Shallow groundwater inhibits soil respiration and favors carbon uptake in a wet alpine meadow ecosystem

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Abstract

Wet alpine meadow ecosystems generally act as a significant carbon sink due to their higher rate of photosynthesis than the rate of decomposition. However, it remains unclear whether the low decomposition rate is determined by low temperatures or by nearly-saturated soil conditions. Using five years of measurements from two sites on the Tibetan Plateau with significantly different soil water conditions, we showed that compared to the dry site (which had a deep water table), the much larger carbon sink at the site with a shallow groundwater was mainly caused by the inhibiting effects of the nearly-saturated soil condition on soil respiration rather than by the low temperature. The findings suggested that thawing of frozen soil may partially slow down soil carbon decomposition through increasing soil water. We highlights that a warming-induced shrinking cryosphere may largely affect the carbon dynamics of wet and cold ecosystems through changes in soil hydrology.

Abstract:

Wet alpine meadow ecosystems generally act as a significant carbon sink due to their higher rate of photosynthesis than the rate of decomposition. However, it remains unclear whether the low decomposition rate is determined by low temperatures or by nearly-saturated soil conditions. Using five years of measurements from two sites on the Tibetan Plateau with significantly different soil water conditions, we showed that compared to the dry site (which had a deep water table), the much larger carbon sink at the site with a shallow groundwater was mainly caused by the inhibiting effects of the nearly-saturated soil condition on soil respiration rather than by the low temperature. The findings suggested that thawing of frozen soil may partially slow down soil carbon decomposition through increasing soil water. We highlights that a warming-induced shrinking cryosphere may largely affect the carbon dynamics of wet and cold ecosystems through changes in soil hydrology.

INTRODUCTION

Alpine meadow ecosystems are sensitive to climate change and human activities due to their extremely cold and fragile environment (Marcolla *et al.* 2011; Hu *et al.* 2016; Knowles *et al.* 2015; Wang *et al.* 2020). These ecosystems generally act as a carbon sink (Kato *et al.* 2006; Li *et al.* 2016; Scholz *et al.* 2018), which however is expected to be reduced and potentially turns into a carbon source in response to future warming, due to the accelerated soil carbon decomposition (Virkkala*et al.* 2017; Ganjurjav *et al.* 2018; Sun *et al.*2019). Many previous studies reported that climate warming and human activities will change the soil hydrologic conditions and further affecting the soil carbon dynamics of several cold ecosystems, including Arctic tundra, northern peatlands, mires, and bogs (Ise *et al.*2008; Dorrepaal *et al.* 2009; Dinsmore *et al.* 2010; McVeigh*et al.* 2014; Schädel *et al.* 2016; Drollinger *et al.*2019; Gockede *et al.* 2019; Korkiakoski *et al.*

2019; Stover & Henry 2019; Swindles *et al.* 2019). However, the mechanisms by which the soil hydrological conditions, such as the shallow groundwater level, affect carbon exchanges in alpine meadow ecosystem are poorly understood. To maintain the carbon sink capacity of the ecosystem and predict its potential changes in response to future warming, it is critical to better understand this eco-hydrological coupling process.

The Tibetan Plateau (TP) is the highest plateau in the world, with an average elevation of 4000 m above sea level (Yang *et al.* 2014). It has been experiencing large increases in temperature during recent decades (Gao *et al.* 2015). The alpine meadow/grassland is the dominant ecosystem over the TP, covering more than 50% of the whole TP (Liu *et al.* 2010). Both a warming climate and increasing anthropogenic activities have caused significant changes in carbon exchanges of the alpine meadow ecosystem over the TP (Piao *et al.* 2012). Many studies have investigated the relationships between carbon exchanges and environmental factors of this ecosystem (Kato *et al.* 2006; Lin *et al.* 2011; Chen*et al.* 2015; Hu *et al.* 2016; Fu *et al.* 2018; Ganjurjav *et al.* 2018; Liu *et al.* 2018; Zhang *et al.* 2018; Wang *et al.* 2019; Lv *et al.* 2020; Yu *et al.* 2020). These studies mainly focused on the effects of temperature, precipitation, soil moisture (SM), soil temperature (ST), and grazing on net ecosystem exchange (NEE), gross primary productivity (GPP), and ecosystem respiration (Re), and rarely considered the effects of soil hydrological conditions, such as groundwater conditions and water table depth.

For cold and wet ecosystems, a shallow water table can largely affect carbon exchange by controlling oxygen diffusion, enzyme dynamics, and osmoregulation in soils (Moyano *et al.* 2013; Yan *et al.*2018). For example, in northern peatlands a shallower water table level (WTL) lowers the decomposition rate of soil organic carbon (Korkiakoski*et al.* 2019) and therefore results in a high sensitivity of peat decomposition to climate change through WTL feedbacks (Ise *et al.*2008; Helfter *et al.* 2015). For tundra ecosystems, an increased shallow WTL can strongly lower ecosystem respiration by reducing soil oxygen availability; a decreased WTL increases GPP and Re, while it negatively affects NEE because the increases in root and microbial activity are greater than in photosynthesis (Olivas *et al.* 2010). Several previous studies reported that the wet alpine meadow ecosystems on the TP act as significant carbon sinks (Kato *et al.* 2006; Li*et al.* 2019; Sun *et al.* 2019), while it remains unclear whether the large carbon sink is determined by the low temperature or by the nearly-saturated soil conditions (i.e., shallow ground water).

The TP is also known as the "Asian Water Tower" because of its large water storage (Immerzeel *et al.* 2010). In wet alpine regions at the TP, the groundwater level is usually shallow and is significantly changing with climate warming (Ge *et al.* 2008; Ge *et al.*2011; Wu *et al.* 2013). We hypothesize that the large carbon sink and high carbon sequestration efficiency (CSE, defined as the ratio of net ecosystem productivity to GPP) of the wet alpine meadow ecosystem of the TP is determined by the inhibiting effects of the shallow groundwater rather than that of the low temperature on soil respiration. To test this hypothesis, we analyzed five years of measurements from two sites in the northeastern TP with low temperature and significantly different soil water conditions.

MATERIAL AND METHODS

2.1 Study area and site information

The study area is located at the upper reach of the Heihe River basin, northeast TP, China (Fig. 1a). The area is characterized by a tundra climate (Kottek *et al.* 2006), with a mean annual temperature (MAT) of 2 and a mean annual precipitation (MAP) of 350 mm (Sun*et al.* 2019). The elevation in the area ranges from 1637 m to 5706 m above sea level. Most of the area is covered by alpine meadows and shrubs (Fig. 1a & b). The study area serves as the main contributing area for the runoff of the Heihe River watershed due to glaciers and snow melt. Most of the land is seasonally frozen, and permafrost occurs at high elevation. More details about the regions can be found in Li et al. (2018).

Several eddy-covariance (EC) and automatic meteorological towers were successively established in the study area since 2012 (Li *et al.*2013). The carbon exchange and meteorological measurements of the Dashalong and Arou sites were used in this study (Fig. 1a). The dominant vegetation species are *Kobresia tibetica Maxim* and *Carex*at Dahshalong and *Elymus nutans* and *Roegneria nutans* at Arou (Sun *et al.* 2019). The elevations, MATs, and MAPs are distinctly different between the two sites, with values of 3739 m and 3033 m, –3.4 degC and 0.6 degC, and 388.6 and to 464.1 mm for Dashalong and Arou, respectively. Dashalong has a shallow groundwater table of ~ 40 cm (Fig. 1c), while the groundwater table is deep at Arou (Fig. 1d). The Arou site is located in an enclosed pasture without grazing. The vegetation around Dashalong is grazed by yaks and sheep during the growing-season.

EC and Meteorological measurements

The EC systems were installed at 3.5 m and 4.5 m above the ground at Arou and Dashalong, respectively. Each EC instrument consists of a 3-D sonic anemometer (CSAT3, Campbell Scientific, Inc., Logan, UT, USA) and an infrared gas analyzer (Li- 7500A, LI-COR Biosciences, Lincoln, NE, USA). The instruments started collecting data from December, 2012 at Arou and from August, 2013 at Dashalong.

The meteorological and soil variables were simultaneously measured with the EC systems, including air temperature (), precipitation (mm), air relative humidity (%), wind direction, air pressure (hPa) and four-component radiation (W m^{-2}), soil temperature and soil moisture. The soil temperature (109/109ss-L, Campbell Scientific, Inc.) and soil moisture (CS616, Campbell Scientific, Inc.) were measured at 4, 10, 20, 40, 80, 120, and 160 cm depths at Dashalong, and at 2, 4, 6, 10, 15, 20, 30, 40, 60, 80, 120, 160, 200, 240, 280, and 320 cm depths at Arou. More details on the measurements and sensors can be found in Che et al. (2019) and Liu et al. (2018).

Data preprocessing

The measurements collected from January 2013 to December 2017 at Arou and from September 2013 to December 2017 at Dashalong were examined. The EC half hour CO_2 measurements were firstly preprocessed with the EdiRe software (The University of Edinburgh, 2012) and then converted to NEE following Hollinger et al. (1994). The details and criteria of data quality control and conversion can be found in Liu et al. (2011).

The percentages of missing NEE data were 25% and 39% for Arou and Dashalong, respectively. The REddyProcWeb tool (Wutzler *et al.*2018) was used to perform gap filling, friction velocity u* filtering, and NEE partitioning procedures. The tool was also used to calculate the vapor pressure deficit (VPD). The gap filling method is similar to Falge et al. (2001), but considers the co-variation of fluxes with meteorological variables and the temporal auto-correlation of the fluxes (Reichstein *et al.* 2005). The u* thresholds for filtering were estimated according to Papale et al. (2006), and the flux measurements below the thresholds were replaced with gap-filled values. The flux partitioning algorithm was based on Reichstein et al. (2005), in which respiration is estimated from night-time data and extrapolated to day-time. The outputs gap-filling data from the tool were classified into three classes according to their reliability (most reliable, medium, and least reliable). The least reliable data were removed from the analyses.

For meteorological and soil data, the small gaps ([?] 4 steps, i.e., 2 h) were filled using linear interpolation, and continuous large gaps were removed. Leaf area index (LAI) was derived from the MODIS LAI product (MCD15A3H version 6) (Myneni *et al.* 2015), which has spatial and temporal resolutions of 500 m and 4-day, respectively. The LAI values at the sites were the values of the MCD15A3H LAI pixels that encompassed the EC towers.

Methods

Because we lacked direct WTL measurements at the sites, we used the multi-layer SM measurements to indirectly infer the shallow groundwater table. The measurement range of the CS616 SM sensor is 0-50%, depends on soil properties, and is generally lower for very sandy soil (Campbell Scientific, 2002; Zhu *et al.* 2019). Based on the measurements during the high WTL period (Fig. 1c), we deemed that deep soils (> 40 cm) are nearly-saturated when the measurements are larger than ~ 0.38 (Knowles *et al.* 2015).

To explore whether the low rate in soil organic carbon decomposition and thus the higher CSE and larger carbon sink was determined by the low temperature or by the shallow groundwater at the wet site, we firstly compared the observation-based soil moisture and soil temperature profiles to Re at the two sites; and then examined the relationships between Re and SM and between Re and ST at the nearly-saturated soil layer of the wet site during the unfrozen seasons. The unfrozen seasons of the sites were defined as periods from the first day that temperature at 160 cm soil depth was above 0 to the first day that temperature of surface soil was below 0 . Consequently, the unfrozen seasons were 25 May - 30 September and 1 July - 30 September for the Arou and Dashalong sites, respectively.

Finally, we used linear mixed-effects models to evaluate the effects of SM and ST on Re in each soil layer at the sites. The linear mixed-effects models have the advantages to include both fixed and random effects, and have been widely used in ecology (Harrison *et al.* 2018). We used the lmer package (Bates *et al.* 2015) to run the linear mixed-effects models in R software (version 3.5.2, R Core Team, 2018). The afex package (*http://afex.singmann.science/*) was used to conduct analysis of variance (ANOVA) analyses and compare the model fits. The best fitting model was selected according to comparison of the model fits. Our best fitting model had a model structure in which observational years were the subjects (random effects), both soil moisture and soil temperature were predictors of Re (fixed effects), and there was no an interaction term between soil moisture and soil temperature. The response variable in linear mixed-effects models was the transformed log10 (Re) instead of Re.

RESULTS

Environmental conditions of the ecosystem

Based on the observations collected during 2013-2017, both air temperature and precipitation were much lower at Dashalong than at Arou (Fig. S1). The daily mean air temperature and daily precipitation at Dashalong were within -25.3 - 13.6 and 0 - 39.2 mm, respectively; the MAT and MAP were -3.7 and 363.0 mm, respectively. At Arou, the daily mean air temperature and daily precipitation ranged from -23.3 to 17.3 and from 0 to 30.7 mm, respectively; the MAT and MAP were 0.3 and 458.7 mm, respectively. The daily mean wind speed ranged from 1.2 to 9.7 m s^{-1} at the sites. The daily mean VPD at the sites was within 0.3-10.1 hPa, and the mean annual VPD was 2.4 hPa and 3.3 hPa for Dashalong and Arou, respectively. The RH of both sites varied largely across seasons; the mean annual RH was 56.8% and 59.3% for Dashalong and Arou, respectively. The ST (4 cm depth) and pressure were consistently higher at Arou than at Dashalong; the daily mean ST and pressure were 4.1 and 730.0 hPa at Arou and -0.1 and 642.2 hPa at Dashalong, respectively. The surface SM (4 cm depth) of the sites varied considerably, ranging between 6.2%-56.6%. The Rn at Dashalong was slightly larger than at Arou, with mean annual values of 79.8 and 66.1 W m-^{2}, respectively. In contrast, the LAI of Arou was much higher than that of Dashalong, with mean annual values of 1.3 and 0.4, respectively.

Carbon exchanges at the sites

The GPP at Arou was significantly larger than at Dashalong, with annual mean values of 826.6 g C m^{-2} and 468.3 g C m^{-2}, respectively (Table S1). The daily GPP ranged from 0 to 13.3 g C m^{-2} at Arou during 2014-2017, with a standard deviation (SD) of 3.3 g C m^{-1}. It was nearly double that of Dashalong during the peak periods (Fig. 2a). At Dashalong, the daily GPP was within 0-7.2 g C m^{-2}, with a SD value of 1.6 g C m^{-2}. Compared to GPP, the differences in Re between the sites were much larger (Fig. 2b). The mean annual Re at Arou was 619.1 g C m^{-2}, while it was only 184.8 g C m^{-2} at Dashalong. The daily Re ranged from 0 to 3.7 g C m^{-2} and from 0 to 12.2 g C m^{-2}, with SD values of 0.7 g C $m^{-2}$and 2.4 g C m^{-2} at Dashalong and Arou, respectively. In contrast to GPP and Re, the Dashalong site had a lager carbon sink (-280.2 g C m^{-2} yr^{-1}) than that of Arou (-195.8 g C m^{-2} yr^{-1}) due to the much lower annual Re (Fig. 2c). The daily NEE ranged from -5.7 to 0.9 g C m^{-2} at Dashalong and from -6.5 to 3.9 g C m^{-2} at Arou, with SD values of 1.2 g C m^{-2} and 1.5 g C m^{-2}, respectively. Consequently, the Dashalong site had a significantly higher CSE than that of Arou during the unfrozen seasons (Fig. 2d). The daily CSE ranging from -28% to 89% and from -46% to 78% at Dashalong and Arou, respectively. The annual CSE reached 60% at Dashalong, while it was much lower at Arou, with a value of 24%.

Effects of soil water and soil temperature on Re

To clarify whether the lower temperature or the shallow groundwater (Fig. 1c) determined the lower Re and further caused the larger carbon sink and higher CSE at Dashalong than at Arou, we first examined the soil hydrological conditions and soil temperature at the two sites using multi-layer SM and ST measurements (Fig. S2 & S3), and then compared them to the Re. At Dashalong, SM showed significant seasonal variations at depths from 4 cm to 160 cm. During the unfrozen months, SM ranged from 0.25 to 0.58; the SMs in the top layers ([?] 40 cm) fluctuated with greater magnitude over time than those in the deep layers ($>$ 40 cm), indicating that a shallow groundwater table might exist with recharge from the melting cryosphere; this was further confirmed by the field survey (Fig. 1c). As expected, during the frozen periods, SM was very low in each layer, with an average value of 0.15 +- 0.09. At Arou, SM of the top layers ($>$ 60 cm) exhibited large fluctuations during the unfrozen months, with an average value of 0.34 +- 0.05. While, during the frozen months SM was below 0.10 in each soil layer, because of the conversion of liquid to frozen water. Different from topsoil, SM of deep soil remained almost unchanged across seasons, indicating that there should be no shallow ground water existed throughout a whole year, which was consistent with our observations (Fig. 1d). Soil temperature of both sites varied largely across seasons for all layers (Fig. S3). The daily mean soil temperature ranged from -18 to 15 at Dashalong and from -12 to 19 at Arou. As expected, the temperature of the topsoil fluctuated more greatly than that of the deep soil in response to the strong effects of the atmospheric forcing. That is, during the unfrozen periods, the temperature of the topsoil was much higher than that of the deep soil; in contrast, it was much lower than that of the deep soil during the frozen months.

The comparisons between Re and soil moisture profiles showed that consistent with the large differences in Re, the soil water conditions were highly and significantly different between the two sites (Fig. 3). The SM of deep soil ($>$ 50 cm) was significantly high at Dashalong than it at Arou site during the unfrozen seasons. At Dashalong, SM remained above 0.23 from topsoil to deep soil, and the Re was lower than 3.7 g C m^{-2} day^{-1}, with a mean value of 1.1 +- 0.7 g C m^{-2}day^{-1}. At Arou, SM was comparable to that of Dashalong in topsoil during the unfrozen seasons; while it was much lower in deep soil, with values below 0.10, confirming that there was no shallow groundwater. The Re of Arou was within 0.5-13.5 g C m^{-2} day^{-1}, with a mean value of 4.3 +- 2.4 g C m^{-2} day^{-1} during the unfrozen seasons. In contrast to SM, the ST profiles of the two sites were comparable during the unfrozen seasons (Fig. 4). The temperature in topsoil at Arou was higher than it at Dashalong, while they were close in deep soil.

We also compared the SM in deep soil ($>$ 40 cm) and Re at the sites during the unfrozen seasons (Fig. S4). The results expectedly showed that the SM had small fluctuations at 40 cm depth, and almost remained unchanged in deeper soil at Dashalong, due to the exist of shallow groundwater. At Arou, SM was highly fluctuant in soil at 40 cm depth, while it almost kept dry ($<$ 0.1) in deeper soil. To verify our hypothesis that the nearly-saturated soil suppressed Re during the unfrozen seasons and caused the larger carbon sink at Dashalong when compared that at Arou, we examined the relationships between Re and SM, and between Re and ST at the 40 cm soil layers of the sites (Fig. 5). At Dashalong, Re was significantly decreased with increasing SM ($R^2 = 0.28$, $p < 0.001$) when soil was nearly-saturated ($>$ 0.38) during the unfrozen seasons; while it expectedly increased with rising ST, conforming a significantly exponential relationship, with aR^2 of 0.25 ($p < 0.001$). The SM of Arou was lower than 0.32 at 40 cm depth across the unfrozen seasons, and there was no a significantly relationship between Re and SM; while, there was also a significantly exponential relationship between Re and ST, with a R^2 of 0.28 ($p < 0.001$).

We further used the mixed-effects model to examine the influences of SM and ST on Re at the sites during the unfrozen seasons. The results clearly showed that at Dashalong site SM negatively affected Re in each soil layer during the unfrozen seasons; although the effects were not significant in soil above 120 cm ($p >$ 0.05), they were overall enhanced with increasing soil depths (Table 1). In contrast, ST significantly and positively affected Re in top soil ($<$ 40 cm); it negatively affected Re in deep soil, but the effects were not significant ($p > 0.05$). At Arou site, both SM and ST had positive effects on Re during the unfrozen seasons (Table S2). The ST significantly affect Re at each soil layer, and the magnitudes of its effects were much larger than that of SM on Re. The effects of SM on Re were not significant in the soil layers except for 20 cm depth. These distinctly different effects of SM on Re between the Dashalong and Arou sites further verify our hypothesis that the relatively low Re and high carbon sink of wet alpine meadow ecosystems are mainly caused by the suppressed effects of the nearly-saturated SM on Re rather than that of the low ST.

DISCUSSION

Impacts of shallow groundwater on carbon exchange of wet alpine meadow ecosystem

Both low temperature and high soil water content could be responsible for the low decomposition rates in cold and wet ecosystems (Yurova*et al.* 2007; Ise *et al.* 2008; Dorrepaal *et al.*2009; Moyano *et al.* 2013; Knowles *et al.* 2015; Drollinger*et al.* 2019; Gockede *et al.* 2019). To reveal whether the low temperature or the high SM suppressed soil respiration and caused a large carbon sink in the wet alpine meadow ecosystem of the TP, we compared continuous carbon exchange, soil temperature, and SM measurements at a site with a shallow groundwater table (Dashalong) to the site with no shallow groundwater (Arou). The comparisons showed that there were large differences in Re and SM and relative small differences in ST between the two sites, indicating that the much smaller Re and larger carbon sink at Dashalong might be mainly caused by the suppressed effects of the potential shallow groundwater table on soil respiration during the unfrozen seasons. In contrast, the lack of presence of groundwater table with a large space for microbial activity might promote Re and thus resulted in less CO_2 sink at Arou. During the frozen seasons, the soil was frozen and the GPP was zero; both Re and NEE was small at both sites (Fig. 2). During the unfrozen months, the Re was much lower at Dashalong than at Arou (Fig. 3), due to a much smaller unsaturated room for microbial activities. In contrast, at Arou the deep soil was dryer with a larger unsaturated room and Re was much higher than that at Dashalong site. The mixed-effects models' analyses suggested that at Dashalong the high SM negatively affected Re during the unfrozen seasons. In contrast, at Arou SM showed positive effects on Re. The ST expectedly had significant and positive effects on Re at both of the Dashalong and Arou sites. These results confirmed that nearly-saturated conditions largely suppressed soil respiration and further caused a large carbon sink. This finding was consistent with the situations in several wet ecosystems, such as tropical peatlands, northern peatlands, and Arctic tundra (Knowles *et al.* 2015; Korkiakoski *et al.* 2019; Hoyt *et al.* 2019). For example, Knowles et al. (2015) reported that in a wet tundra ecosystem in the Colorado Rocky Mountains there was a significantly negative relationship between SM and soil respiration when soil moisture was above 0.38; they explained this result through the fact that soil respiration switched from moisture-limited to oxygen diffusion-limited with increasing SM. A mechanism explanation for these negative effects of groundwater table on soil respiration is that the metabolic activity of aerobic organisms decreases as soil is in nearly-saturated condition; soil water can largely and negatively affect soil respiration through physical (diffusion), physiological (osmoregulation), biochemical (enzyme dynamics), and ecological processes (microbial community composition and trophic interactions) (Manzoni & Porporato 2007; Moyano *et al.*2013; Bond-Lamberty *et al.* 2018). Therefore, we concluded that the large carbon sink in the wet alpine meadow ecosystem on the TP is responsible for inhibiting the effects of the nearly-saturated soil condition (i.e., shallow groundwater table) rather than the low temperature on soil respiration. These findings may partially explain why the land surface models which consider changing temperature as key climatic factor that affects soil respiration poorly simulated soil carbon dynamics in cold and wet ecosystems such as Arctic-Boreal (Huntzinger *et al.* 2020); and may helpful for improving the models' in these regions.

Implications for carbon uptake under a changing climate

The alpine meadow on the TP is experiencing fast warming (Gao *et al.* 2015; Guo *et al.* 2019; Hu *et al.* 2019). As a consequence, both the permafrost and the seasonal frozen land of the ecosystem are expected to further decline, with decreases in permafrost area and increases in active layer thickness (Zhao *et al.* 2004; Marchenko *et al.* 2007; Wu & Zhang 2008; Guo & Wang 2013; Hu*et al.* 2019). These changes distinctly alter the soil hydrological conditions, such as the groundwater table, and the conditions are likely to deteriorate with further warming (Walvoord*et al.* 2012; Kurylyk *et al.* 2014; Liljedahl *et al.*2016; Walvoord & Kurylyk 2016; Cheng *et al.* 2019).

Even small changes in WTL exert appreciable effects on frozen soil carbon dynamics (Ise *et al.* 2008; Zona *et al.* 2011; Virkkala *et al.* 2017; Luan *et al.* 2018; Yu *et al.*2020). A decrease in shallow WTL increases both Re and GPP; the increase in Re is always greater than that in GPP, resulting in a decreased carbon sequestration efficiency and carbon sink (Olivas *et al.*2010; Helfter *et al.* 2015). In contrast, rising WTL would suppress Re due to the reducing soil oxygen availability and favor photosynthesis, and thus positively affect carbon uptake (Hirano*et al.* 2009; Baldocchi *et al.* 2018). In most cases, for the wet and cold ecosystems warming-induced changes in the cryosphere cause increasing soil water content (Cheng *et al.* 2019), and may generate a rising WTL (Bense *et al.* 2012; Gao *et al.*2018). Therefore, the warming-induced rising WTL might have played an important role in retaining soil organic carbon in wet and cold regions, and will be more effective under future warming. In the meantime, to our knowledge, the relative magnitude of this inhibiting effect on soil carbon remains unclear. In addition, this situation is not sustainable for relatively dry regions, because these regions lack a sustainable cryosphere moisture supply. The warming and drying-induced decreases in WTL will enhance Re and decrease GPP, and thus cause a reduced carbon sink, and might shift ecosystems that have been historically serving as a CO_2 sink to a CO_2 source (Olivas*et al.* 2010; Helfter *et al.* 2015; Drollinger *et al.*2019; Swindles *et al.* 2019; Yu *et al.* 2020). Moreover, field measurements demonstrated that SM is increasing in the bottom active layer, while it is decreasing or remains unchanged in the upper layer with climate change (Xue *et al.* 2009; Zhang *et al.*2020); multi-model simulations suggested extensive and larger decreases in surface SM (upper 10 cm) and increasing SM in deep soil in northern middle to high latitudes with global warming (Berg *et al.* 2017). These differences in responses to climate warming between top soil and deep soil mean that thaw-induced changes in soil water condition may cause large CO_2 emission from the top soil (Lawrence*et al.* 2015), while it may also contribute to a remaining stability or slowdown in the decomposition of the old carbon in the deep soil, thus counterbalancing direct warming effects on permafrost carbon pools (Dorrepaal *et al.* 2009; Wilson *et al.* 2016; Gockede*et al.* 2019; Kwon *et al.* 2019). However, our knowledge on these different responses of Re to the changing soil water conditions between top soil and deep soil at a large scale is still limited.

CONCLUSION

We explored whether low temperature or the nearly-saturated soil water suppressed soil respiration and thus caused a large carbon sink in a cold and wet alpine ecosystem on the TP by comparing continuous measurements from two EC sites with quite different soil water and temperature conditions. The results showed that although it had a lower mean annual GPP (468.3 g C m^{-1}), the site with a shallow groundwater table during the unfrozen seasons had a high carbon sequestration efficiency (60% in annual) and large carbon sink (280.2 g C m^{-1} yr^{-1}) due to the very low Re (184.8 g C m^{-1} yr^{-1}); the site without a shallow groundwater had a high mean annual GPP (826.6 g C m^{-1}), while its carbon sequestration efficiency (24% in annual) and carbon sink were relatively low (195.8 g C m^{-1} yr^{-1}) and because of the large Re (619.1 g C m^{-1}). The high SM negatively affected Re at the site with a shallow groundwater table during the unfrozen seasons. While, SM had positive effects on Re at the site without a shallow groundwater. The ST expectedly had large and positive effects on Re at both of the two sites. Thus, the high carbon sequestration efficiency and large carbon sink of the wet alpine meadow ecosystem was caused by the inhibiting effects of the nearly-saturated soil water rather than by the low temperature controls on soil respiration. These findings suggest that warming-induced declines in the cryosphere could largely affect carbon dynamics of the ecosystems through changing soil hydrological conditions. Future studies should focus on investigating the different responses of soil carbon to warming between top soil and deep soil at a large scale.

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References

Baldocchi, D., Chu, H. & Reichstein, M. (2018). Inter-annual variability of net and gross ecosystem carbon fluxes: A review.*Agric. For. Meteorol., 249* , 520-533.

Bates, D., Machler, M., Bolker, B. & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw., 67* . https://doi.org/10.18637/jss.v067.i01

Bense, V.F., Kooi, H., Ferguson, G. & Read, T. (2012). Permafrost degradation as a control on hydrogeological regime shifts in a warming climate. *J. Geophys. Res., 117* , F03036.

Berg, A., Sheffield, J. & Milly, P.C.D. (2017). Divergent surface and total soil moisture projections under global warming. *Geophys. Res. Lett., 44* , 236-244.

Bond-Lamberty, B., Bailey, V.L., Chen, M., Gough, C.M. & Vargas, R. (2018). Globally rising soil heterotrophic respiration over recent decades. *Nature, 560* , 80-83.

Campbell Scientific. (2002). CS616 and CS625 water content reflectometers. *Campbell Scientific* . https://www.campbellsci.eu/cs616-reflectometer

Che, T., Li, X., Liu, S., Li, H., Xu, Z., Tan, J. *et al.* (2019). Integrated hydrometeorological – snow – frozen ground observations in the alpine region of the Heihe River Basin, China. *Earth Syst. Sci. Data, 11* , 1483-1499.

Chen, J., Shi, W. & Cao, J. (2015). Effects of grazing on ecosystem CO_2 exchange in a meadow grassland on the Tibetan Plateau during the growing season. *Environ. Manage., 55* , 347-359.

Cheng, M., Zhong, L., Ma, Y., Zou, M., Ge, N., Wang, X. & Hu, Y. (2019). A study on the assessment of multi-source satellite soil moisture products and reanalysis data for the Tibetan Plateau.*Remote Sens., 11,* 1196.

Dinsmore, K.J., Billett, M.F., Skiba, U.M., Rees, R.M., Drewer, J. & Helfter, C. (2010). Role of the aquatic pathway in the carbon and greenhouse gas budgets of a peatland catchment. *Glob. Change Biol., 16* , 2750-2762.

Dorrepaal, E., Toet, S., van Logtestijn, R.S.P., Swart, E., van de Weg, M.J., Callaghan, T. V. *et al.* (2009). Carbon respiration from subsurface peat accelerated by climate warming in the subarctic.*Nature, 460* , 616-619.

Drollinger, S., Maier, A. & Glatzel, S. (2019). Interannual and seasonal variability in carbon dioxide and methane fluxes of a pine peat bog in the Eastern Alps, Austria. *Agric. For. Meteorol., 275* , 69-78.

Fu, G., Shen, Z.-X. & Zhang, X.-Z. (2018). Increased precipitation has stronger effects on plant production of an alpine meadow than does experimental warming in the Northern Tibetan Plateau. *Agric. For. Meteorol., 249* , 11-21.

Ganjurjav, H., Hu, G., Wan, Y., Li, Y., Danjiu, L. & Gao, Q. (2018). Different responses of ecosystem carbon exchange to warming in three types of alpine grassland on the central Qinghai-Tibetan Plateau.*Ecol. Evol., 8* , 1507-1520.

Gao, B., Yang, D., Qin, Y., Wang, Y., Li, H., Zhang, Y. *et al.*(2018). Change in frozen soils and its effect on regional hydrology, upper Heihe basin, northeastern Qinghai-Tibetan Plateau.*Cryosphere, 12* , 657-673.

Gao, Y.H., Li, X., Leung, L.R., Chen, D.L. & Xu, J.W. (2015). Aridity changes in the Tibetan Plateau in a warming climate. *Environ. Res. Lett., 10* , 034013.

Ge, S., McKenzie, J., Voss, C. & Wu, Q. (2011). Exchange of groundwater and surface-water mediated by permafrost response to seasonal and long term air temperature variation. *Geophys. Res. Lett., 38* , L11402.

Ge, S., Wu, Q.B., Lu, N., Jiang, G.L. & Ball, L. (2008). Groundwater in the Tibet Plateau, western China. *Geophys. Res. Lett., 35* , L18403.

Gockede, M., Kwon, M.J., Kittler, F., Heimann, M., Zimov, N. & Zimov, S. (2019). Negative feedback processes following drainage slow down permafrost degradation. *Glob. Change Biol., 25* , 3254-3266.

Guo, D. & Wang, H. (2013). Simulation of permafrost and seasonally frozen ground conditions on the Tibetan Plateau, 1981-2010. *J. Geophys. Res., 118* , 5216-5230.

Guo, D., Sun, J., Yang, K., Pepin, N. & Xu, Y. (2019). Revisiting recent elevation-dependent warming on the Tibetan Plateau using satellite-based data sets. *J. Geophys. Res., 114* , 8511-8521.

Harrison, X.A., Donaldson, L., Correa-Cano, M.E., Evans, J., Fisher, D.N., Goodwin, C.E.D. *et al.* (2018). A brief introduction to mixed effects modelling and multi-model inference in ecology.*PeerJ, 6* , e4794.

Helfter, C., Campbell, C., Dinsmore, K.J., Drewer, J., Coyle, M., Anderson, M. *et al.* (2015). Drivers of long-term variability in CO_2 net ecosystem exchange in a temperate peatland.*Biogeosciences, 12* , 1799-1811.

Hirano, T., Jauhiainen, J., Inoue, T. & Takahashi, H.J.E. (2009). Controls on the carbon balance of tropical peatlands. *Ecosystems, 12* , 873-887.

Hollinger, D.Y., Kelliher, F.M., Byers, J.N., Hunt, J.E., McSeveny, T.M. & Weir, P.L. J. E. (1994). Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere.*Ecology, 75* , 134-150.

Hoyt, A.M., Gandois, L., Eri, J., Kai, F.M., Harvey, C.F. & Cobb, A.R. (2019). CO_2 emissions from an undrained tropical peatland: Interacting influences of temperature, shading and water table depth. *Glob. Change Biol., 25,* 2885-2899.

Hu, G., Zhao, L., Li, R., Wu, X., Wu, T., Xie, C. *et al.* (2019). Variations in soil temperature from 1980 to 2015 in permafrost regions on the Qinghai-Tibetan Plateau based on observed and reanalysis products. *Geoderma, 337* , 893-905.

Hu, Y., Jiang, L., Wang, S., Zhang, Z., Luo, C., Bao, X. *et al.*(2016). The temperature sensitivity of ecosystem respiration to climate change in an alpine meadow on the Tibet plateau: A reciprocal translocation experiment. *Agric. For. Meteorol., 216* , 93-104.

Huntzinger, D.N., Schaefer, K., Schwalm, C., Fisher, J.B., Michalak, A.M., Wei, Y. *et al.* (2020). Evaluation of simulated soil carbon dynamics in Arctic-Boreal ecosystems. *Environ. Res. Lett., 15* , 025005.

Immerzeel, W.W., van Beek, L.P.H. & Bierkens, M.F.P. (2010). Climate change will affect the asian water towers. *Science, 328* , 1382-1385.

Ise, T., Dunn, A.L., Wofsy, S.C. & Moorcroft, P.R. (2008). High sensitivity of peat decomposition to climate change through water-table feedback. *Nat. Geosci., 1* , 763-766.

Kato, T., Tang, Y., Gu, S., Hirota, M., Du, M., Li, Y. *et al.*(2006). Temperature and biomass influences on interannual changes in CO_2 exchange in an alpine meadow on the Qinghai-Tibetan Plateau. *Glob. Change Biol., 12* , 1285-1298.

Knowles, J.F., Blanken, P.D. & Williams, M.W. (2015). Soil respiration variability across a soil moisture and vegetation community gradient within a snow-scoured alpine meadow. *Biogeochemistry, 125* , 185-202.

Korkiakoski, M., Tuovinen, J.-P., Penttila, T., Sarkkola, S., Ojanen, P., Minkkinen, K. *et al.* (2019). Greenhouse gas and energy fluxes in a boreal peatland forest after clear-cutting. *Biogeosciences, 16* , 3703-3723.

Kottek, M., Grieser, J., Beck, C., Rudolf, B. & Rubel, F. (2006). World map of the Koppen-Geiger climate classification updated. *Meteorol. Zeitschrift, 15* , 259-263.

Kurylyk, B.L., MacQuarrie, K.T.B. & McKenzie, J.M. (2014). Climate change impacts on groundwater and soil temperatures in cold and temperate regions: Implications, mathematical theory, and emerging simulation tools. *Earth-Sci. Rev., 138* , 313-334.

Kwon, M.J., Natali, S.M., Hicks Pries, C.E., Schuur, E.A.G., Steinhof, A., Crummer, K.G. *et al.* (2019). Drainage enhances modern soil carbon contribution but reduces old soil carbon contribution to ecosystem respiration in tundra ecosystems. *Glob. Change Biol., 25,* 1315-1325.

Lawrence, D.M., Koven, C.D., Swenson, S.C., Riley, W.J. & Slater, A.G. (2015). Permafrost thaw and resulting soil moisture changes regulate projected high-latitude CO_2 and CH4 emissions.*Environ. Res. Lett., 10* , 094011.

Li, H., Zhang, F., Li, Y., Wang, J., Zhang, L., Zhao, L. *et al.*(2016). Seasonal and inter-annual variations in CO_2fluxes over 10 years in an alpine shrubland on the Qinghai-Tibetan Plateau, China. *Agric. For. Meteorol., 228* , 95-103.

Li, H., Zhu, J., Zhang, F., He, H., Yang, Y., Li, Y. *et al.*(2019). Growth stage-dependant variability in water vapor and CO_2 exchanges over a humid alpine shrubland on the northeastern Qinghai-Tibetan Plateau. *Agric. For. Meteorol., 268* , 55-62.

Li, X. (2019). Integrated hydrometeorological – snow – frozen ground observations in the alpine region of the Heihe River Basin, China. Cold and Arid Regions Science Data Center at Lanzhou (CARD). https://doi.org/10.3972/hiwater.001.2019.db.

Li, X., Cheng, G., Ge, Y., Li, H., Han, F., Hu, X. *et al.* (2018). Hydrological cycle in the Heihe River basin and its implication for water resource management in endorheic basins. *J. Geophys. Res., 123* , 890-914.

Liljedahl, A.K., Boike, J., Daanen, R.P., Fedorov, A.N., Frost, G.V., Grosse, G. *et al.* (2016). Pan-Arctic ice-wedge degradation in warming permafrost and its influence on tundra hydrology. *Nat. Geosci., 9* , 312-318.

Lin, X., Zhang, Z., Wang, S., Hu, Y., Xu, G., Luo, C. *et al.*(2011). Response of ecosystem respiration to warming and grazing during the growing seasons in the alpine meadow on the Tibetan plateau.*Agric. For. Meteorol., 151* , 792-802.

Liu, D., Li, Y., Wang, T., Peylin, P., MacBean, N., Ciais, P. *et al.* (2018). Contrasting responses of grassland water and carbon exchanges to climate change between Tibetan Plateau and Inner Mongolia.*Agric. For. Meteorol., 249* , 163-175.

Liu, J., Zhang, Z., Xu, X., Kuang, W., Zhou, W., Zhang, S. *et al.*(2010). Spatial patterns and driving forces of land use change in China during the early 21st century. *J. Geogr. Sci., 20* , 483-494.

Liu, S, Xu, Z, Wang, W, Jia, Z, Zhu, M, Bai, J. *et al.* (2011). A comparison of eddy-covariance and large aperture scintillometer measurements with respect to the energy balance closure problem.*Hydrol. Earth Syst. Sci., 15* , 1291-1306.

Liu, S., Li, X., Xu, Z., Che, T., Xiao, Q., Ma, M. *et al.* (2018). The Heihe integrated observatory network: A basin-scale land surface processes observatory in China. *Vadose Zone J., 17* . https://doi.org/10.2136/vzj2018.04.0072

Luan, J., Liu, S., Wu, J., Wang, M. & Yu, Z. (2018). The transient shift of driving environmental factors of carbon dioxide and methane fluxes in Tibetan peatlands before and after hydrological restoration.*Agric. For. Meteorol., 250-251* , 138-146.

Lv, W., Luo, C., Zhang, L., Niu, H., Zhang, Z., Wang, S. *et al.*(2020). Net neutral carbon responses to warming and grazing in alpine grassland ecosystems. *Agric. For. Meteorol., 280,* 107792.

Manzoni, S. & Porporato, A. (2007). A theoretical analysis of nonlinearities and feedbacks in soil carbon and nitrogen cycles.*Soil Biol. Biochem., 39* , 1542-1556.

Marchenko, S.S., Gorbunov, A.P. & Romanovsky, V.E. (2007). Permafrost warming in the Tien Shan Mountains, Central Asia. *Glob. Planet. Change, 56* , 311-327.

Marcolla, B., Cescatti, A., Manca, G., Zorer, R., Cavagna, M., Fiora, A.*et al.* (2011). Climatic controls and ecosystem responses drive the inter-annual variability of the net ecosystem exchange of an alpine meadow. *Agric. For. Meteorol., 151* , 1233-1243.

McVeigh, P., Sottocornola, M., Foley, N., Leahy, P. & Kiely, G. (2014). Meteorological and functional response partitioning to explain interannual variability of CO_2 exchange at an Irish Atlantic blanket bog. *Agric. For. Meteorol., 194* , 8-19.

Moyano, F.E., Manzoni, S. & Chenu, C. (2013). Responses of soil heterotrophic respiration to moisture availability: An exploration of processes and models. *Soil Biol. Biochem., 59* , 72-85.

Myneni, R., Knyazikhin, Y. & Park, T. (2015). MCD15A3H MODIS/Terra+Aqua Leaf Area Index/FPAR 4-day L4 Global 500m SIN Grid V006. *NASA EOSDIS Land Processes DAAC* . http://doi.org/10.5067/MODIS/MCD15A3H.006.

Natali, S.M., Schuur, E.A.G., Trucco, C., Hicks Pries, C.E., Crummer, K.G. & Baron Lopez, A.F. (2011). Effects of experimental warming of air, soil and permafrost on carbon balance in Alaskan tundra.*Glob. Change Biol., 17* , 1394-1407.

Olivas, P.C., Oberbauer, S.F., Tweedie, C.E., Oechel, W.C. & Kuchy, A. (2010). Responses of CO_2 flux components of Alaskan Coastal Plain tundra to shifts in water table. *J. Geophys. Res., 115* . https://doi.org/10.1029/2009jg001254

Papale, D., Reichstein, M., Aubinet, M., Canfora, E., Bernhofer, C., Kutsch, W. *et al.* (2006). Towards a standardized processing of Net Ecosystem Exchange measured with eddy covariance technique: algorithms and uncertainty estimation. *Biogeosciences, 3* , 571-583.

Piao, S., Tan, K., Nan, H., Ciais, P., Fang, J., Wang, T. *et al.*(2012). Impacts of climate and CO_2 changes on the vegetation growth and carbon balance of Qinghai–Tibetan grasslands over the past five decades. *Glob. Planet. Change, 98-99* , 73-80.

Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P. *et al.* (2005). On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. *Glob. Change Biol., 11* , 1424-1439.

Schadel, C., Bader, M.K.F., Schuur, E.A.G., Biasi, C., Bracho, R., Capek, P. *et al.* (2016). Potential carbon emissions dominated by carbon dioxide from thawed permafrost soils. *Nat. Clim. Change, 6,* 950-953.

Scholz, K., Hammerle, A., Hiltbrunner, E. & Wohlfahrt, G. (2018). Analyzing the effects of growing season length on the net ecosystem production of an alpine grassland using model–data fusion.*Ecosystems, 21* , 982-999.

Stover, H. J. & Henry, H. A. L. (2019). Interactions between soil heterogeneity and freezing: Implications for grassland plant diversity and relative species abundances. *Glob. Change Biol., 25* , 2275-2284.

Sun, S., Che, T., Li, H., Wang, T., Ma, C., Liu, B. *et al.*(2019). Water and carbon dioxide exchange of an alpine meadow ecosystem in the northeastern Tibetan Plateau is energy-limited. *Agric. For. Meteorol., 275* , 283-295.

Swindles, G.T., Morris, P.J., Mullan, D.J., Payne, R.J., Roland, T.P., Amesbury, M.J. *et al.* (2019). Widespread drying of European peatlands in recent centuries. *Nat. Geosci., 12* , 922-928.

Virkkala, A.-M., Virtanen, T., Lehtonen, A., Rinne, J. & Luoto, M. (2017). The current state of CO_2 flux chamber studies in the Arctic tundra. *Prog. Phys. Geogr., 42* , 162-184.

Walvoord, M. A. & Kurylyk, B. L. (2016). Hydrologic impacts of thawing permafrost — A review. *Vadose Zone J., 15* . https://doi.org/10.2136/vzj2016.01.0010

Walvoord, M.A., Voss, C.I. & Wellman, T.P. (2012). Influence of permafrost distribution on groundwater flow in the context of climate-driven permafrost thaw: Example from Yukon Flats Basin, Alaska, United States. *Water Resour. Res., 48* , 7.

Wang, H., Liu, H., Cao, G., Ma, Z., Li, Y., Zhang, F. *et al.*(2020). Alpine grassland plants grow earlier and faster but biomass remains unchanged over 35 years of climate change. *Ecol Lett, 23* , 701-710.

Wang, L., Liu, H., Sun, J. & Shao, Y. (2017). Biophysical effects on the interannual variation in carbon dioxide exchange of an alpine meadow on the Tibetan Plateau. *Atmospheric Chem. Phys., 17* , 5119-5129.

Wang, Q., Lv, W., Li, B., Zhou, Y., Jiang, L., Piao, S. *et al.*(2019). Annual ecosystem respiration is resistant to changes in freeze – thaw periods in semi-arid permafrost. *Glob. Change Biol., 26* , 2630-2641.

Wilson, R.M., Hopple, A.M., Tfaily, M.M., Sebestyen, S.D., Schadt, C.W., Pfeifer-Meister, L. *et al.* (2016). Stability of peatland carbon to rising temperatures. *Nat. Commun., 7,* 13723.

Wu, G.-L., Ren, G.-H., Wang, D., Shi, Z.-H. & Warrington, D. (2013). Above- and below-ground response to soil water change in an alpine wetland ecosystem on the Qinghai-Tibetan Plateau, China. *J. Hydrol., 476* , 120-127.

Wu, Q. & Zhang, T. (2008). Recent permafrost warming on the Qinghai-Tibetan Plateau. *J. Geophys. Res., 113* , D13.

Wutzler, T., Lucas-Moffat, A., Migliavacca, M., Knauer, J., Sickel, K., Šigut, L. *et al.* (2018). Basic and extensible post-processing of eddy covariance flux data with REddyProc. *Biogeosciences, 15* , 5015-5030.

Xue, X., Guo, J., Han, B., Sun, Q. & Liu, L. (2009). The effect of climate warming and permafrost thaw on desertification in the Qinghai–Tibetan Plateau. *Geomorphology, 108* , 182-190.

Yan, Z., Bond-Lamberty, B., Todd-Brown, K.E., Bailey, V.L., Li, S., Liu, C. *et al.* (2018). A moisture function of soil heterotrophic respiration that incorporates microscale processes. *Nat. Commun., 9* , 2562.

Yang, K., Wu, H., Qin, J., Lin, C., Tang, W. & Chen, Y. (2014). Recent climate changes over the Tibetan Plateau and their impacts on energy and water cycle: A review. *Glob. Planet. Change, 112* , 79-91.

Yu, L., Wang, H., Wang, Y., Zhang, Z., Chen, L., Liang, N. *et al* . (2020). Temporal variation in soil respiration and its sensitivity to temperature T along a hydrological gradient in an alpine wetland of the Tibetan Plateau. *Agric. For. Meteorol., 282-283* , 107854.

Yurova, A., Wolf, A., Sagerfors, J. & Nilsson, M. (2007). Variations in net ecosystem exchange of carbon dioxide in a boreal mire: Modeling mechanisms linked to water table position. *J. Geophys. Res., 112,*G2.

Zhang, T., Zhang, Y., Xu, M., Zhu, J., Chen, N., Jiang, Y. *et al.*(2018). Water availability is more important than temperature in driving the carbon fluxes of an alpine meadow on the Tibetan Plateau.*Agric. For. Meteorol., 256-257* , 22-31.

Zhang, Y., Parazoo, N.C., Williams, A.P., Zhou, S. & Gentine, P. (2020). Large and projected strengthening moisture limitation on end-of-season photosynthesis. *Proc. Natl Acad. Sci. USA* , 117, 9216-9222.

Zhao, L., Ping, C.-L., Yang, D., Cheng, G., Ding, Y. & Liu, S. (2004). Changes of climate and seasonally frozen ground over the past 30 years in Qinghai–Xizang (Tibetan) Plateau, China. *Glob. Planet. Change, 43* , 19-31.

Zhu, Y., Irmak, S., Jhala, A. J., Vuran, M.C. & Diotto, A. (2019). Time-domain and frequency-domain reflectomenyry type soil soil moisture sensor performace and soil temperature effects in fine-and coarse-textured soils. *Appl. Eng. Agric., 35* , 117-134.

Zona, D., Lipson, D.A., Zulueta, R.C., Oberbauer, S.F. & Oechel, W.C. (2011). Microtopographic controls on ecosystem functioning in the Arctic Coastal Plain. *J. Geophys. Res., 116,* G4.

Figures

Fig. 1 Location of the study area and eddy covariance sites (a), the alpine meadow ecosystem landscape (b), and soil measured profiles at Dashalong (c) and Arou (d, modified from Fig. 6a in Che *et al.* 2019).

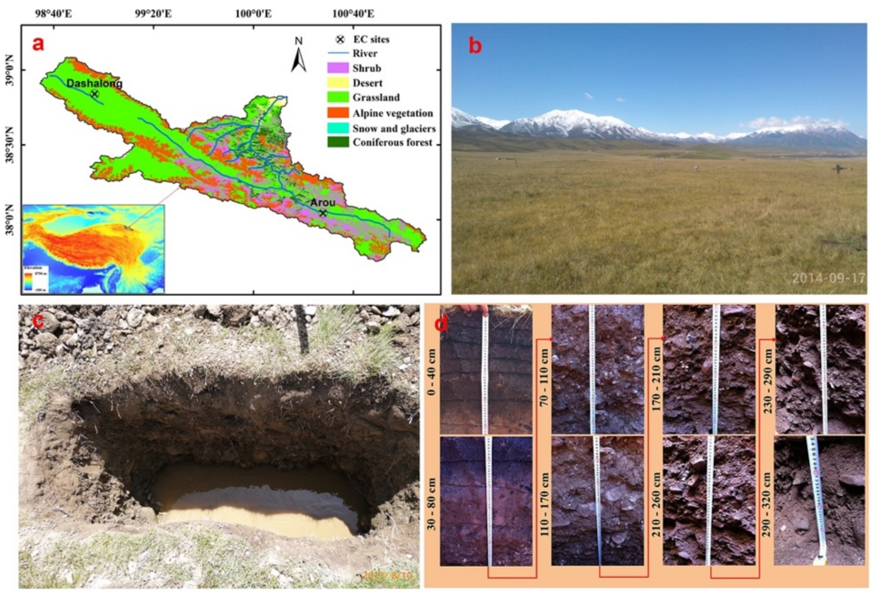


Fig. 2 Daily GPP (a), Re (b), NEE (c), and CSE (d) at the sites during 2013-2017. The CSE was calculated during the unfrozen seasons of the sites. A weekly moving-average was applied.

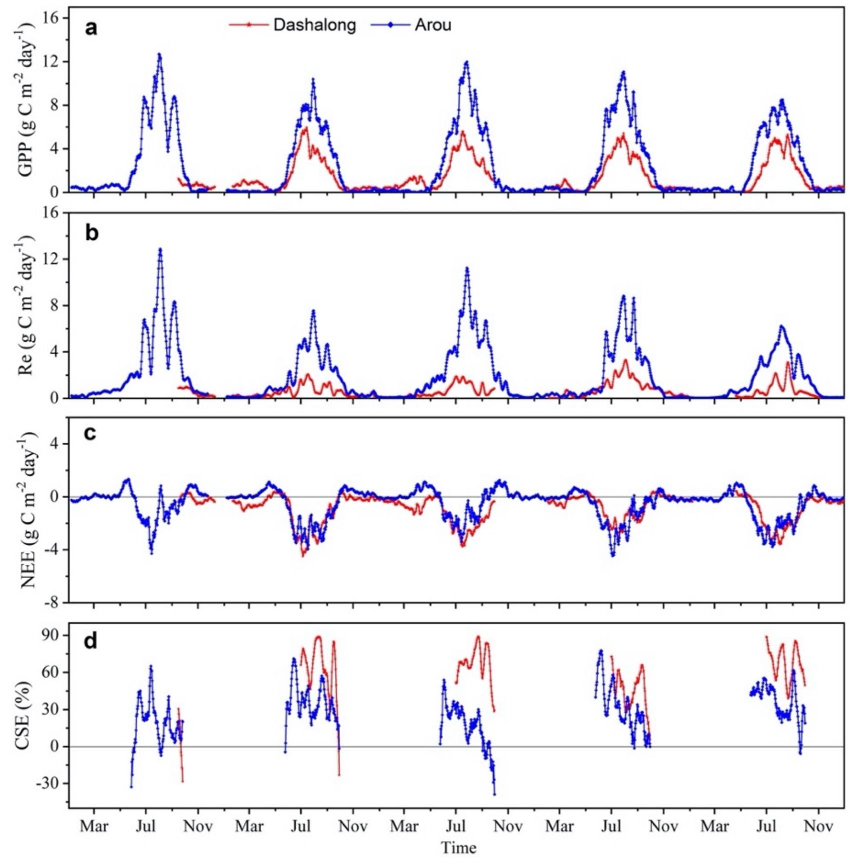


Fig. 3 Comparisons between daily Re and daily mean soil moisture profile at Dashalong (top) and Arou (bottom) during 2013-2017. A weekly moving-average was applied to the Re series. Gray strips indicated data gaps.

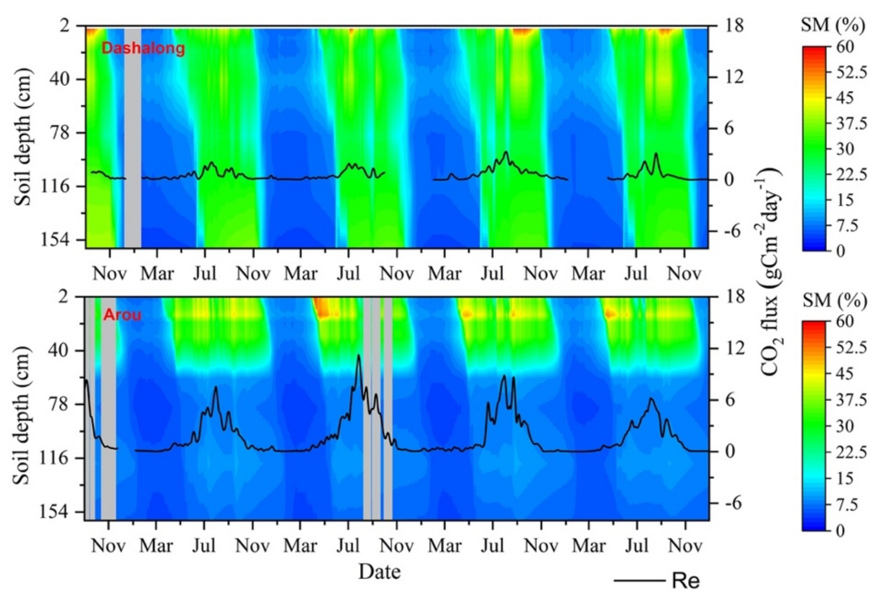


Fig. 4 Comparisons between daily carbon fluxes and daily mean soil temperature profile at Dashalong (top) and Arou (bottom) during 2013-2017. A weekly moving-average was applied to the Re series. Gray strips indicated data gaps.

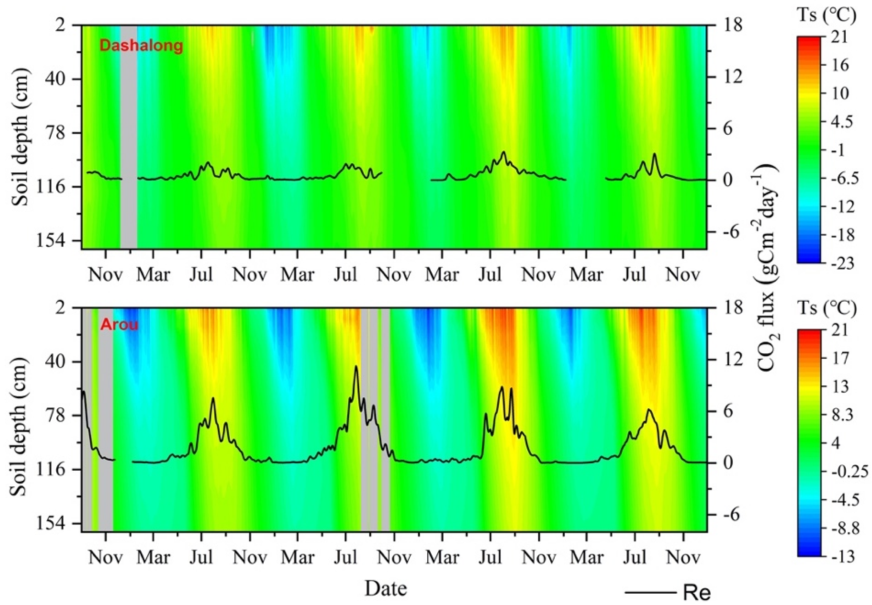
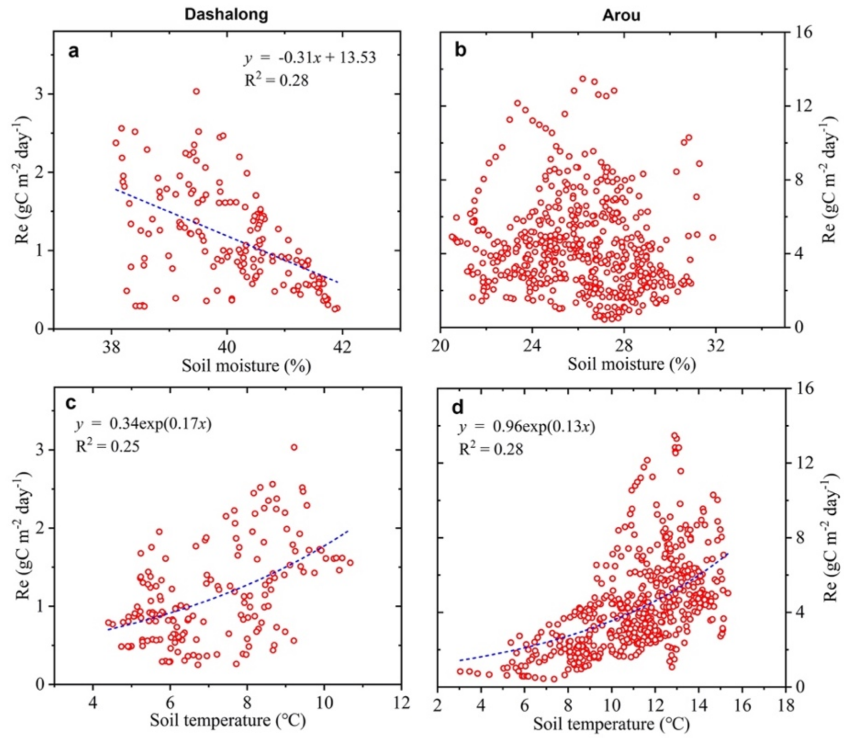


Fig. 5 Relationships between the nearly-saturated SM (> 0.38) at 40 cm depth and Re at Dashalong (a), and between the corresponding ST and Re (c). Relationships between the SM at 40 cm depth and Re at Arou (b), and between the corresponding ST and Re (d).



Tables

Table 1 Results of linear mixed-effects models for the effects of SM and ST on Re during the unfrozen seasons at Dashalong site.

Soil depth (cm)	Explanatory variable	Estimate	Standard error	Degrees of freedom	t value	p value
4	SM	-0.003	0.006	3.660	-0.561	0.607
	ST	0.041	0.014	4.359	2.967	0.037 *
10	SM	-0.004	0.008	5.684	-0.513	0.627
	ST	0.057	0.007	8.047	7.746	< 0.001 *
20	SM	-0.003	0.009	4.332	-0.379	0.722
	ST	0.063	0.010	4.626	6.104	0.002 *
40	SM	-0.006	0.007	5.550	-0.861	0.425
	ST	0.053	0.025	4.231	2.180	0.091
80	SM	-0.012	0.010	3.775	-1.265	0.278
	ST	-0.015	0.052	3.946	-0.285	0.790
120	SM	-0.049	0.012	4.340	-4.199	0.011 *
	ST	-0.085	0.125	4.366	-0.684	0.529
160	SM	-0.107	0.019	16.595	-5.614	< 0.001
	ST	-0.018	0.041	6.519	-0.430	0.681

* indicates a significant level of $p < 0.05$