation gradient ($R^2 = 0.316$, $P = 0.352$; Fig. 4c). However, the Q_{10} values were significantly higher in the alpine meadow than in the wetland ($F = 7.657$, $P < 0.001$; Fig. 4d).

E_a increased to some extent with decreasing soil moisture ($R^2 = 0.394$, $P = 0.256$; Fig. 4a) and E_a was highest in the alpine meadow. The average E_a value in the wetland was significantly lower than that of the alpine meadow ($F = 5.713$, $P = 0.010$; Fig. 4b).

E_a related to substrate quality

The E_a values decreased significantly with increasing substrate quality index (*Q*) for all locations. The logarithmic equations fit the negative relationships well ($R^2 = 0.254$, $P < 0.001$; Fig. 5a), and the

Table 2 Effects of sampling location, incubation temperature, and duration on SOM decomposition rates and accumulation

	Decomposition rate of SOM		Accumulation of SOM decomposition	
	F	*p*	*F*	*p*
Sampling position (P)	139.305	<0.001	175.216	<0.001
Incubation temperature (T)	80.880	<0.001	111.805	<0.001
Incubation duration (D)	6.927	<0.001	152.974	<0.001
P × T	4.298	<0.001	5.800	<0.001
P × D	0.413	0.990	7.393	<0.001
T × D	0.652	0.875	4.829	<0.001
P × T × D	0.226	1.000	0.264	1.000

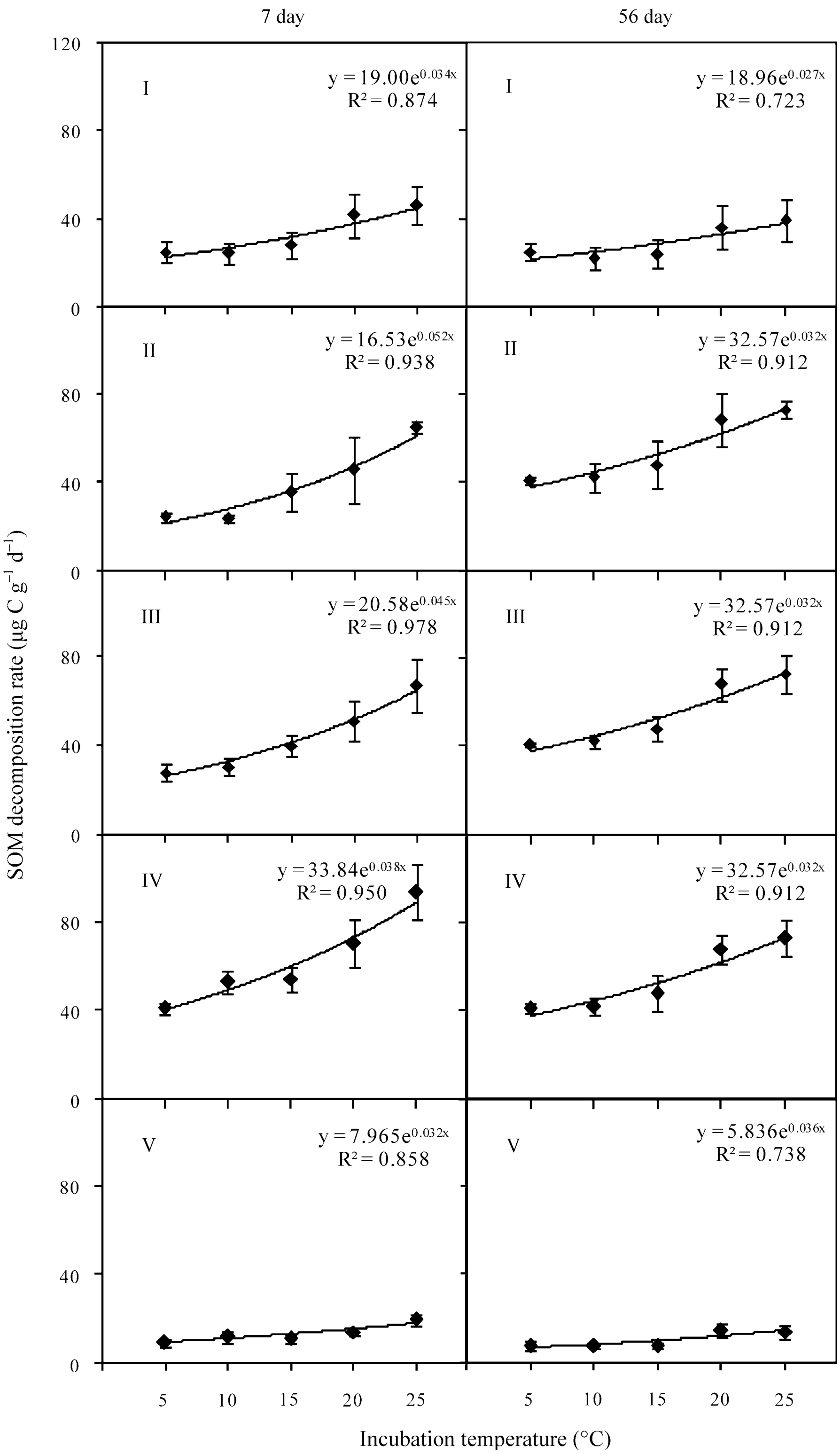

Fig. 2 Effect of incubation temperature on SOM decomposition rate in alpine wetland and meadow. I, II, III, IV, and V represent different sampling locations (Fig. 1). The data are mean ± SE ($n = 9$)

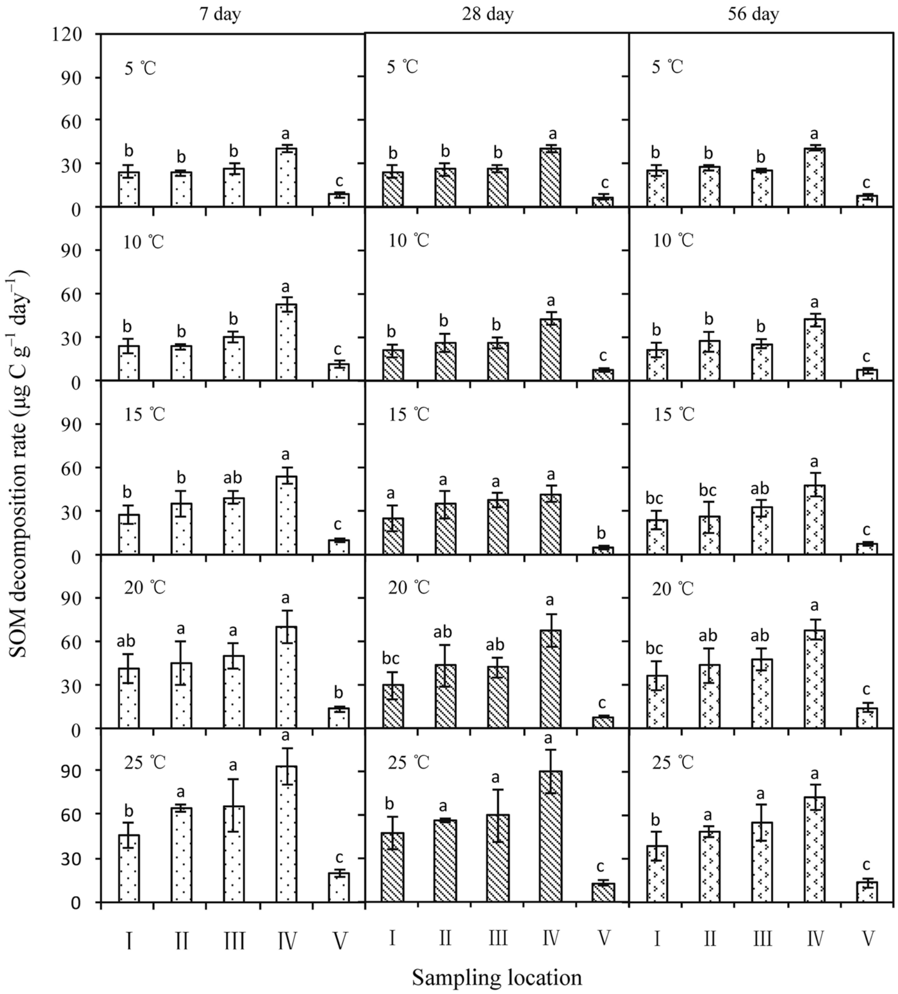

Fig. 3 Changes in SOM decomposition rates among different sampling positions. I, II, III, IV, and V indicate different sampling locations (Fig. 1). Data are mean ± SE ($n = 9$)

relationship was stronger in the alpine meadow (site V, Fig. 5f). Except for location III, E_a deceased significantly with increasing Q in the wetland sites ($R^2 = 0.147$, $P = 0.006$ for I; $R^2 = 0.093$, $P = 0.034$ for II; $R^2 = 0.173$, $P = 0.002$ for IV) (Fig. 5b–e).

Discussion

Rising temperature accelerates SOM decomposition in the alpine wetland

It has become clear that *Rs* is positively correlated with temperature (Du et al. 2014; Hartley and Ineson 2008; Jenkinson et al. 1991; Knorr et al. 2005; Mitsch and Gosselink 2007). Our findings demonstrated that *Rs* increased exponentially with increasing temperature in the Zoige alpine wetland and meadow. Similarly, Wang et al. (2010) reported that temperature played an important role in *Rs* in permafrost wetlands in the Great Hing′an Mountains of China. A study of Mediterranean forest soils in Italy showed that *Rs* increased exponentially with increasing temperature when soil moisture or other factors were not limiting (Rey et al. 2005). Higher temperatures are conducive to microbial activity and enzymatic activity increase with temperature; thus, increased temperatures in the future would improve substrate utilization and result in higher *Rs* (Craine et al. 2010b;

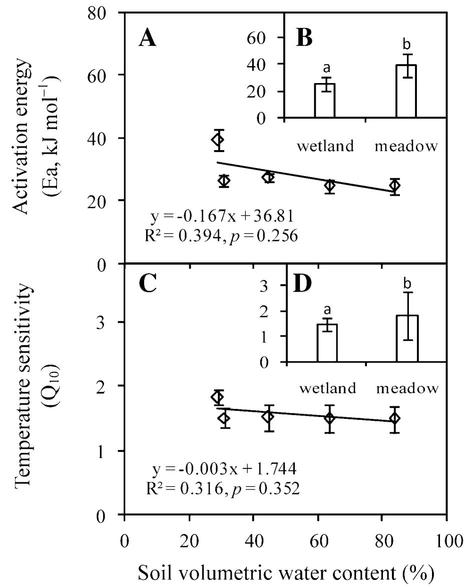

Fig. 4 Changes in activation energy (E_a) and temperature sensitivity (Q_{10}) with soil moisture gradient (sampling location). Data in scatter panels (**a**, **c**) represent E_a and Q_{10} of I, II, III, IV, and V. Data in inset column panels (**b**, **d**) are derived from wetlands (I, II, III, and IV) and meadow (V)

Gershenson et al. 2009; von Lutzow and Kogel-Knabner 2009).

Changes in substrate and microbial communtiy lead different SOM decomposition

The gradual increases in *Rs* with decreasing soil moisture in different wetlands indicate that changes in soil substrate and aerobic microbial communtiy lead the difference in SOM decomposition. The findings support our assumption that *Rs* may first increase and then decrease during the process of degradation of wetland to meadow. When moisture content is moderate, aerobic conditions promote soil enzyme activity, which accelerates SOM decomposition (Carrera et al. 2011; Toberman et al. 2008). Moreover, lower oxygen concentrations in saturated and inundated soils inhibit phenol oxidase activity; which results in the accumulation of phenolic compounds that inhibit the activity of hydrolase enzymes and reduce *Rs* (Freeman et al. 2001). However, this inhibition is quickly reversible when wetland soils become aerobic (Davidson and Janssens 2006), and can result in higher *Rs* and larger C loss with the degradation process of alpine wetlands (Shang and Yang 2012; Tian et al. 2004). The lower *Rs* observed in the alpine meadow may be linked to C constraints. Furthermore, some studies have demonstrated that changes in soil enzyme activity are important determinants resulting from lower C quality (Shackle et al. 2000) and different C content of different vegetation types (Neff and Hooper 2002).

The alpine wetland has lower temperature sensitivity than the alpine meadow

The significant differences in Q_{10} between alpine wetlands and meadows provide new evidence that models involving specific Q_{10} value can better predict the influences of warming climate on the C budget in alpine ecosystems. However, we did not observe a significant trend of Q_{10} along the wetland degradation gradient. In a study of peatlands in northern Manitoba, Canada, Ise et al. (2008) found that a falling water table increased the sensitivity of peat decomposition to temperature. Soil water content in the alpine wetlands was high, which depressed air diffusion, enzyme activity, and substrate availability (Rey et al. 2005; Tang et al. 2012; Wang et al. 2010); this may have obscured the influences of increasing temperature and resulted in a lack of significant differences in Q_{10} among different alpine wetlands. Moreover, the alpine wetlands were rich in high-quality SOM, therefore Q_{10} values should not increase significantly until better-quality SOM is progressively depleted (Hartley and Ineson 2008). According to the CQT hypothesis, similar substrate quality is associated with similar Q_{10} (Bosatta and Agren 1999; Craine et al. 2010b; Gershenson et al. 2009), which should explain the differences in temperature sensitivity between alpine wetland and alpine meadow to some extent.

C quality-temperature hypothesis is applicable to the alpine wetland and meadow

E_a decreased logarithmically with increasing substrate quality in both alpine wetland and meadow, which supported the CQT hypothesis that the temperature sensitivity (Q_{10}) of soil organic matter (SOM) decomposition is inversely related to organic carbon (C) quality or E_a (Bosatta and Agren 1999; Xu et al. 2012). Substrate quality is particularly important (Giardina and Ryan 2000; Hartley et al. 2009; Mikan et al. 2002). Bosatta and Agren (1999) developed the

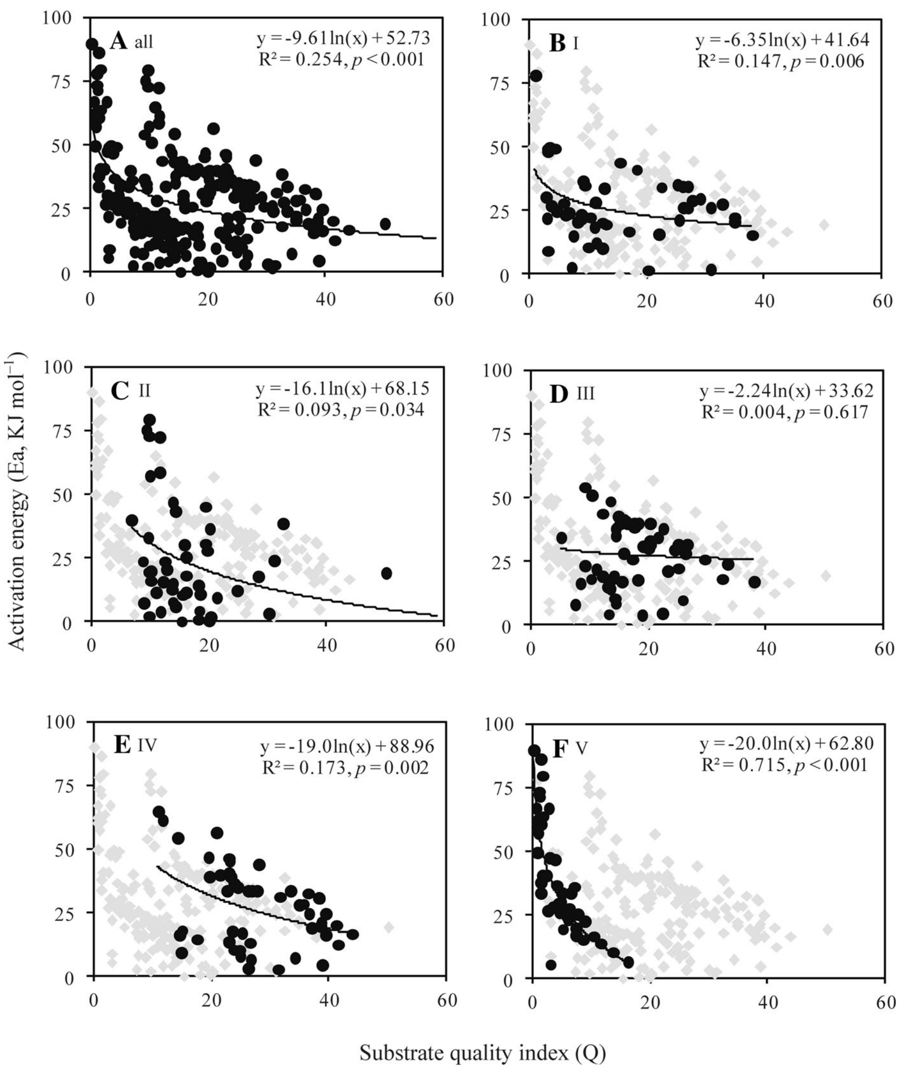

Fig. 5 Relationships between activation energy (E_a) and substrate quality index (Q) in alpine wetlands and meadows. The Q values were calculated by exponential models ($SR = Q \times e^{bT}$). The *grey points* represent the relationship between E_a and Q of all locations. The *black points* in **b**, **c**, **d**, **e**, and **f** represent the relationship between *Ea* and Q in the locations I, II, III, IV, and V

CQT hypothesis based on principles of enzyme kinetics, wherein the energy required for SOM decomposition is correlated with substrate quality. In other words, the higher activation energy associated with the breakdown of recalcitrant substrates should result in greater Q_{10} (Conen et al. 2008). In accordance with previous studies (Fierer et al. 2005; Koch et al. 2007; Wetterstedt et al. 2010), we used a C quality index calculated from exponential equations, and found that the observed Q_{10} and E_a were inversely related to substrate quality indices in both alpine wetland and meadow. Xu et al. (2012) also used the C quality index to represent the overall C quality of SOM being utilized by microbes at a special time point. Using different approaches, Hartley and Ineson (2008) found that Q_{10} values increased significantly with incubation duration, suggesting that substrate recalcitrance increases as the labile SOC pool is depleted, and that incubation time could reflect substrate quality.

SOM decomposition rates in the Zoige alpine wetlands increased significantly with rising temperature. Lower Q_{10} values in alpine wetlands could be explained by changes in soil moisture, enzyme activity, and substrate availability during the degradation process. The activation energy of SOM decomposition decreased logarithmically with increasing substrate quality in both alpine wetland and meadow, indicating that the CQT hypothesis is applicable to these types of sites. The influence of wetland degradation on the Q_{10} of SOM decomposition provides new insights to improve the prediction of C budget in alpine wetlands under warming scenarios.

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