Geoderma 288 (2017) 166–174

Contents lists available at ScienceDirect

Geoderma

journal homepage: www.elsevier.com/locate/geoderma

Changes of carbon stocks in alpine grassland soils from 2002 to 2011 on the Tibetan Plateau and their climatic causes

Litong Chen [a,*], Xin Jing [b], Dan F.B. Flynn [c], Yue Shi [b,d], Peter Kühn [e], Thomas Scholten [e], Jin-Sheng He [a,b]

[a] Key Laboratory of Adaptation and Evolution of Plateau Biota, Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining 810008, China
[b] Department of Ecology, College of Urban and Environmental Sciences, and Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, Beijing, 100871, China
[c] The Arnold Arboretum of Harvard University, 1300 Centre Street, Boston, MA, USA
[d] State Key Laboratory of Vegetation an Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China
[e] Department of Geosciences, Soil Science and Geomorphology, University of Tüebingen, Tüebingen 72079, Germany

ARTICLE INFO

Article history:
Received 21 May 2016
Received in revised form 28 October 2016
Accepted 10 November 2016
Available online 16 November 2016

Keywords:
Soil organic carbon (SOC)
SOC stocks
Repeated soil inventory
Alpine meadow
Alpine steppe
Tibetan Plateau

ABSTRACT

Based on field observations, remote sensing, and modeling, recent studies have reported inconsistent changes in soil organic carbon (SOC) stocks in grasslands of the Tibetan Plateau over the past few decades. However, direct evidence about the changes in SOC stocks in the plateau's grasslands coming from in situ, site-by-site, repeated surveys is rare. In this study, we carried out a repeated soil sampling to assess the changes in SOC stocks in the alpine grasslands across the Tibetan Plateau. Across all 41 sites in the alpine grasslands, SOC stocks exhibited a significant increase from 2002 to 2011 at an overall rate of 4.66 g C m^{-2} yr^{-1}. Mesic and low-temperature-limited alpine meadows showed an average carbon gain of 25.8 g C m^{-2} yr^{-1}, whereas the relatively dry alpine steppes exhibited a slight carbon loss of 11.9 g C m^{-2} yr^{-1}. Spatially, the changes in SOC stocks were significantly related to the original SOC stocks across alpine steppes, and soils with low carbon tended to gain carbon. Moreover, the changes in SOC stocks were also associated with March–April precipitation in alpine meadows, and with mean annual precipitation (MAP) in alpine steppes, with drier sites generally gaining carbon. Overall, the alpine grasslands of the Tibetan Plateau significantly accumulated SOC over this 10-year period, but many more site surveys are needed to comprehensively access the changes in SOC stocks across alpine grasslands on the plateau; and management strategies enhancing the ability of C sequestration should differ between alpine meadows and steppes due to their contrasting climate conditions.

1. Introduction

In terrestrial ecosystems, soils represent the largest stock of organic carbon (C), holding approximately 1500 Pg (10^{15} g) C (estimated at 0–100 cm depth), which is about twice the amount held in the atmosphere and thrice the amount contained in terrestrial vegetation (Kutsch et al., 2009). Even small changes in soil organic carbon (SOC) pools, caused by either climatic change or human activity and land use change may have a large impact on the global C cycle (Johnson et al., 2007; Don et al., 2009). Owing to the role they can play in mitigating or promoting the effects of elevated atmospheric CO_2 and associated global warming (Johnston et al., 2004), accurate assessments of SOC pools and their changes over time are of vital importance (Don et al., 2007). Accurate calculation of the dynamics of SOC stocks is also important for mechanistic understanding of the C cycle, and for assessing the feedbacks between SOC and climate change (Smith et al., 2012).

The Tibetan Plateau covers an area of an approximately 2.5×10^6 km^2 at an average altitude of 4000 m above sea level (a.s.l.), and can be regarded as the third pole (Qiu, 2008). Similar to the high-latitude tundra in the polar regions, approximately two-thirds of the total area of the high-altitude Tibetan Plateau was affected by permafrost (Zhao et al., 2000). This area contains a large amount of SOC, as estimated at 7.4–33.52 Pg in alpine grasslands (Wang et al., 2002; Wu et al., 2003; Yang et al., 2008), and its ecosystems are particularly sensitive to global warming (Yao et al., 1995; Liu and Chen, 2000; Zhang et al., 2013; Wang et al., 2014a; Zhang et al., 2016). The plateau has experienced a pronounced warming in recent decades (Liu and Chen, 2000; Chen et al., 2013), and this warming is predicted to continue in the 21st century (Chen et al., 2013). The high-altitude Tibetan Plateau therefore provides a very good opportunity to explore the feedback between SOC and climate change (Li et al., 2013; Li et al., 2014).

Recently, a number of studies have explored the SOC changes in the Tibetan Plateau's alpine grasslands. However, the results are conflicting. For instance, using a satellite-based approach, Yang et al. (2009) found that SOC stocks in the Tibetan Plateau's alpine grasslands had a slight decrease with a change rate of 0.6 g C m^{-2} yr^{-1} (−36.5 to 35.8 g C m^{-2} yr^{-1} at 95% confidence) between the 1980s and 2004.

* Corresponding author.
E-mail address: litong_chen@nwipb.cas.cn (L. Chen).

http://dx.doi.org/10.1016/j.geoderma.2016.11.016
0016-7061/

Based on soil data from the Second State Soil Survey of China (SSSSC), Xie et al. (2007) indicated that SOC in China's grasslands (including the Tibetan Plateau's alpine grasslands) declined by 3.56 Pg from the 1980s to 2000s. Fang et al. (2010) reviewed the dynamics of soil C stocks in China's grasslands over the past 20 years, and found that China's grasslands ecosystems were C neutral. By contrast, a process-based biogeochemical modeling study suggested that during the 20th century, soils in Tibetan Plateau's grasslands shifted from being a carbon source or neutral in the early part of the century to a carbon sink later. Furthermore, flux observations carried out over a short time period showed that soils in alpine meadows acted as a carbon sink of 120.9 g C m^{-2} yr^{-1} (ranging from 78.5 to 192.5 g C m^{-2} yr^{-1}) from 2002 to 2004 (Kato et al., 2006). Finally, a recent synthesis of flux measurements demonstrated that the alpine meadows on the eastern edge of the plateau were a strong carbon sink of 61.64 ± 34.51 g C m^{-2} yr^{-1} in the early 21st century (Yu et al., 2013). The large variability and inconsistency in SOC changes in alpine grasslands of the plateau observed among these above-mentioned studies can be partly attributed to the insufficient observations and/or the inconsistent methodologies. Consequently, direct measurements by repeated soil inventories are urgently needed to accurately assess the changes in SOC stocks across the Tibetan Plateau's alpine grasslands.

Generally, human disturbances (e.g. grazing) and climatic variables are considered as the two main factors affecting the C dynamics in grasslands all over the world. The effects of grazing on SOC stock and its changes in alpine grasslands on the Tibetan Plateau have therefore been well characterized in recent years (Dong et al., 2012; Su et al., 2015; Hu et al., 2016); however, there is little knowledge on how the climate change influences the changes in alpine grasslands' SOC stocks on this plateau. Currently, two hypotheses have been put forward to predict the potential dynamics of SOC stocks in the future changing environment (Garten, 2004). The first hypothesis, defined here as the temperature-loss hypothesis, predicts that since the decomposition of SOC is more sensitive to temperature change than net primary production (NPP) (Jenkinson et al., 1991; Cox et al., 2000; Davidson and Janssens, 2006), increasing temperature will result in a net loss of SOC. The second hypothesis, defined here as the nitrogen-gain hypothesis, predicts that due to the fertilization by nitrogen deposition, SOC stocks might gain more carbon than they lose in a nitrogen-rich and warming environment. Since the Tibetan Plateau is very sensitive to warming, we predicted that SOC stocks in mesic and low-temperature-limited alpine meadows would show a declining trend under the temperature-loss hypothesis and would show an increasing trend under the nitrogen-gain hypothesis. By contrast, in water-limited alpine steppes, SOC stocks would exhibit no changes or even decrease under the nitrogen-gain hypothesis since nitrogen deposition would have minor effects, whereas increased temperature would intensify soil aridity under water-limited condition.

To test our hypotheses, we analyzed changes in SOC stocks in alpine grasslands across the Tibetan Plateau during the past decade from 2002 to 2011. During the summer of 2011, we sampled 205 soil profiles from 41 sites selected from the 2002–2003 soil inventory (Yang et al., 2008). We addressed the following three questions. (i) To what extend have SOC stocks in the Tibetan Plateau's alpine grasslands changed over this 10-year period? (ii) Have the changes in SOC stocks in alpine meadows and steppes exhibited consistent responses? (iii) Since climatic variables widely affect the potentials for C sequestration in ecosystems, at the spatial scale, how do climatic factors affect the changes of SOC stocks in alpine meadows and steppes?

2. Materials and methods

2.1. Study area

Our study was conducted in the alpine grasslands on the Tibetan Plateau, which has experienced substantial climate change during the past decade. Mean annual temperature (MAT) has significantly increased at a rate of 0.087 °C yr^{-1}, whereas mean annual precipitation (MAP) varied only slightly (Fig. S1). The alpine meadows and alpine steppes are two major vegetation types on the plateau, with covering >60% of the plateau's total surface which corresponds to an area of 1.6×10^8 ha and comprises 40% of the national Chinese grassland area (Wu, 1980). Alpine meadows is the most widely distributed vegetation type on the plateau (Zhou, 2001) occurring at elevations ranging from 3200 to 5200 m a.s.l. (Kato et al., 2004). The dominant plant species found in alpine meadows are *Kobresia pygmaea*, *Kobresia humilis*, *Polygonum gentiana*, and *Saussurea* sp. Alpine steppes vegetation consists mainly of *Stipa purpurea*, *Stipa subsessiliflora* and *Carex moorcroffiana* (Chang, 1981). The soil types in alpine meadows and steppes are felty and cold calcic soils, respectively (Xiong and Li, 1987); these are defined as cambisols based on the World Reference Base for soil resources (WRB) (Shi et al., 2010).

2.2. Original sampling

In order to quantify the storage and patterns of SOC in alpine grasslands, four consecutive sampling campaigns were conducted by Peking University, China, during the summer (July and August) of 2001–2004 (in most cases in 2002/03). Four hundred five soil profiles from 135 sites across the Tibetan Plateau were surveyed (i.e. three soil profiles at each site) (Yang et al., 2008). For each soil profile, the soil pit was excavated to collect soil samples at depth increments of 0–10, 10–20, 20–30, 30–50, 50–70, and 70–100 cm. Soil samples were taken to the laboratory, air-dried, weighed, and sieved through a 2 mm mesh, and then these samples were handpicked to remove plant residuals and then ground on a ball mill for SOC analysis by the Walkley-Black's method (Nelson and Sommers, 1982). Bulk density samples were obtained for each layer using a standard container with 100 cm^3 in volume (50.46 mm in diameter and 50 mm in height) and weighed to the nearest 0.1 g, and then were oven-dried at 105 °C to a constant mass to determine its determining bulk density. For details about the field investigation and laboratory analysis, see Yang et al. (2008).

2.3. Resampling

To detect changes in SOC stocks (top 30 cm) in grasslands of the Tibetan Plateau, we carried out a resampling of soil profiles during the summer of 2011 (July and August), surveying 205 profiles from 41 sites (i.e. five profiles at each site) randomly selected from the 2002/03 sampling campaigns according to the original longitude and latitude as well as original sampling profile of each site (Fig. 1, Table S1). Of the 41 sites, 18 were alpine meadows and 23 were alpine steppes. Following the almost same procedure as in the original sampling, soil samples were collected by hand with a steel core (5 cm in inner diameter) in four soil increments (0–5, 5–10, 10–20, 20–30 cm) at each profile in each site. Three to eight cores were mixed as a replicate in each soil increments (Chen et al., 2015). Soil samples were air-dried, sieved through a 2 mm mesh, handpicked to remove plant detritus, and then ground into a fine powder. SOC content was measured by the Walkley-Black's method (Nelson and Sommers, 1982). Five replicates of bulk density sample at each site were obtained for each layer using a standard container of 100 cm^3 in volume, and thus it was calculated as the ratio of the oven-dried (105 °C) soil mass to the container volume.

2.4. SOC calculation and climate data

We only concerned the SOC changes in top 30 cm, SOC density (C stock per land area) in the top 30 cm therefore was calculated with Eq. (1).

$$\mathrm{SOCD} = \sum_{i=1}^{n} \mathrm{T_i} \times \mathrm{BD_i} \times \mathrm{SOC_i} \times \frac{1 - \frac{\mathrm{C_i}}{100}}{100} \tag{1}$$

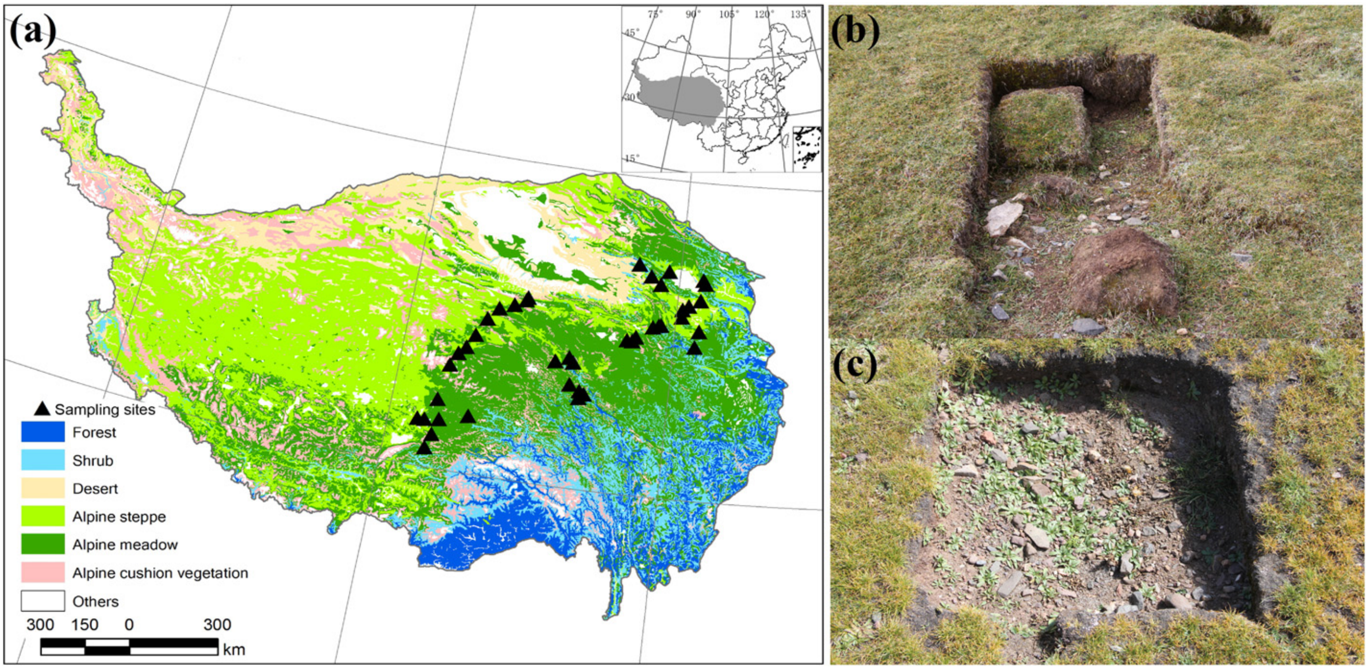

Fig. 1. Location of the repeated sampling sites (a) and original sampling profiles (b, c) across the Tibetan Plateau, shown on the background of China's vegetation atlas (Chinese Academy of Sciences, 2001).

where SOCD, T_i, BD_i, SOC_i, and C_i are SOC density (kg C m^{-2}), soil thickness (cm), buck density (g cm^{-3}), SOC (g kg^{-1}), and percentage of rock fraction (>2 mm) at layer i, respectively (Yang et al., 2008).

The climatic variables of the sampling sites were obtained from the WorldClim data set (http://www.worldclim.org) (Hijmans et al., 2005), including: mean annual temperature (MAT), mean annual precipitation (MAP) and precipitation seasonality (PS, coefficient of variation).

2.5. Statistical analysis

We determined the differences in SOCD in alpine meadows and steppes between 2002 and 2011 using a one-sided, paired *t*-test. The $SOCD_{2002}$ and $SOCD_{2011}$ were log_{10}-transformed to normalize the distributions before analysis. We employed multiple regression to test whether MAT, MAP, PS, and $SOCD_{2002}$ were significant predictors for the effects of original SOCD and climatic variables on SOC changes across the 41 sampling sites. Since MAT had no effect on SOC changes (Fig. 4b, d), the final results of multiple regression analysis showed only the effects of MAP, PS, and $SOCD_{2002}$ on the SOC changes, and $SOCD_{2002}$ was log10-transformed to normalize the distributions before analysis. To evaluate potential collinearity problems between model covariates, we calculated variance-inflation factors (VIFs) for each covariate in each model using VIF ( ) from the package car in R. VIFs for all covariates were lower than 3; far below than the threshold of 10 above which collinearity may adversely affect regression results. All statistical analyses were performed using R 3.0.3 (R Development Core Team, 2014).

3. Results

3.1. Temporal trend of SOC stocks from 2002 to 2011

Across the 41 resampled sites, SOCD in the top 30 cm of alpine grasslands varied from 0.98 to 16.11 kg C m^{-2} with an average of 5.564 kg C m^{-2} in 2011, and from 0.39 to 14.56 kg C m^{-2} with an average of 5.518 kg C m^{-2} in 2002 (Table 1, Table S1, Figs. S2a, S2d). During the last ten years, SOC stocks showed a significant increasing trend, with an overall rate of 4.66 g C m^{-2} yr^{-1} at the 95% confidence interval of $-30.40 - 39.73$ kg C m^{-2} yr^{-1} (Table 1, paired *t*-tests $P = 0.034$, $t = 1.876$ on 40 DF).

SOCD in alpine meadows and steppes also exhibited large variations, ranging 1.94–16.11 kg C m^{-2} and 0.98–9.33 kg C m^{-2} in 2011, and 0.93–14.56 kg C m^{-2} and 0.39–10.45 kg C m^{-2} in 2002, respectively (Table S1). Mean SOCD in alpine meadows and steppes were 6.861 and 4.549 kg C m^{-2} in 2011, 6.603 and 4.668 kg C m^{-2} in 2002, respectively (Table 1, Figs. S2b, S2e, S2c, S2f). SOCDs in alpine meadows and steppes during 2011 samplings were strongly correlated with those measured during 2002–2003 samplings with the slopes of 1.021 and 0.897 ($R^2 = 0.984$, $P < 0.001$; $R^2 = 0.959$, $P < 0.001$), respectively (Fig. 2a, b). From 2002 to 2011, in alpine meadows, SOCD increased by 0.258 kg C m^{-2} at the 95% confidence interval of $-0.232 - 0.748$ kg C m^{-2} with a relatively weak significance (paired *t*-tests $P = 0.069$, $t = 1.560$ on 17 DF; Table 1, Fig. 2a); by contrast, in alpine steppes, it declined by 0.119 kg C m^{-2} at the 95% confidence interval of $-0.636 - 0.398$ kg C m^{-2} but not significantly (paired *t*-tests $P = 0.102$, $t = -1.306$ on 22 DF; Table 1, Fig. 2b).

3.2. Relationships between spatial variability of SOC stocks and original SOCD and climatic variables

The bivariate and multiple regression analyses showed that there was no correlation between SOC changes and original SOCD across alpine meadows, but their relationship was very strong and negative across alpine steppes ($R^2 = 0.552$, $P < 0.001$; Table 2, Fig. 3).

At the spatial scale, water availability, rather than temperature, significantly influenced on SOC changes across alpine grasslands when Site 6 and Site 22/23 were excluded from the statistical analysis in alpine meadows and steppes, respectively (Table 2, Figs. 4, 5). For instance, across alpine meadows, SOC changes had a significant and positive correlation with precipitation seasonality (Table 2, Fig. 5a); for example, the amount of precipitation from March to April before the start of the growing season had a significantly negative effect on SOC changes in alpine meadows (Fig. 5c). By contrast, SOC changes had a significant and negative correlation with mean annual precipitation across alpine steppes (Fig. 4c). Both precipitation form March to

Table 1
Mean values of soil organic carbon (SOC) density in the 0–30 cm and its changes in Tibetan alpine grassland and with its two major grassland types (alpine meadows and steppes) between 2002 and 2011. Values in parenthesis denote 95% confidence intervals. $SOCD_{2002}$ and $SOCD_{2011}$ denote SOC density during the two repeated sampling periods, respectively.

	Alpine grassland	Alpine meadow	Alpine steppe
$SOCD_{2002}$ (kg C m^{-2})	5.518 [4.454, 6.581]	6.603 [4.857, 8.350]	4.668 [3.344, 5.992]
$SOCD_{2011}$ (kg C m^{-2})	5.564 [4.593, 6.536]	6.861 [5.127, 8.596]	4.549 [3.547, 5.551]
SOC change (kg C m^{-2})	0.047 [−0.304, 0.397]	0.258 [−0.232, 0.748]	−0.119 [−0.636, 0.398]
Rate of SOC change (g C m^{-2} yr^{-1})	4.66 [−30.40, 39.73]	25.80 [−23.19, 74.79]	−11.88 [−63.57, 39.81]

April and growing season precipitation all had significant negative effects on the SOC changes (Fig. 5d, f).

4. Discussions

4.1. SOC changes in alpine grassland ecosystems

Regarding the magnitude and direction of SOC variations in grassland ecosystems, current evidence comes mainly from the observations and models in European and New Zealand temperate grasslands (Bellamy et al., 2005; Janssens et al., 2005; Lettens et al., 2005; Schipper et al., 2007; Soussana et al., 2007; Hopkins et al., 2009; Schulze et al., 2009; Schipper et al., 2010). Consistent with the findings of Lettens et al. (2005), who performed a repeated soil inventory between 2002 and 2011, our results showed that SOC stocks exhibited a significant increase in the Tibetan Plateau grasslands from 2002 to 2011, at the overall rate of 4.66 g C m^{-2} yr^{-1} in alpine grasslands and, 25.80 g C m^{-2} yr^{-1} and −11.88 g C m^{-2} yr^{-1} in alpine meadows and steppes (Table 1). These values are lower than, but comparable to the rates of SOC changes in these above-mentioned studies (e.g. 23 g C m^{-2} yr^{-1} of Lettens et al. (2005); 60 g C m^{-2} yr^{-1} of Janssens et al. (2005); 57 ± 34 g C m^{-2} yr^{-1} of Schulze et al. (2009); −104 ± 73 g C m^{-2} yr^{-1} of Soussana et al. (2007); −106− −73 g C m^{-2} yr^{-1} of Schipper et al. (2007) and 52 g C m^{-2} yr^{-1} of Schipper et al. (2010)). Our findings are contrary to the results obtained by Yang et al. (2009), but similar to those of Zhuang et al. (2010) in the Tibetan Plateau grasslands. In other alpine ecosystems, such as Arctic tundra, the direct evidence regarding SOC changes is relatively scarce. Compiling the 40 years of CO_2 flux observations, Belshe et al. (2013) indicated that on an annual basis, tundra ecosystems were currently CO_2 sources, particularly from 2004 to 2010. However, based on the estimates from observations, process-based models, and inversion models, McGuire et al. (2012) showed that Arctic tundra was a C sink of 110 Tg C yr^{-1} from 1990 to 2006, but with large uncertainty ranged from being a sink of 291 Tg C yr^{-1} to a source of 80 Tg C yr^{-1}.

Although a generally increasing trend of SOC stocks is found on the Tibetan Plateau, contrasting temporal trends existed in alpine meadows and steppes. During the past decade SOC stocks in alpine meadows displayed a weakly significant increase with an average rate of 25.8 g C m^{-2} yr^{-1}. This is relatively lower than, but comparable to, the eddy-flux data showing that on the eastern edge of the Tibetan Plateau, alpine meadows was a strong C sink of 61.64 (±34.51) to 120.9 (varying from 78.5 to 192.5) g C m^{-2} yr^{-1} in the early 21st century (Kato et al., 2006; Yu et al., 2013).

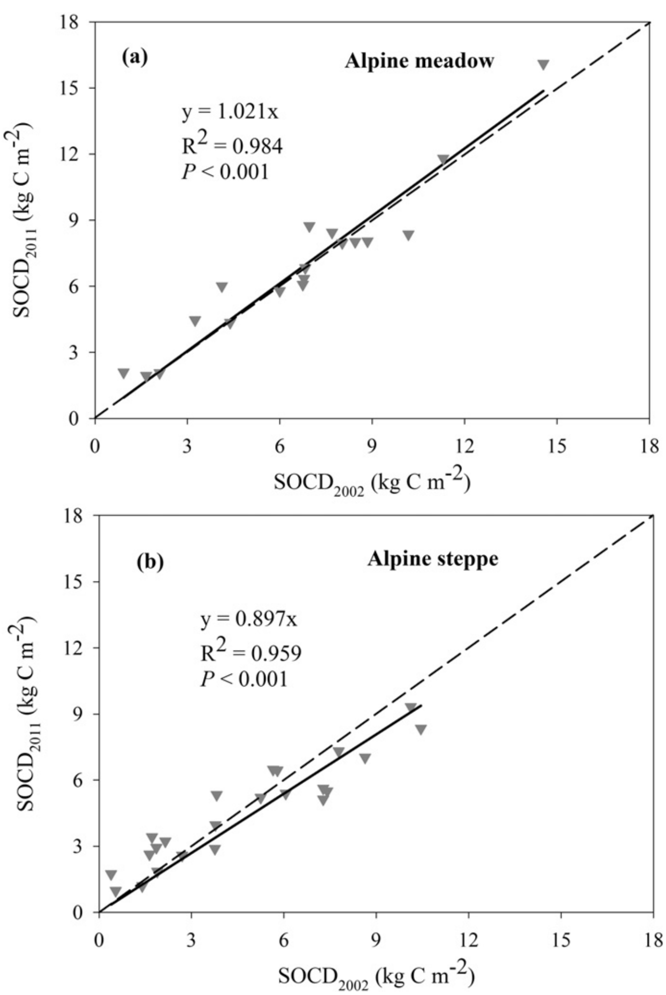

Fig. 2. Statistical comparisons of soil organic carbon (SOC) density and its changes between 2002 and 2011 in alpine meadows (a) and steppes (b) on the Tibetan Plateau. $SOCD_{2002}$ and $SOCD_{2011}$ denote SOC density during the two repeated sampling periods.

Table 2
Multiple regression parameters for the reletive SOC changes in alpine meadows (without site 6) and alpine steppes predicted by mean annual precipitation (MAP), precipitation seasonality (PS), and the original SOC density ($SOCD_{2002}$). The $SOCD_{2002}$ was log_{10}-transformed to normalize the distributions.

Grassland type	Regression parameter	Estimate	Std. error	*t* value	*P*
Alpine meadow	Intercept	−10.568816	4.743464	−2.228	**0.0442**
	MAP	0.004289	0.003468	1.237	0.2381
	PS	0.082459	0.032611	2.529	**0.0252**
	$SOCD_{2002}$	−0.356172	0.888416	−0.401	0.6950
Alpine steppe	Intercept	4.070530	3.079669	1.322	0.201948
	MAP	0.002321	0.003270	0.710	0.486397
	PS	−0.032756	0.025735	−1.273	0.218428
	$SOCD_{2002}$	−2.695694	0.690226	−3.906	**0.000951**

P-values ≤ 0.05 are in bold.

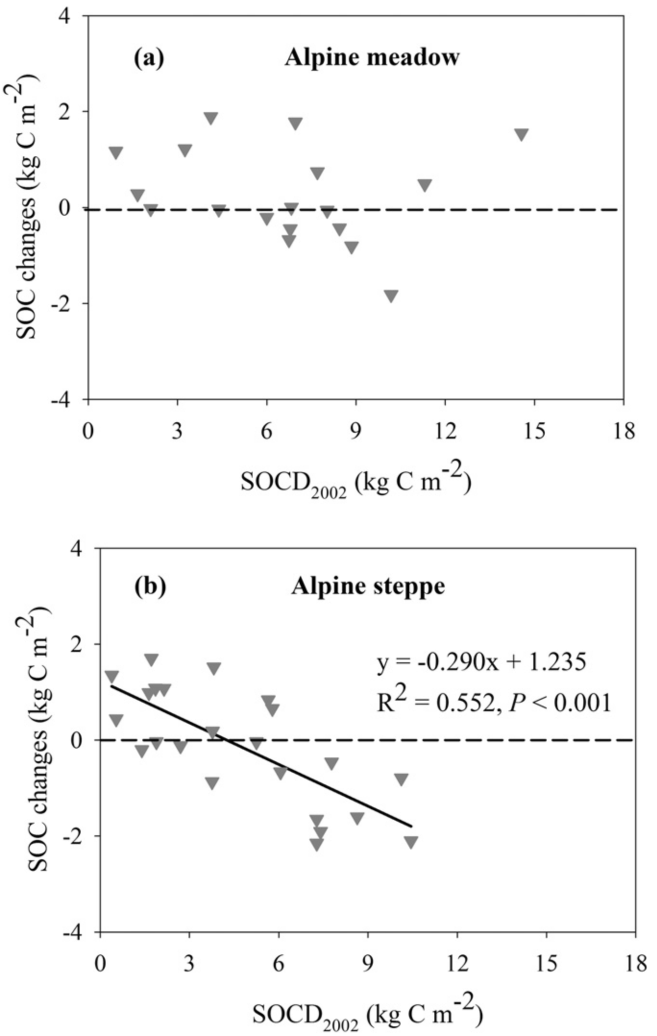

Fig. 3. Relationships between SOC changes and $SOCD_{2002}$ across alpine meadows (a) and steppe s(b) on the Tibetan Plateau.

4.2. Contrasting temporal changes in SOC stocks in alpine meadows and steppes

In the present study, the increase in SOC stocks, particularly in alpine meadows, which are mainly limited by low-temperatures, appears to have been triggered by the increasing temperatures across the grassland area. This is contrary to the prediction by the temperature-loss hypothesis. Our analysis indicated that the Tibetan Plateau experienced an apparent warming trend at a rate of 0.087 °C yr^{-1} from 2000 to 2010 (Fig. S1). Other studies have also demonstrated an ongoing warming trend in the plateau during the past 30 years (Liu and Chen, 2000; Chen et al., 2013). On the one hand, increases in temperature stimulate plant growth and thus the gross and net primary production. It has been reported that the vegetation net primary production in the Tibetan Plateau's grasslands, especially in alpine meadows, showed a significant increase via enhanced plant growth due to increased temperature from 1982 to 1999 (Piao et al., 2006) and from 2000 to 2009 (Zhao and Running, 2010). A field experiment also indicated that warming significantly increased the aboveground net primary production (ANPP) in an alpine meadow on the Tibetan Plateau between 2006 and 2010 (Wang et al., 2012). In the other tundra ecosystems such as the Arctic, contemporary summer warming significantly increased vegetation productivity between 1980 and 2010 (Elmendorf et al., 2012). Direct evidence revealed that a twenty-year summer warming significantly increased mineral soil stocks by 31% in an Alaskan tundra ecosystem (Sistla et al., 2013). On the other hand, the rising temperatures may influence the vegetation phenology such as green-up dates, and thus the length of the growing season. It has been currently suggested that the start of the vegetation growing season (SOS) in the Tibetan Plateau experienced a continuous advancing trend at a rate of ~1.04 day yr^{-1} from 1982 to 2011(Zhang et al., 2013). The marked advancement in vegetation SOS may extend the length of the plant-growing season, and subsequently increase the gross and net primary production, and thus the C sink function of the grassland ecosystem in the Tibetan Plateau.

Nitrogen (N) deposition from agricultural fertilizer usage and the combustion of fossil fuels can be another important factor affecting the changes in SOC stocks in alpine meadows over the past decade. It has already been noted that N deposition significantly increased at a mean rate of 0.17 kg N ha^{-1} yr^{-1} were found in the Tibetan Plateau from the 1980s to 2010 (Liu et al., 2013). Since the potential of terrestrial ecosystems to take up carbon is constrained globally by the availability of nutrients required for plant production, particularly N (LeBauer and Treseder, 2008), increased N deposition may therefore increase the biological N availability. Under increased N deposition, the enhanced SOC stocks could be probably illustrated by the below two mechanisms. Firstly, increased N availability could increase NPP and/or root mass and subsequently litter and thus organic carbon (OC) inputs (Fornara and Tilman, 2012; Ziter and MacDougall, 2013). Secondly, although higher N content might stimulate litter decomposition it seems to suppress humus decay in later stages (Jandl et al., 2007), thus leading to stabilization of soil organic matter (SOM) in mineral-associated fractions (Dörfer et al., 2013). Consequently, warming and increased N deposition stimulate more plant growth and subsequently increase in gross and net primary production than soil respiration (Zhuang et al., 2010), thereby increasing SOC stocks in alpine meadow. This is consistent with the nitrogen-gain hypothesis of nitrogen deposition leading to SOC gain: namely, that soil C stocks appear to gain more carbon than they loss in a nitrogen-rich and warming environment. Furthermore, the soil acidification partially caused by N deposition over the past twenty years observed by Yang et al. (2012) could inhibit SOC loss from soils in alpine meadows since there is a negative relationship between soil pH and SOC found by Shi et al. (2012) in Mongolian and Tibetan grasslands.

In more than half of the global ecosystem, primary productivity is substantially constrained by water availability (Heimann and Reichstein, 2008). In contrary to alpine meadows, steppe ecosystems are apparently water-limited. Hence, soil water availability may be a dominant driver influencing carbon dynamics of alpine steppes under warming climate conditions (Baumann et al., 2009). In the Tibetan Plateau, temperature showed a significance increasing trend; however, precipitation had almost no change during the past one decade (Fig. S1), which could lead to increased soil aridity in alpine steppes. Substantial evidence indicates that large-scale droughts induced by global warming have recently occurred in many regions and countries around the world, resulting in major effects on vegetation productivity markedly and thus carbon balance across ecosystems from grasslands to forests (Breshears et al., 2005; Saleska et al., 2007; Allen et al., 2010; Scott et al., 2010; Zhao and Running, 2010). Furthermore, recent studies showed that grassland productivity is highly sensitive to temporal variability in precipitation, especially in water-limited ecosystems (Fay et al., 2003; Fay et al., 2008; Heisler-White et al., 2008; Heisler-White et al., 2009). For instance, one study conducted in a semi-desert grassland suggested that because seasonal photosynthesis was more sensitive than respiration to rainfall variation, the severe drought years led to low gross ecosystem production and subsequently resulted in a net carbon release (Scott et al., 2010). Another study also indicated that gross ecosystem productivity had a higher sensitivity than soil respiration to soil moisture in a semiarid steppe in Inner Mongolia, and thus decreased soil water availability causes carbon release

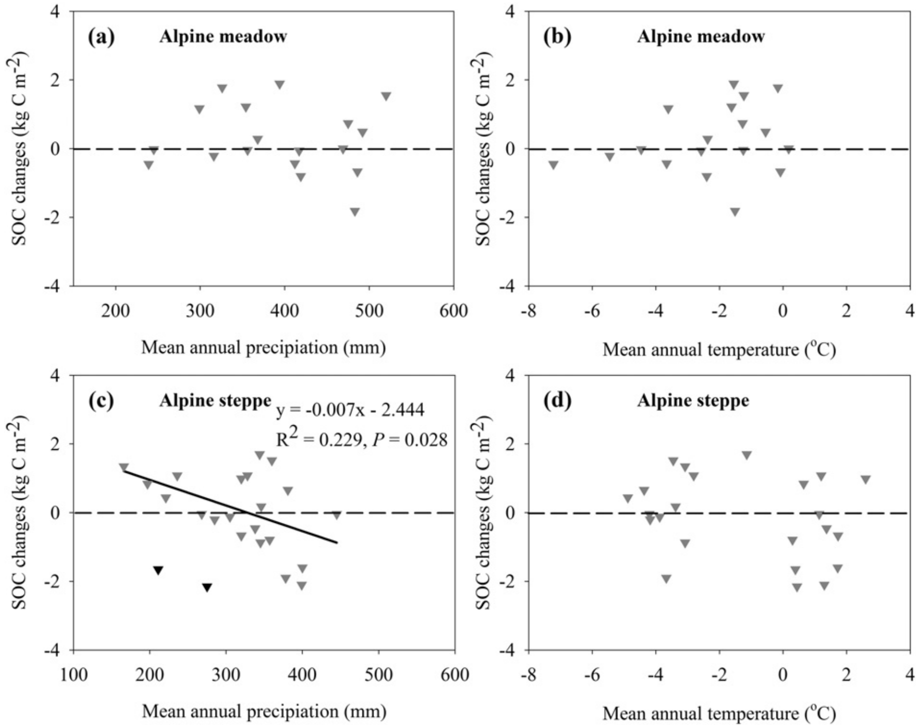

Fig. 4. Relationships between SOC changes and mean annual temperature (a, b) and precipitation (c, d) across alpine meadows and steppes on the Tibetan Plateau (Site 22/23 (black triangles) are excluded).

(Chen et al., 2009). Therefore, we hypothesized that the decreased soil water availability caused by climate warming is a key factor resulting in the observed decrease in the SOC stocks of alpine steppes.

4.3. Relationship between SOC changes and original SOCD

Consistent with previous studies (Bellamy et al., 2005; Stevens and van Wesemael, 2008; Grüneberg et al., 2014), our analyses also indicated that the amplitude of SOC losses in alpine steppes was strongly related to the original SOC density (Fig. 3b). Such a pattern suggested that SOC stocks in alpine steppes decreased much more at those sites with higher SOC density. The higher rate of SOC losses in areas with higher SOC levels may be explained by the one fact that in alpine steppes the dominant plants are main the lignin-rich species, such as *S. purpurea*, *S. subsessiliflora* and *C. moorcroffiana*. More organic soils necessarily contain a greater proportion of slowly decaying organic matter such lignin, and its rate of turnover may be more sensitive to temperature changes than that of more labile organic matter (Knorr et al., 2005). In addition, Grüneberg et al. (2014) demonstrated that compared to the high clayed-loamy soils of the mountains and hills, low-clay sandy lowland soils with low initial C stocks and C concentrations sequestered larger amounts of C due to reduced decomposition. In our study, the rate of carbon sequestration declined significantly with soil silt and clay contents (Fig. S3), and Yang et al. (2009) also confirmed the positive relationship between SOC stocks and soil silt and clay contents. Baumann et al. (2014) showed the same relationship for the central-eastern Tibetan Plateau, interrelated to weathering processes and pedogenesis under permafrost conditions. These finding suggest that low decomposition may be another important factor resulting in carbon gains in low-silt and clay sites with low initial SOC stocks across alpine steppes, but further verification is very needed; however, under the condition of degraded grasslands, sandy soils loss more SOC than clayed soils (Dlamini et al., 2016).

4.4. Contributions of climatic variables to spatial variability of SOC changes

We found that SOC gains declined apparently with increasing March–April precipitation and MAP across alpine meadows and steppes, respectively (Figs. 5c, 4c). Although current studies regarding SOC dynamics across a large-scale precipitation gradient using repeated soil inventories in native vegetation are few, SOC accumulations under forestation or woody plant invasion decreased significantly across increasing precipitation gradients (Jackson et al., 2002; Berthrong et al., 2012; Eclesia et al., 2012). These studies generally suggest that SOC accumulations increase in arid sites but decrease in wet ones. However, a meta-analysis comparing SOC stocks in the topsoil of non-degraded and degraded grassland soils showed greater SOC losses from degraded grasslands under dry climates (Dlamini et al., 2016). Although the observed patterns of SOC dynamics across the precipitation gradients in our study and in these above-mentioned studies were similar, the mechanisms underlying these SOC changes were different. Berthrong et al. (2012) suggested that soils in xeric regions store C through increases in the soil C:N ratio, whereas in more humid areas, increased decomposition and N leaching losses through leaching lead to C losses. And Eclesia et al. (2012) examined variability in SOC stocks along a precipitation gradient with different C inputs to the soil because of variability of C uptake by the vegetation. Additionally, some other studies indicated that soil organic nitrogen (SON) is one of the primary factors driving SOC losses (Kirschbaum et al., 2008; Parfitt and Ross, 2011); and hence in humid regions, N losses resulted from decomposition and leaching might constrain SOC accumulations in tree plantations (Kirschbaum et al., 2008). In the present study, March–April precipitation rather than MAP is a primary factor controlling SOC changes in alpine meadows. This may be partially explained by soil C releases during soil freezing and thawing processes under sufficient water conditions before the start of the growing season. This was confirmed in our recent study, which revealed that during non-growing seasons, soil respiration was mainly affected by freezing and thawing processes (Wang et al., 2014b). By contrast, across alpine steppes, MAP is an

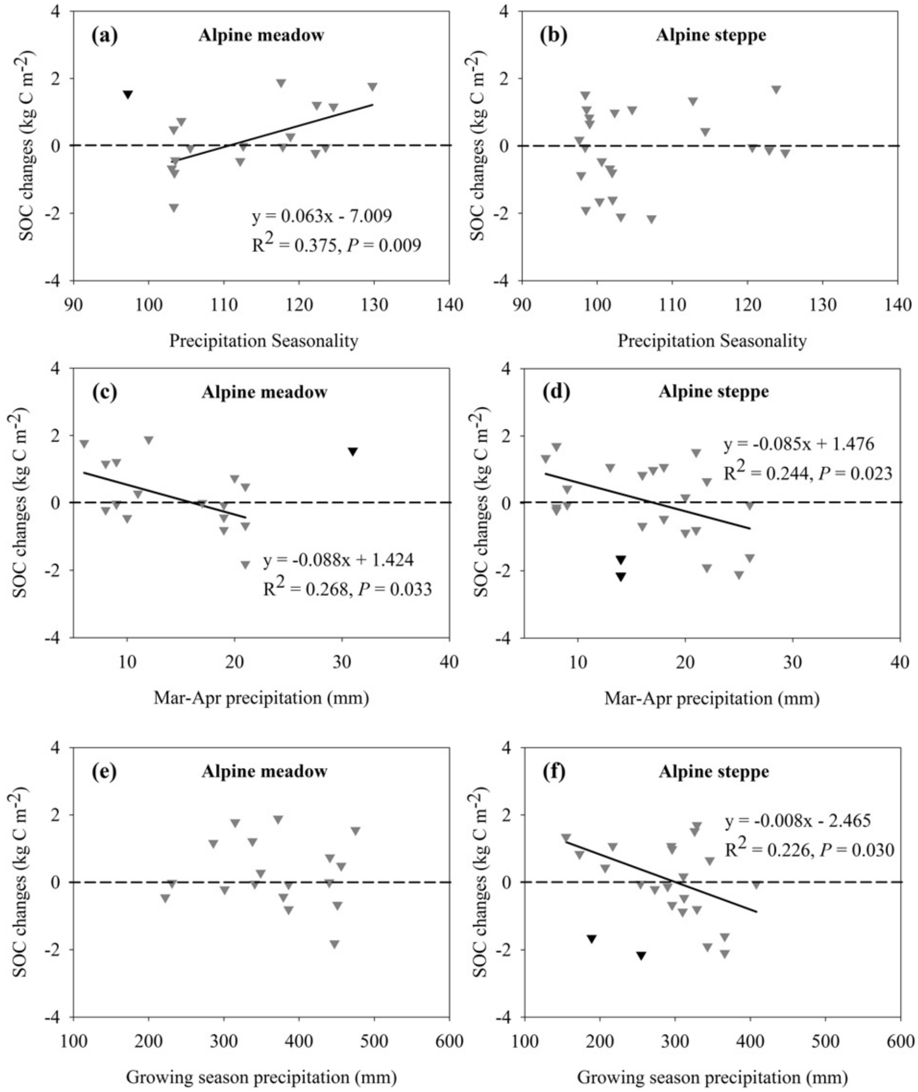

Fig. 5. Relationships between SOC changes and seasonality (a, b), March–April precipitation (c, d) and growing season precipitation (e, f) across alpine meadows and steppes on the Tibetan Plateau (Site 22/23 and Site 6 (black triangles) are excluded).

important factor driving SOC variations. This may be caused by increased decomposition with increased MAP, since the rates of soil respiration during growing-seasons increased with soil moisture in alpine grasslands (Geng et al., 2012).

In addition, we should conclude how climatic factors affect SOC changes in grasslands with more cautions because human activities, such as grazing or grazing exclusion, also have significant effects on it. For example, a few studies indicated that SOC declined markedly in severely degraded grasslands caused by over-grazing in the headwaters areas of the Tibetan Plateau (Dong et al., 2012; Su et al., 2015), and a synthesis showed that grazing exclusion significantly increased soil C content in Chinese grasslands (Hu et al., 2016).

5. Conclusions

We used repeated soil surveys from the years 2002 and 2011 to assess alterations of SOC stocks in Tibetan Plateau's alpine grasslands across 41 sites. We found that SOC stocks in alpine grasslands showed a significant upward trend. The temporally shifting trends in alpine meadows and steppes differed apparently: the former increased with a weak significance, while the latter declined insignificantly. Spatially, the main climatic variable affecting SOC dynamics across alpine meadows was the precipitation in March and April: i.e. before the start of the growing season. By contrast, mean annual precipitation (MAP) was the most important factor driving SOC dynamics across alpine steppes. The alpine grasslands of Tibetan Plateau showed a negative carbon feedback in a nitrogen-rich and warming world, but many more sites studies are needed to comprehensively evaluate the changes in SOC stocks across alpine grasslands. More importantly, the different management strategies should be employed to enhance the ability of soil C sequestration in alpine meadows and steppes, considering the contrasting climatic conditions between them.

Acknowledgements

We thank the editor and the two anonymous reviewers for their constructive comments. This research was funded by the Strategic Priority Research Program – “Climate Change: Carbon Budget and Relevant Issues” of the Chinese Academy of Sciences (grant no. XDA05050404), the National Natural Science Foundation of China (grant no. 31570481) and National Basic Research Program of China (grant no. 2014CB954004).

Appendix A. Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.geoderma.2016.11.016.

References

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manag. 259, 660–684.

Baumann, F., He, J.S., Schmidt, K., Kühn, P., Scholten, T., 2009. Pedogenesis, permafrost, and soil moisture as controlling factors for soil nitrogen and carbon contents across the Tibetan Plateau. Glob. Chang. Biol. 15, 3001–3017.

Baumann, F., Schmidt, K., Dorfer, C., He, J.S., Scholten, T., Kuhn, P., 2014. Pedogenesis, permafrost, substrate and topography: plot and landscape scale interrelations of weathering processes on the central-eastern Tibetan plateau. Geoderma 226, 300–316.

Bellamy, P.H., Loveland, P.J., Bradley, R.I., Lark, R.M., Kirk, G.J., 2005. Carbon losses from all soils across England and Wales 1978–2003. Nature 437, 245–248.

Belshe, E.F., Schuur, E.A., Bolker, B.M., 2013. Tundra ecosystems observed to be CO_2 sources due to differential amplification of the carbon cycle. Ecol. Lett. 16, 1307–1315.

Berthrong, S.T., Pineiro, G., Jobbagy, E.G., Jackson, R.B., 2012. Soil C and N changes with afforestation of grasslands across gradients of precipitation and plantation age. Ecol. Appl. 22, 76–86.

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B., Meyer, C.W., 2005. Regional vegetation die-off in response to global-change-type drought. Proc. Natl. Acad. Sci. U. S. A. 102, 15144–15148.

Chang, D.H.S., 1981. The vegetation zonation of the Tibetan Plateau. Mt. Res. Dev. 29-48.

Chen, S.P., Lin, G.H., Huang, J.H., Jenerette, G.D., 2009. Dependence of carbon sequestration on the differential responses of ecosystem photosynthesis and respiration to rain pulses in a semiarid steppe. Glob. Chang. Biol. 15, 2450–2461.

Chen, H., Zhu, Q.A., Peng, C.H., Wu, N., Wang, Y.F., Fang, X.Q., Gao, Y.H., Zhu, D., Yang, G., Tian, J.Q., Kang, X.M., Piao, S.H., Ouyang, H., Xiang, W.H., Luo, Z.B., Jiang, H., Song, X.Z., Zhang, Y., Yu, G.R., Zhao, X.Q., Gong, P., Yao, T.D., Wu, J.H., 2013. The impacts of climate change and human activities on biogeochemical cycles on the Qinghai-Tibetan Plateau. Glob. Chang. Biol. 19, 2940–2955.

Chen, L.T., Flynn, D.F.B., Jing, X., Kuhn, P., Scholten, T., He, J.S., 2015. A comparison of two methods for quantifying soil organic carbon of alpine grasslands on the Tibetan Plateau. PLoS One 10, e0126372.

Chinese Academy of Sciences, 2001. Vegetation Atlas of China (1:1,000,000). Science Press, Beijing, p. 260.

Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A., Totterdell, I.J., 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408, 750.

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

Dlamini, P., Chivenge, P., Chaplot, V., 2016. Overgrazing decreases soil organic carbon stocks the most under dry climates and low soil pH: a meta-analysis shows. Agric. Ecosyst. Environ. 221, 258–269.

Don, A., Schumacher, J., Scherer-Lorenzen, M., Scholten, T., Schulze, E.D., 2007. Spatial and vertical variation of soil carbon at two grassland sites - implications for measuring soil carbon stocks. Geoderma 141, 272–282.

Don, A., Scholten, T., Schulze, E.D., 2009. Conversion of cropland into grassland: implications for soil organic-carbon stocks in two soils with different texture. J. Plant Nutr. Soil Sci. 172, 53–62.

Dong, S.K., Wen, L., Li, Y.Y., Wang, X.X., Zhu, L., Li, X.Y., 2012. Soil-quality effects of grassland degradation and restoration on the Qinghai-Tibetan plateau. Soil Sci. Soc. Am. J. 76, 2256.

Dörfer, C., Kühn, P., Baumann, F., He, J.S., Scholten, T., 2013. Soil organic carbon pools and stocks in permafrost-affected soils on the Tibetan Plateau. PLoS One 8, e57024.

Eclesia, R.P., Jobbagy, E.G., Jackson, R.B., Biganzoli, F., Piñeiro, G., 2012. Shifts in soil organic carbon for plantation and pasture establishment in native forests and grasslands of South America. Glob. Chang. Biol. 18, 3237–3251.

Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Bjork, R.G., Boulanger-Lapointe, N., Cooper, E.J., Cornelissen, J.H.C., Day, T.A., Dorrepaal, E., Elumeeva, T.G., Gill, M., Gould, W.A., Harte, J., Hik, D.S., Hofgaard, A., Johnson, D.R., Johnstone, J.F., Jonsdottir, I.S., Jorgenson, J.C., Klanderud, K., Klein, J.A., Koh, S., Kudo, G., Lara, M., Levesque, E., Magnusson, B., May, J.L., Mercado-Diaz, J.A., Michelsen, A., Molau, U., Myers-Smith, I.H., Oberbauer, S.F., Onipchenko, V.G., Rixen, C., Schmidt, N.M., Shaver, G.R., Spasojevic, M.J., Porhallsdottir, P.E., Tolvanen, A., Troxler, T., Tweedie, C.E., Villareal, S., Wahren, C.H., Walker, X., Webber, P.J., Welker, J.M., Wipf, S., 2012. Plot-scale evidence of tundra vegetation change and links to recent summer warming. Nat. Clim. Chang. 2, 453–457.

Fang, J., Yang, Y., Ma, W., Mohammat, A., Shen, H., 2010. Ecosystem carbon stocks and their changes in China's grasslands. Sci. China Life Sci. 53, 757–765.

Fay, P.A., Carlisle, J.D., Knapp, A.K., Blair, J.M., Collins, S.L., 2003. Productivity responses to altered rainfall patterns in a C_4-dominated grassland. Oecologia 137, 245–251.

Fay, P.A., Kaufman, D.M., Nippert, J.B., Carlisle, J.D., Harper, C.W., 2008. Changes in grassland ecosystem function due to extreme rainfall events: implications for responses to climate change. Glob. Chang. Biol. 14, 1600–1608.

Fornara, D.A., Tilman, D., 2012. Soil carbon sequestration in prairie grasslands increased by chronic nitrogen addition. Ecology 93, 2030–2036.

Garten, C.T., 2004. Soil Carbon Dynamics Along an Elevation Gradient in the Southern Appalachian Mountains. US Department of Energy, Environmental Science Division, Oak Ridge National Laboratory ORNL/TM-2004/50.

Geng, Y., Wang, Y.H., Yang, K., Wang, S.P., Zeng, H., Baumann, F., Kühn, P., Scholten, T., He, J.S., 2012. Soil respiration in Tibetan alpine grasslands: belowground biomass and soil moisture, but not soil temperature, best explain the large-scale patterns. PLoS One 7, e34968.

Grüneberg, E., Ziche, D., Wellbrock, N., 2014. Organic carbon stocks and sequestration rates of forest soils in Germany. Glob. Chang. Biol. 20, 2644–2662.

Heimann, M., Reichstein, M., 2008. Terrestrial ecosystem carbon dynamics and climate feedbacks. Nature 451, 289–292.

Heisler-White, J.L., Knapp, A.K., Kelly, E.F., 2008. Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland. Oecologia 158, 129–140.

Heisler-White, J., Blair, J.M., Kelly, E.F., Harmoney, K., Knapp, A.K., 2009. Contingent productivity responses to more extreme rainfall regimes across a grassland biome. Glob. Chang. Biol. 15, 2894–2904.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978.

Hopkins, D.W., Waite, I.S., McNicol, J.W., Poulton, P.R., Macdonald, A.J., O'Donnell, A.G., 2009. Soil organic carbon contents in long-term experimental grassland plots in the UK (Palace Leas and Park Grass) have *not* changed consistently in recent decades. Glob. Chang. Biol. 15, 1739–1754.

Hu, Z. M., Li, S. G., Guo, Q., Niu, S. L, He, N. P., Li, L. H., Yu, G. R., 2016. A synthesis of the effect of grazing exclusion on carbon dynamics in grasslands in China. Glob. Chang. Biol. 22, 1385–1393.

Jackson, R.B., Banner, J.L., Jobbagy, E.G., Pockman, W.T., Wall, D.H., 2002. Ecosystem carbon loss with woody plant invasion of grasslands. Nature 418, 623–626.

Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Johnson, D.W., Minkkinen, K., Byrne, K.A., 2007. How strongly can forest management influence soil carbon sequestration? Geoderma 137, 253–268.

Janssens, I.A., Freibauer, A., Schlamadinger, B., Ceulemans, R., Ciais, P., Dolman, A.J., Heimann, M., Nabuurs, G.J., Smith, P., Valentini, R., Schulze, E.D., 2005. The carbon budget of terrestrial ecosystems at country-scale - a European case study. Biogeosciences 2, 15–26.

Jenkinson, D., Adams, D., Wild, A., 1991. Model estimates of CO_2 emissions from soil in response to global warming. Nature 351, 304–306.

Johnson, D.W., Todd, D.E., Trettin, C.F., Sedinger, J.S., 2007. Soil carbon and nitrogen changes in forests of walker branch watershed, 1972 to 2004. Soil Sci. Soc. Am. J. 71, 1639–1646.

Johnston, C.A., Groffman, P., Breshears, D.D., Cardon, Z.G., Currie, W., Emanuel, W., Gaudinski, J., Jackson, R.B., Lajtha, K., Nadelhoffer, K., Nelson, D., Post, W.M., Retallack, G., Wielopolski, L., 2004. Carbon cycling in soil. Front. Ecol. Environ. 2, 522–528.

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

Kato, T., Tang, Y., Gu, S., Hirota, M., Du, M., Li, Y., Zhao, X., 2006. Temperature and biomass influences on interannual changes in CO_2 exchange in an alpine meadow on the Qinghai-Tibetan Plateau. Glob. Chang. Biol. 12, 1285–1298.

Kirschbaum, M.U.F., Bin Guo, L., Gifford, R.M., 2008. Why does rainfall affect the trend in soil carbon after converting pastures to forests? A possible explanation based on nitrogen dynamics. For. Ecol. Manag. 255, 2990–3000.

Knorr, W., Prentice, I.C., House, J.I., Holland, E.A., 2005. Long-term sensitivity of soil carbon turnover to warming. Nature 433, 298–301.

Kutsch, W., Bahn, M., Heinemeyer, A., 2009. Soil Carbon Dynamics: An Integrated Methodology. Cambridge University Press .

LeBauer, D.S., Treseder, K.K., 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. Ecology 89, 371–379.

Lettens, S., van Orshoven, J., van Wesemael, B., Muys, B., Perrin, D., 2005. Soil organic carbon changes in landscape units of Belgium between 1960 and 2000 with reference to 1990. Glob. Chang. Biol. 11, 2128–2140.

Li, Y., Dong, S., Wen, L., Wang, X., Wu, Y., 2013. The effects of fencing on carbon stocks in the degraded alpine grasslands of the Qinghai-Tibetan Plateau. J. Environ. Manag. 128, 393–399.

Li, Y.-Y., Dong, S.-K., Wen, L., Wang, X.-X., Wu, Y., 2014. Soil carbon and nitrogen pools and their relationship to plant and soil dynamics of degraded and artificially restored grasslands of the Qinghai–Tibetan Plateau. Geoderma 213, 178–184.

Liu, X.D., Chen, B.D., 2000. Climatic warming in the Tibetan Plateau during recent decades. Int. J. Climatol. 20, 1729–1742.

Liu, X.J., Zhang, Y., Han, W.X., Tang, A.H., Shen, J.L., Cui, Z.L., Vitousek, P., Erisman, J.W., Goulding, K., Christie, P., Fangmeier, A., Zhang, F.S., 2013. Enhanced nitrogen deposition over China. Nature 494, 459–462.

McGuire, A.D., Christensen, T.R., Hayes, D., Heroult, A., Euskirchen, E., Kimball, J.S., Koven, C., Lafleur, P., Miller, P.A., Oechel, W., Peylin, P., Williams, M., Yi, Y., 2012. An assessment of the carbon balance of Arctic tundra: comparisons among observations, process models, and atmospheric inversions. Biogeosciences 9, 3185–3204.

Nelson, D.W., Sommers, L.E., 1982. Total Carbon, Organic Carbon, and Organic Matter. Methods of Soil Analysis II. American Society of Agronomy, Madison, pp. 539–579.

Parfitt, R.L., Ross, D.J., 2011. Long-term effects of afforestation with *Pinus radiata* on soil carbon, nitrogen, and pH: a case study. Soil Res. 49, 494–503.

Piao, S.L., Fang, J.Y., He, J.S., 2006. Variations in vegetation net primary production in the Qinghai-Xizang Plateau, China, from 1982 to 1999. Clim. Chang. 74, 253–267.

Qiu, J., 2008. The third pole. Nature 454, 393–396.

Saleska, S.R., Didan, K., Huete, A.R., da Rocha, H.R., 2007. Amazon forests green-up during 2005 drought. Science 318, 612.

R Development Core Team, 2014. R: A Language and Environment for Statistical Computing. R Development Core Team, Austria, Vienna .
Schipper, L.A., Baisden, W.T., Parfitt, R.L., Ross, C., Claydon, J.J., Arnold, G., 2007. Large losses of soil C and N from soil profiles under pasture in New Zealand during the past 20 years. Glob. Chang. Biol. 13, 1138–1144.
Schipper, L.A., Parfitt, R.L., Ross, C., Baisden, W.T., Claydon, J.J., Fraser, S., 2010. Gains and losses in C and N stocks of New Zealand pasture soils depend on land use. Agric. Ecosyst. Environ. 139, 611–617.
Schulze, E.D., Luyssaert, S., Ciais, P., Freibauer, A., Janssens, I.A., Schulze, E.D., Soussana, J.F., Smith, P., Grace, J., Levin, I., Thiruchittampalam, B., Heimann, M., Dolman, A.J., Valentini, R., Bousquet, P., Peylin, P., Peters, W., Rödenbeck, C., Etiope, G., Vuichard, N., Wattenbach, M., Nabuurs, G.J., Poussi, Z., Nieschulze, J., Gash, J.H., et al., 2009. Importance of methane and nitrous oxide for Europe's terrestrial greenhouse-gas balance. Nat. Geosci. 2, 842–850.
Scott, R.L., Hamerlynck, E.P., Jenerette, G.D., Moran, M.S., Barron-Gafford, G.A., 2010. Carbon dioxide exchange in a semidesert grassland through drought-induced vegetation change. J. Geophys. Res. 115, G03026.
Shi, X.Z., Yu, D.S., Xu, S.X., Warner, E.D., Wang, H.J., Sun, W.X., Zhao, Y.C., Gong, Z.T., 2010. Cross-reference for relating Genetic Soil Classification of China with WRB at different scales. Geoderma 155, 344–350.
Shi, Y., Baumann, F., Ma, Y., Song, C., Kühn, P., Scholten, T., He, J.S., 2012. Organic and inorganic carbon in the topsoil of the Mongolian and Tibetan grasslands: pattern, control and implications. Biogeosciences 9, 2287–2299.
Sistla, S.A., Moore, J.C., Simpson, R.T., Gough, L., Shaver, G.R., Schimel, J.P., 2013. Long-term warming restructures Arctic tundra without changing net soil carbon storage. Nature 497, 615–618.
Smith, P., Davies, C.A., Ogle, S., Zanchi, G., Bellarby, J., Bird, N., Boddey, R.M., McNamara, N.P., Powlson, D., Cowie, A., Noordwijk, M., Davis, S.C., Richter, D.D.E.B., Kryzanowski, L., Wijk, M.T., Stuart, J., Kirton, A., Eggar, D., Newton-Cross, G., Adhya, T.K., Braimoh, A.K., 2012. Towards an integrated global framework to assess the impacts of land use and management change on soil carbon: current capability and future vision. Glob. Chang. Biol. 18, 2089–2101.
Soussana, J.F., Allard, V., Pilegaard, K., Ambus, P., Amman, C., Campbell, C., Ceschia, E., Clifton-Brown, J., Czobel, S., Domingues, R., Flechard, C., Fuhrer, J., Hensen, A., Horvath, L., Jones, M., Kasper, G., Martin, C., Nagy, Z., Neftel, A., Raschi, A., Baronti, S., Rees, R.M., Skiba, U., Stefani, P., Manca, G., Sutton, M., Tuba, Z., Valentini, R., 2007. Full accounting of the greenhouse gas (CO_2, N_2O, CH_4) budget of nine European grassland sites. Agric. Ecosyst. Environ. 121, 121–134.
Stevens, A., van Wesemael, B., 2008. Soil organic carbon dynamics at the regional scale as influenced by land use history: a case study in forest soils from southern Belgium. Soil Use Manag. 24, 69–79.
Su, X.K., Wu, Y., Dong, S.K., Wen, L., Li, Y.Y., Wang, X.X., 2015. Effects of grassland degradation and re-vegetation on carbon and nitrogen storage in the soils of the Headwater Area Nature Reserve on the Qinghai-Tibetan Plateau, China. J. Mt. Sci. 12, 582–591.
Wang, G.X., Qian, J., Cheng, G.D., Lai, Y.M., 2002. Soil organic carbon pool of grassland soils on the Qinghai-Tibetan Plateau and its global implication. Sci. Total Environ. 291, 207–217.
Wang, S.P., Duan, J.C., Xu, G.P., Wang, Y.F., Zhang, Z.H., Rui, Y.C., Luo, C.Y., Xu, B., Zhu, X.X., Chang, X.F., Cui, X.Y., Niu, H.S., Zhao, X.Q., Wang, W.Y., 2012. Effects of warming and grazing on soil N availability, species composition, and ANPP in an alpine meadow. Ecology 93, 2365–2376.
Wang, X., Dong, S., Gao, Q., Zhou, H., Liu, S., Su, X., Li, Y., 2014a. Effects of short-term and long-term warming on soil nutrients, microbial biomass and enzyme activities in an alpine meadow on the Qinghai-Tibet Plateau of China. Soil Biol. Biochem. 76, 140–142.
Wang, Y.H., Liu, H.Y., Chung, H., Yu, L.F., Mi, Z.R., Geng, Y., Jing, X., Wang, S.P., Zeng, H., Cao, G.M., Zhao, X.Q., He, J.S., 2014b. Non-growing-season soil respiration is controlled by freezing and thawing processes in the summer monsoon-dominated Tibetan alpine grassland. Glob. Biogeochem. Cycles 28, 1081–1095.
Wu, Z.Y., 1980. Vegetation of China. Science Press, Beijing .
Wu, H.B., Guo, Z.T., Peng, C.H., 2003. Distribution and storage of soil organic carbon in China. Glob. Biogeochem. Cycles 17, 1048.
Xie, Z.B., Zhu, J.G., Liu, G., Cadisch, G., Hasegawa, T., Chen, C.M., Sun, H.F., Tang, H.Y., Zeng, Q., 2007. Soil organic carbon stocks in China and changes from 1980s to 2000s. Glob. Chang. Biol. 13, 1989–2007.
Xiong, Y., Li, Q.K., 1987. Soils of China (in Chinese). Science Press, Beijing, China .
Yang, Y.H., Fang, J.Y., Tang, Y.H., Ji, C.J., Zheng, C.Y., He, J.S., Zhu, B., 2008. Storage, patterns and controls of soil organic carbon in the Tibetan grasslands. Glob. Chang. Biol. 14, 1592–1599.
Yang, Y.H., Fang, J.Y., Smith, P., Tang, Y.H., Chen, A.P., Ji, C.J., Hu, H.F., Rao, S., Tan, K., He, J.S., 2009. Changes in topsoil carbon stock in the Tibetan grasslands between the 1980s and 2004. Glob. Chang. Biol. 15, 2723–2729.
Yang, Y.H., Ji, C.J., Ma, W.H., Wang, S.F., Wang, S.P., Han, W.X., Mohammat, A., Robinson, D., Smith, P., 2012. Significant soil acidification across northern China's grasslands during 1980s–2000s. Glob. Chang. Biol. 18, 2292–2300.
Yao, T.D., Thompson, L.G., Jiao, K.Q., Mosleythompson, E., Yang, Z.H., 1995. Recent warming as recorded in the Qinghai-Tibetan cryosphere. Ann. Glaciol. 21, 196–200.
Yu, G.R., Zhu, X.J., Fu, Y.L., He, H.L., Wang, Q.F., Wen, X.F., Li, X.R., Zhang, L.M., Zhang, L., Su, W., Li, S.G., Sun, X.M., Zhang, Y.P., Zhang, J.H., Yan, J.H., Wang, H.M., Zhou, G.S., Jia, B.R., Xiang, W.H., Li, Y.N., Zhao, L., Wang, Y.F., Shi, P.L., Chen, S.P., Xin, X.P., Zhao, F.H., Wang, Y.Y., Tong, C.L., 2013. Spatial patterns and climate drivers of carbon fluxes in terrestrial ecosystems of China. Glob. Chang. Biol. 19, 798–810.
Zhang, G.L., Zhang, Y.J., Dong, J.W., Xiao, X.M., 2013. Green-up dates in the Tibetan Plateau have continuously advanced from 1982 to 2011. Proc. Natl. Acad. Sci. U. S. A. 110, 4309–4314.
Zhang, Y., Dong, S.K., Gao, Q.Z., Liu, S.L., Zhou, H.K., Ganjurjav, H., Wang, X.X., 2016. Climate change and human activities altered the diversity and composition of soil microbial community in alpine grasslands of the Qinghai-Tibetan Plateau. Sci. Total Environ. 562, 353–363.
Zhao, M.S., Running, S.W., 2010. Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. Science 329, 940–943.
Zhao, L., Cheng, G.D., Li, S.X., Zhao, X.M., Wang, S.L., 2000. Thawing and freezing processes of active layer in Wudaoliang region of Tibetan Plateau. Chin. Sci. Bull. 45, 2181–2187.
Zhou, X.M., 2001. "Kobresia" Meadow Ecosystem in China. Science and Technology Press, Beijing .
Zhuang, Q., He, J., Lu, Y., Ji, L., Xiao, J., Luo, T., 2010. Carbon dynamics of terrestrial ecosystems on the Tibetan Plateau during the 20th century: an analysis with a process-based biogeochemical model. Glob. Ecol. Biogeogr. 19, 649–662.
Ziter, C., MacDougall, A.S., 2013. Nutrients and defoliation increase soil carbon inputs in grassland. Ecology 94, 106–116.