Radiation, soil water content, and temperature effects on carbon cycling in an alpine swamp meadow of the northeastern Qinghai-Tibetan Plateau

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Abstract. Predicted intensified climate warming will likely alter the ecosystem net carbon (C) uptake of the Qinghai-Tibetan Plateau (QTP). Variations in C sink/source responses to climate warming have been linked to water availability; however, the mechanisms by which net C uptake responds to soil water content in saturated swamp meadow ecosystems remain unclear. To explore how soil moisture and other environmental drivers modulate net C uptake in the QTP, field measurements were conducted using the eddy covariance technique in 2014, 2015, 2017, and 2018. The alpine swamp meadow presented in this study was a persistent and strong C sink of CO_2 (-168.0 ± 62.5 g C m^{-2} y^{-1}, average ± standard deviation) across the entire 4-year study period. A random forest machine-learning analysis suggested that the diurnal and seasonal variations of net ecosystem exchange (NEE) and gross primary productivity (GPP) were regulated by temperature and net radiation. Ecosystem respiration (Re), however, was found mainly regulated by the variability of soil water content (SWC) at different temporal aggregations, followed by temperature, the second contributing driver. We further explored how Re is controlled by nearly saturated soil moisture and temperature comparing two different periods featuring almost identical temperatures and significant differences on SWC and vice versa. Our data suggest that, despite the relatively abundant

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water supply, periods with a substantial decrease of SWC or increase of temperature produced higher Re and therefore weakened the C sink strength. Our results reveal that nearly saturated soil conditions during the growing seasons can help maintain lower ecosystem respiration rates and thus enhance the overall C sequestration capacity in this alpine swamp meadow. We argue that soil respiration and subsequent ecosystem C sink magnitude in alpine swamp meadows could likely be affected by future changes in soil hydrological conditions caused by permafrost degradation or accelerated thawing-freezing cycling due to climate warming.

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1. Introduction

Wetlands play a significant role in the global carbon (C) cycle due to a large amount of C stored in their soils. The Qinghai-Tibetan Plateau (QTP), with an average altitude of over 4,000 m a.s.l., has approximately 10×10^4 km^2 of natural wetlands, of which ~ 50% (4.9×10^4 km^2) are alpine swamp meadows. These ecosystems are predominantly located in permafrost areas and are typically soil nutrient-rich and water-logged (Bai et al., 2019; Zhao et al., 2005). Climate change and human disturbance can have profound consequences on permafrost regions (Biskaborn et al., 2019) and significantly impact their hydrological regimes (Lafrenière and Lamoureux, 2019). Hydrological regimes have an important role in controlling wetland functioning (Bohn et al., 2007; Christensen et al., 2003), and the changes of hydrological regimes may put the wetland functioning of the QTP under pressure (Hruby, 1999; Woodward and Wui, 2001; Foti et al., 2013).

The QTP is forecasted to be warmer and wetter in the future (Chen et al., 2015; Cheng et al., 2011). Warming may accelerate the microbial breakdown of alpine soil organic C and subsequently increase CO_2 emissions (Zhu et al., 2015a). Warming could also improve C sequestration capacity by enhancing the photosynthetic inputs and growth rates of alpine plants (Fu et al., 2015). Therefore, the potential increase of CO_2 emissions due to warming in alpine regions could be partially offset by enhanced C uptake (Schuur et al., 2009), triggering different net C uptake responses to climate warming. For example, an increase in temperature in the QTP has been associated with net C sinks in the Zoige alpine wetlands (Kang et al., 2014) but also with net C sources in the Damxung alpine swamp meadow (Niu et al., 2017).

According to recent studies in QTP alpine grasslands, water conditions such as soil water content (SWC) can be a key factor that changes water-use patterns and ecophysiological characteristics of alpine plants (Wu et al., 2019) and modulate the warming-mediated increase of ecosystem C uptake (Ganjurjav et al. 2016; Peng et al. 2014). Ecosystem C processes such as net C uptake and soil respiration may increase with SWC in dry environments, but decrease with SWC in water-logged environments (Quan et al., 2019; Taylor et al., 2017). Warming in conjunction with increased precipitation can turn an ecosystem from net source to a sink of C (Zhao et al., 2019), increasing both photosynthesis and respiration rates during warmer and wetter years (López-Blanco et al., 2017, 2018). However, when warming occurs in soils associated with low moisture, soil drought can change ecosystems from C sinks to sources (Ganjurjav et al., 2017). Studies in QTP alpine meadows have indicated that warming significantly stimulates ecosystem net C uptake in wet years but does not affect ecosystem net C uptake in dry years, because the positive effects of warming on net C uptake are compensated by the negative effects of lower soil moisture (Peng et al., 2014).

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However, the existing studies concerning ecosystem C dynamics on the QTP mainly focused on alpine meadows (Saito et al., 2009; Zhao et al., 2005, 2010; Zhu et al., 2015b), only a few analyses have been conducted to specifically characterize C dynamics in alpine swamp meadows (Zhao et al., 2010; Qi et al., 2021; Liu et al., 2020; Zhu et al., 2020). The magnitudes and interannual variations of net ecosystem exchange (NEE) in alpine wetlands from the QTP are proved to be closely related to radiation, precipitation, and temperature (Cao et al., 2017; Niu et al., 2017). Temperature has been identified as an important driver for ecosystem respiration (Re) in alpine swamp meadows, and Zhao et al. (2005, 2010) found that Re follows an exponential relationship with soil temperature. Other studies also noticed that rainfall is an important determinant of the interannual C sink/source strength in alpine swamp meadows (Liu et al., 2019; Zhu et al. 2020). For example, CO_2 emissions were reported to decrease notably after rain events (Zhao et al., 2010). Even though alpine swamp meadow ecosystems are characterised by high SWC, the role of SWC on C cycling has often been neglected or assumed to be less important. Compared to other factors, the effects of SWC on the net C uptake in alpine swamp meadows are still unclear. Climate warming and the associated enhanced evapotranspiration and permafrost degradation may change soil hydrology dramatically (Andresen et al., 2020; Zhao et al., 2019). Considering the critical role that SWC played in regulating C uptake and soil respiration of other ecosystem types (Ganjurjav et al. 2016; Peng et al., 2014; Quan et al., 2019; Taylor et al., 2017; Wu et al., 2019), it is important to understand whether the change of SWC would aggravate the saturated water stress or trigger drought effects on net C uptake in the alpine swamp meadow ecosystem under future climate warming.

These uncertainties require a detailed investigation to understand wetland C source/sink processes and their potential future C sink strength variations (sign and magnitude). In addition, as compared with alpine meadows, there still needs long-term continuous observations for the alpine swamp meadow to investigate C dynamics during dry and wet years. So a four-year field observation dataset is provided in this study to characterize and quantify the importance of SWC in addition to temperature and net radiation on the C sink strength of an alpine swamp meadow. Therefore, the objectives of this study are to (i) quantify the diurnal and seasonal variations of net ecosystem exchange (NEE), gross primary productivity (GPP), and ecosystem respiration (Re), (ii) identify and quantify the relative importance of different key environmental drivers contributing to the variability observed of NEE, Re, and GPP, and (iii) analyse how these C fluxes respond to soil water availability, temperature, and radiation variation in a QTP alpine swamp meadow. This study would provide new insights into better understanding of the complex C cycle dynamics in the Tibetan Plateau driven by the almost certain future intensified climate warming.

2. Materials and methods

2.1 Site description

The study site (37°35.75′ N, 100°00.47′ E, 3,571 m a.s.l.) is located in Gangcha County, Qinghai Province, in the north-eastern part of the QTP (Fig. 1(a)). The mean annual temperature and precipitation measured at the Gangcha National Weather Station were 0.1 °C and 389.4 mm between 1982 and 2011, respectively (Zhang et al., 2016). The site area has seasonal permafrost featuring frozen soils between January–March and November–December for a total of about 125–135 days (Zhang et al., 2014). The dominant species of the alpine swamp meadow ecosystem is *Kobresia pygmaea*, companied by *Saussurea pulchra*, *Polygonum viviparum*, and *Potentilla saundersiana.* The average plant height at the experimental site is 7.4 ± 1.5 cm, with a 97 ± 2% coverage. Our study defined the growing season as the period between June and September. The early (June–July) and late (August–September) growing

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seasons, as they will be henceforth referred to, correspond with the early growing season and late growing seasons, respectively.

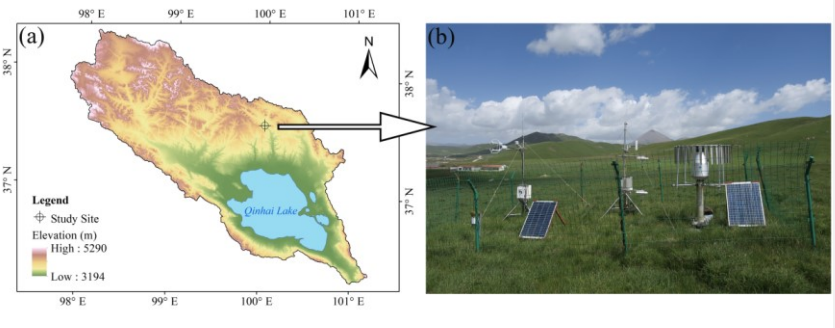

Figure 1. (a) Location of the study site in the Qinghai Lake basin in the northeastern part of the QTP. (b) Eddy covariance system measuring water and CO_2 fluxes between the land surface and the atmosphere in the alpine swamp meadow.

2.2 Field measurements

An Eddy Covariance (EC) system was installed at the study site (Fig. 1b) to measure the CO_2 fluxes at a sampling frequency of 10 Hz from 2014 to 2018. Data for 2016 was missing due to equipment malfunction. The EC system included an open-path CO_2/H_2O infrared gas analyser, which quantified fluctuations in water vapour and CO_2 fluxes. A 3-D sonic anemometer was installed at a 2.0 m height above ground to directly measure horizontal and vertical wind velocity components (u, v, and w). C flux data were recorded with a data logger (Campbell Scientific Inc.). An automated meteorological station was installed near the EC station to measure meteorological variables such as air temperature (Ta; °C), precipitation (P; mm), net radiation (Rn; W m^{-2}), wind speed (WS; m s^{-1}), wind direction (WD; º), relative humidity (RH; %), and vapour pressure deficit (VPD; hPa). The meteorological data were collected at one-minute intervals and subsequently resampled at 30-minute timesteps to keep pace with the EC data. More details on the in-situ instrument specifications are summarised in Table 1.

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Table 1 Information about the sensors installed in the alpine swamp meadow.

	Sensor Names	Sensor type	Installation height/depth	Manufacturer
Eddy Covariance	Open-path CO_2/H_2O infrared gas analyser	EC150	2.0 m	Campbell, US

	Three-dimensional sonic anemometer	CSAT3	2.0 m	Campbell, US
Meteorological observation	Net radiation	NR Lite	1.8 m	Kipp&Zonen, Netherlands
	Wind speed/direction	034B	2m	
	Air temperature/humidity	083E-1-6	0.5 m, 1.5 m	MetOne, US
	Atmosphere pressure	PTB110	In data acquisition box	Vaisala, Finland
	Rain-gauge	7852M-AB	0.7 m	Davis, US

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Soil water content (SWC; %) were measured at depths of 10, 20, 40, 60, and 100 cm from the soil surface with EC-H_2O sensors (Decagon Devices, USA) at a 10-minute recording frequency. The precision of the EC-H_2O sensors for soil moisture measurements was ± 0.03 m^3 m^{-3}. As the roots of *Kobresia* meadows are mainly distributed within the top 20 cm of soil, we focused only on the variation of SWC in the top 20 cm of the soil.

2.3 Eddy Covariance data processing

The half-hourly NEE data was calculated using the EddyPro software (version 5.2, LI-COR) from the 10-Hz raw data. During the calculation, three-dimensional rotation was used to correct the data by removing the effects of instrument tilt irregularity on airflow (Wilczak et al., 2001). Webb, Pearman, and Leuning (WPL) (Webb et al., 1980) correction was applied to calculate the averages of CO_2 covariance, rectifying the air density variations induced by heat and water vapour. The half-hourly flux data were quality-checked based on several filtering algorithms, including: (1) the rejection of outliers in sonic temperature, water vapour density, and CO_2 density (Li et al. 2008; Liu et al., 2011), (2) the elimination of data one hour before and after precipitation events (Li et al. 2008; Liu et al., 2011), (3) the removal of negative NEE during the non-growing season (from November to March) (Cao et al., 2017; Qi et al., 2021) attributed to the self-heating effect from EC instruments (Cao et al., 2017), and (4) the exclusion of measurements with weak turbulence conditions at night time. The weak turbulence periods were identified by bootstrapping friction velocity (u^*) thresholds, as described by Papale et al. (2006). This approach effectively divided the data into 4-year and 7-temperature subsets with similar micro-meteorological conditions (except for u~~*~~). The u~~*~~ thresholds (5%, 50%, and 95% of bootstrapping) were calculated specifically per year and temperature subset.

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Based on those different subsets, we gap-filled and partitioned NEE (into GPP and Re) to spread the uncertainty variability that emerged from the different u* thresholds, similar to López-Blanco et al. (2017). All missing data were marked as -9999 (no data). Negative and positive NEE values represent sink and source of C, respectively. Additionally, a standardised mechanism to fill NEE gaps is needed for adequate data processing (Moffat et al., 2007). Therefore, this study adopted the method described by López-Blanco et al. (2020) using the marginal distribution sampling (MDS) algorithm in the REddyProc gap-filling tool (Reichstein et al., 2016), which was readapted from Reichstein et al. (2005). Finally, NEE was separated into GPP and Re by applying the REddyProc partitioning algorithm (Reichstein et al., 2016) for further analyses. This partitioning method is based on the exponential regression of night-time respiration with temperature using the Lloyd-Taylor-Function (Lloyd and Taylor, 1994). Night-time periods were selected via current combined solar radiation and potential radiation thresholds based on the exact solar time, latitude, and longitude. REddyProc estimates the temperature sensitivity from a short-term period, and based on this short-term temperature sensitivity, it estimates the reference temperature in the continuous period of the entire dataset. These estimates were then used to calculate Re for day-time and night-time, while GPP was estimated based on the difference between NEE and Re.

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2.4 Identifying the importance of environmental drivers

In order to characterize how environmental conditions impact diurnal and seasonal variability of NEE, GPP and Re at this alpine swamp meadow, we used a novel method based on machine learning. Random forest (Breiman, 2001) is a machine learning technique that can be used to quantify and interpret the contribution of environmental drivers (covariates) to the variability of different C fluxes (response variables) by combining multiple individual regression trees. This technique has been increasingly utilized to upscale global C fluxes from eddy covariance data (Zeng et al., 2020) but also to evaluate controls on C cycle processes (Zhang et al., 2017; López-Blanco et al., 2017, 2020). Here, we calculate the relative importance of air temperature (Ta), net radiation (Rn), soil water content (SWC) and vapour pressure deficit (VPD) controlling the C sink strength, photosynthesis, and respiration variability. This random forest algorithm constructs multiple (1000 in this analysis) decision trees during training time with different random subsamples (with replacement) from the same input training dataset. In each cluster classified by random forest, the algorithm generates a multiple linear regression to characterize

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different C fluxes as a function of environmental drivers (López-Blanco et al., 2017, 2020). This algorithm version (Pedregosa et al., 2011) estimates the relative importance of each covariate between 0 and 100%, which correspond to the fraction of decision participating during data clustering. We used the random forest algorithm to evaluate the diurnal and seasonal patterns of the relative importance of Ta, Rn, SWC, and VPD responsible for the variability of C fluxes. We used data from the June-September period aggregated per hour, and we ran multiple random forests with growing season data binned per hour of the day, day of the year and yearly, respectively (Table S1).

Since C fluxes are affected by plant phenology and climate factors, including temperature, soil moisture, and radiation simultaneously, to analyze the effect of a single factor, ideally, other factors need to be identical or at least closed (no significant differences). In each comparison, data of the same period in each year were selected to exclude the influence of plant phenology. To further analyse the effect of soil moisture, radiation, and temperature on C fluxes, we selected a specific group of data for further evaluation other than the entire observation time. The group of data contains two late growing season periods: periods with a significant difference in SWC but almost identical Ta and Rn (i.e., late growing season of 2014 vs 2015) and periods with a significant difference in Ta but almost identical SWC and Rn (i.e., late growing season of 2014 vs 2018). Additionally, in order to analyse the effect of annual temperature on C fluxes, we selected a group of time stamps with significant differences in Ta but almost identical SWC and Rn (i.e., 2017 vs 2014, and 2018 vs 2014). The magnitude of the differences between C fluxes in the same group were analysed by the independent-sample T-test method.

3. Results

3.1 Meteorological variability

Mean daily meteorological variables (including Ta, P, SWC, and Rn) exhibited evident seasonal variability except for VPD; these variables increased progressively in the early growing seasons, reached their maximum in July and decreased gradually afterwards (Fig. 2(a), (b), (c), (d)). Air temperature during the growing season was 7.7 ± 2.6, 7.4 ± 2.6, 8.5 ± 2.9, and 9.2 ± 3.3 °C in 2014, 2015, 2017, and 2018, respectively while precipitation totalled 662.8, 521.4, 661.2, and 624.3 mm for the same years, falling primarily during the growing season. The precipitation measured during the late growing season of 2015 was only half of the amount measured in 2014, 2017, and 2018. The lower precipitation regime

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led to a marked decline in SWC, making the late growing season of 2015 the driest period among all growing seasons during the study period. The greatest difference in SWC occurred in the late growing season of 2014 and 2015, when Ta at the same period were very closed (Ta was 6.8 ± 2.6 and 6.8 ± 2.5℃ in 2014 and 2015, respectively). Compared to 2014, SWC decreased by 15.4% in the late growing season of 2015 (Fig. 2(b); Table S2). Meanwhile, SWC in the late growing season of 2014 and 2018 was almost identical (80.7 ± 4.1 and 80.8 ± 3.8, respectively), but the temperature difference was the largest (25%) compared to any other years (Fig. 2(a); Table S2).

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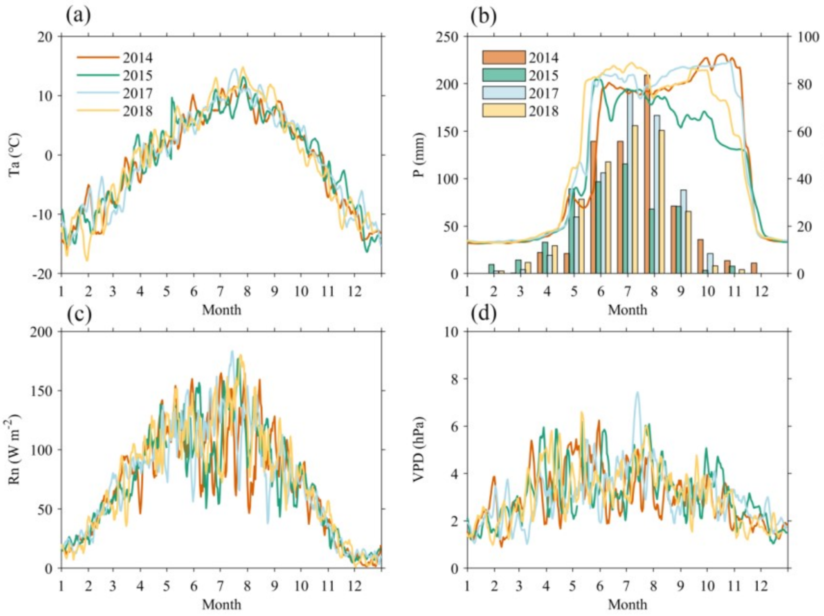

Figure 2. Five-day moving average meteorological variables (Ta, P, SWC, Rn, and VPD) in the studied swamp alpine meadow.

3.2 Diurnal and seasonal variability of CO_2 fluxes

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During the growing season, NEE (Fig. 3, (a1)–(d1)) and GPP (Fig. 3, (a3)–(d3)) featured a clear peak of the diurnal variations; both fluxes reached their summit between 12:00 and 14:00 local time. Re, however, presented a lower daily variability. The rates of NEE, Re, and GPP during the growing season averaged -2.3 ± 0.3, 3.2 ± 1.0, and 5.5 ± 0.9 µmol m^{-2} s^{-1}, respectively, for the entire study period (2014, 2015, 2017 and 2018). For the late growing seasons, the lowest rate of net C uptake was measured in

2015 (-10.0 μmol m^{-2} s^{-1}), whereas 2014 (-12.4 μmol m^{-2} s^{-1}), 2017 (-12.2 μmol m^{-2} s^{-1}), and 2018 (-12.5 μmol m^{-2} s^{-1}) exhibited more negative NEE values (i.e., stronger net C uptake rate). Between the late growing season in 2015 and the late growing seasons in 2014, 2017 and 2018, there was a significant difference in the rates of Re ($p<0.01$) while no significant difference was found in GPP variability ($p>0.05$), suggesting that Re may be the component causing the difference observed in NEE. Specifically, the rates of Re in the late growing season of 2014 and 2015 were 2.4 ± 0.2 and 3.0 ± 0.2 μmol m^{-2} s^{-1}, respectively, which indicated that the drier conditions in 2015 generated a 25% higher Re compared to 2014. In addition, the rate of Re in the late growing season was significantly higher in warmer 2018 (3.5 ± 0.2 μmol m^{-2} s^{-1}) than in 2014 (2.4 ± 0.2 μmol m^{-2} s^{-1}).

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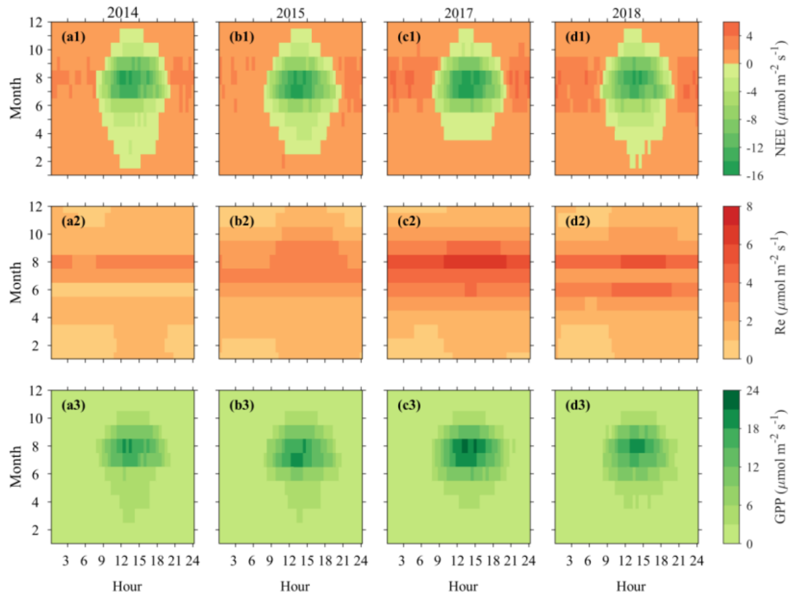

Figure 3. Diurnal variability of gap-filled NEE and partitioned Re and GPP in 2014, 2015, 2017 and 2018.

NEE, Re, and GPP also exhibited a strong seasonal variability; the C fluxes gradually increased from low values in early June to the maximum in the middle of the growing season (late July to early August on average), followed by a decrease towards the end of the growing season (Fig. 4(a), (b), (c)). The C sink strength across the growing season was found lowest in 2018, followed by 2017, whereas 2014 and 2015 exhibited relatively higher values (Fig. 4(a)). Notably, the accumulated Re in the late growing

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season was significantly higher in 2015 compared to 2014 ($P<0.05$), while there was no significant difference in GPP (Fig. 4(b); Table S2). Moreover, the late growing season of 2015 witnessed the lowest SWC while keeping the same Ta compared to the same period in 2014 (Fig. 2(b); Table S2). The substantial decline of SWC observed in 2015 appeared to be responsible for the weaker observed C sink strength. On the other hand, Ta in the late growing season of 2018 was the highest for the same period among all the years while the SWC remained the same as 2014 (Fig. 2(a)). The late growing season of 2018 showed overall higher GPP and Re, but lower net C uptake than 2014. Significantly higher Re in 2018 caused by higher temperatures eventually led to a decrease of the C sink capacity (Fig. 4(a), (b), (c); Table S2).

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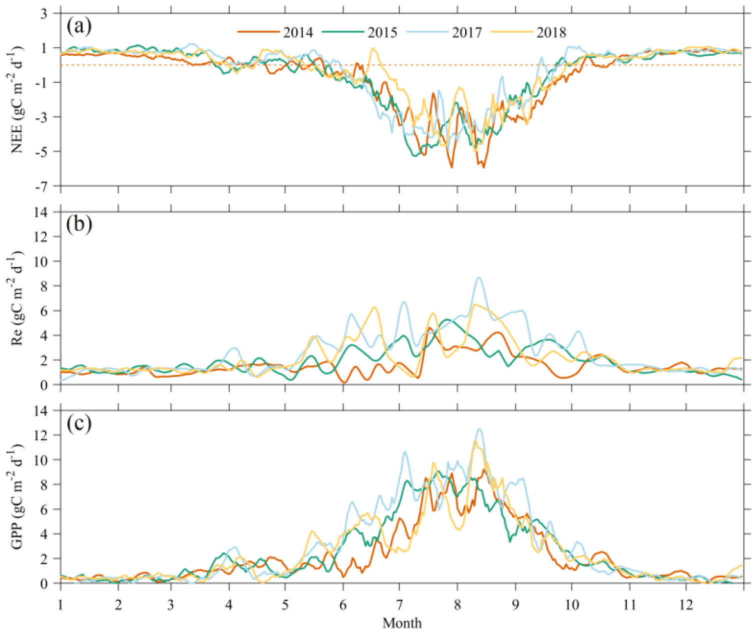

Figure 4. Seasonal variability of daily 5-day moving average daily NEE, Re, and GPP in the swamp alpine meadow.

3.3 The importance of environmental forcing controlling C fluxes

Our data processed by a machine learning technique suggest that the relative importance of the primary environmental drivers (Rn, Ta, VPD, and SWC) regulating C fluxes varies on different time scales (i.e., diurnal and seasonal scales) in this swamp meadow of the QTP (Fig. 5(a), (b), (c)). The diurnal variability

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of NEE and GPP was mostly driven by Ta (Fig. 5(a)), especially in the central hours of the day between 11:00 and 15:00, while Re showed a fairly lower temperature dependence compared to NEE and GPP (Fig. 5(a)). SWC was relatively more important than air temperature controlling the diurnal variability of respiration (Fig. 5(a)). The seasonal variability shaping the terrestrial C fluxes are regulated not only by meteorological variables but also by plant phenology. To separate the role of meteorological variables from phenology, we carried out a random forest analysis every fortnight and assumed that plant phenology changed little during this time span (Fig. 5(b); seasonal variability). The analyses based on random forest revealed a distinct seasonal pattern for different C fluxes from June to September, pointing to a marked contribution of net radiation over NEE and GPP (Fig. 5(b)). Re, however, was found mostly regulated by SWC. The contribution patterns of each environmental driver to the variations of C fluxes on inter-seasonal scale (Fig. 5(c)) are similar to the ones found at the seasonal scale (Fig. 5(b)). The inter-seasonal variability of NEE and GPP were explained clearly by Rn, while SWC revealed a stronger relative importance over Re. Overall, SWC dynamics seem to be the most important variable explaining the variability observed in the Re data, suggesting that soil moisture plays an essential role on diurnal and seasonal basis in this cold swamp meadow ecosystem. Note also that Ta played a secondary role in regulating Re at all assessed time scales (Fig. 5(a), (b), (c)).

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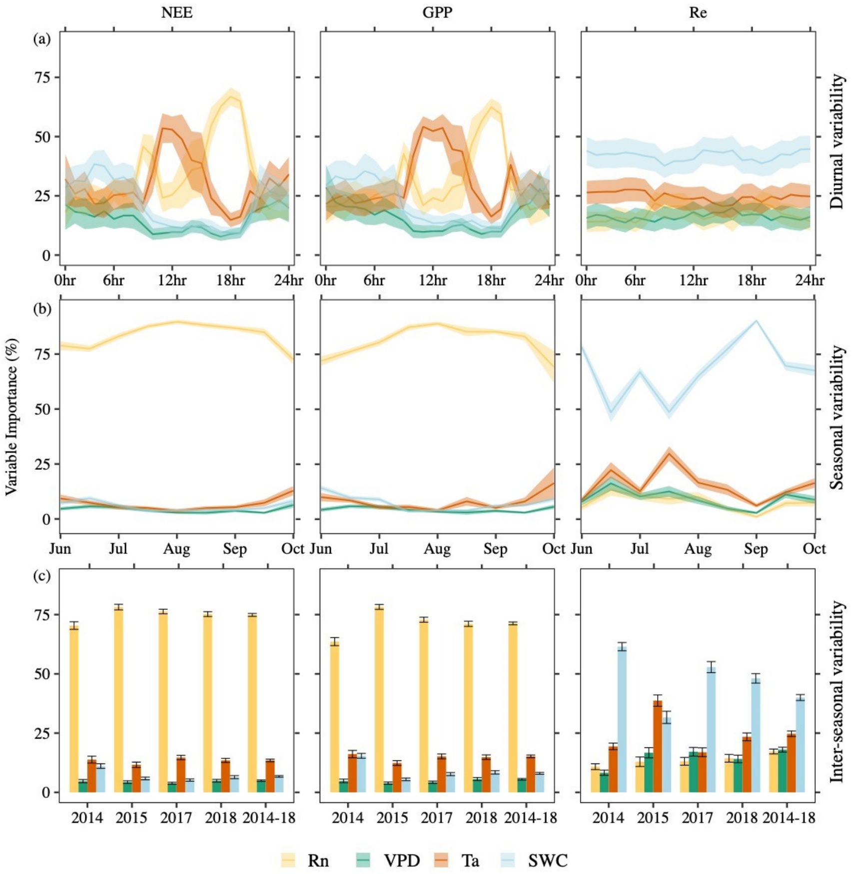
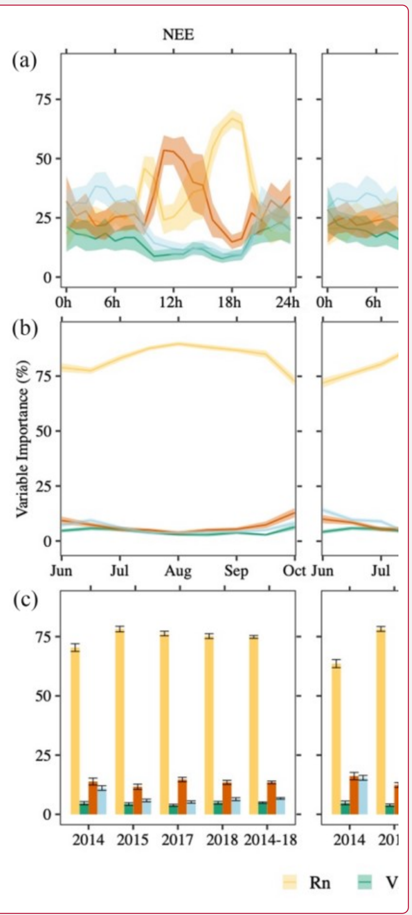


Figure 5. Contribution to diurnal and seasonal variation of NEE, GPP, and Re from different environmental drivers (Rn (yellow), Ta (orange), SWC (blue), and VPD (green)). Solid lines with shades (diurnal and seasonal variability) and bars with error bars (inter-seasonal variability) both illustrate the average ± standard deviation of the importance across 1000 decision trees. Inter-seasonal variability refers to the variability of the integrated growing season of 2014, 2015, 2017, and 2018.

4. Discussion

Since NEE is the difference between Re and GPP, environmental variables affecting Re and GPP could affect NEE indirectly (Song et al., 2011). Radiation affects the magnitude of plant photosynthesis and controls temperature, one of the key factors related to C fluxes. Abundant radiation benefits photosynthesis and respiration and thus directly affects the C sink strength of an alpine wetland



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ecosystem in the Qinghai Lake basin (Cao et al., 2017). In this study, radiation has been identified as the most important factor that regulating diurnal and seasonal variations of GPP and NEE, but soil moisture contributed the most to the variation of Re. On annual scale, Niu et al. (2017) show that 99% of the interannual variation of NEE in an alpine swamp meadow can be well explained by temperature conditions, precipitation and radiation. The results of this study demonstrate that ecosystem C sequestration is regulated not only by radiation and temperature but also by soil moisture in the alpine swamp meadow site studied herein. Given there were no significant differences in net radiation among the four years we studied, the effects of SWC and temperature on C fluxes on diurnal and seasonal scales are therefore discussed in detail below.

4.1 Low soil moisture is associated with enhanced ecosystem respiration

A previous study in alpine meadow ecosystems found that water stress may be the key limiting factor leading to a decline in the photosynthetic rate at noon with a low SWC of 6–21% (Zhang et al., 2018). In this alpine swamp meadow, the soil layer maintained a relatively high SWC due to the frequent precipitation during the growing season. SWC was always greater than 70% during the entire study period (Fig. 2(b)). Therefore, microbial activity, and thus heterotrophic respiration were likely suppressed by the anaerobic environment due to saturated soil water condition (Chimner and Cooper, 2003; Sun et al., 2021). At this site, SWC was found to be a more important factor than temperature controlling the variability of Re at different time aggregations (Fig. 5(a), (b), (c)). This result suggests that even under water-saturated conditions, the C dynamics of this alpine swamp meadow are still highly sensitive to changes in soil moisture and could therefore be significantly influenced by future changes in water supply (Li et al., 2015). In fact, previous studies have stressed that soil moisture will likely interact with temperature to affect Re (Han et al., 2013) and therefore modify the overall C sink strength.

To better understand the underlying mechanisms around how SWC interacts with the C fluxes in the studied alpine swamp meadow ecosystem, we selected two late growing season periods, which have significant differences in SWC but no significant difference in Ta (Fig. 6(a); Table S2).

The most significant difference in C fluxes between the late growing season of 2014 and 2015 was observed in Re (p<0.05). Additionally, on both diurnal and seasonal scales, a 15.4% decrease of SWC in the late growing season of 2015 resulted in a 25.7% increase of Re and a 19.4% decrease in net C uptake

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Since C fluxes are affected by plant phenology and climate factors, including temperature, soil moisture, and radiation simultaneously (Fig. 5), to analyze the effect of a single factor, ideally, other factors need to be identical or at least closed (no significant differences). Based on this theory and t

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compared to 2014 (Figs. 6(a), (b); Table S2). According to Jansson and Hofmockel (2020), the intensification of anaerobic conditions due to water saturated soil can be responsible for weaker respiratory losses. This finding suggests that drier conditions in 2015 likely prevented this alpine swamp meadow from water-logged states, thereby strengthening soil respiration due to improved soil aeration (Wang et al., 2014).

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Although the SWC in September 2015 was much greater than the 6–21% range reported by Zhang et al. (2018), our data suggest that a 22.2% reduction in SWC in September 2015 resulted in a 51.6% decline in net C uptake compared to September 2014 (Fig. S1; Table S3). There is evidence from the literature that the rates of net C uptake in alpine wetlands during the growing season can be lower under drier conditions (Hao et al., 2011), indicating that this alpine swamp meadow ecosystem may be adapted to high levels of SWC (Li et al., 2015). Higher SWC may limit the diffusion of oxygen from the atmosphere to the soil, inhibiting the activity of microorganisms and reducing the decomposition rate of soil organic matter (Chimner and Cooper, 2003). Our comparisons suggest that drying can weaken the overall C sink strength in this alpine swamp meadow ecosystem. Wetlands are predicted to experience lower water tables due to permafrost degradation in the Tibetan Plateau and, therefore, permafrost thaw-induced wetland drying could enhance the response of C emissions to climate warming (Yu et al., 2020).

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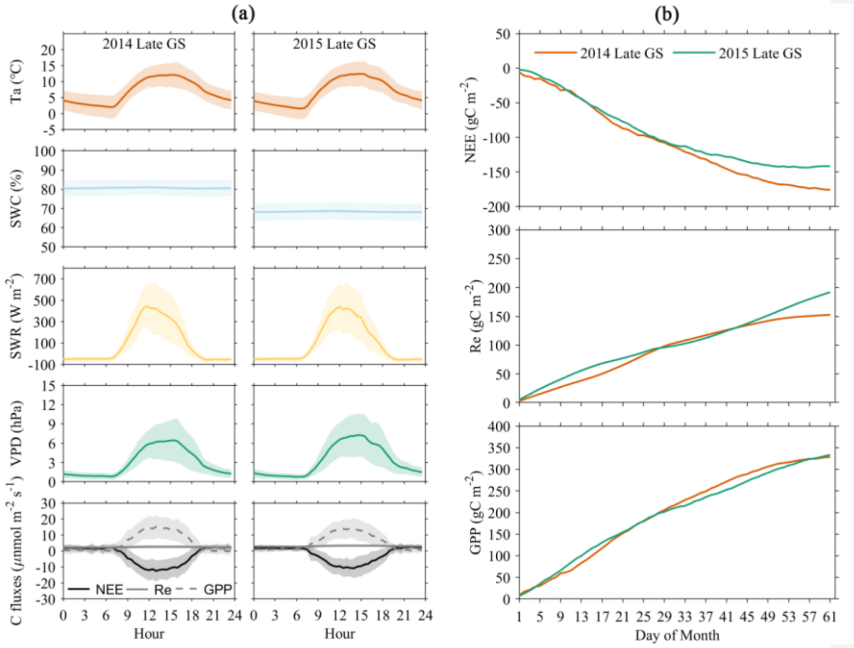

Figure 6. (a) Comparisons of the diurnal variations of environmental drivers (Ta, SWC, Rn, and VPD) and C fluxes (NEE, Re, and GPP) between the late growing season of 2014 and 2015. The shading represents the mean ± standard deviation of the presented variables. (b) Comparisons of the daily accumulated C fluxes (NEE, Re, and GPP) between the late growing season of 2014 and 2015. Note: late GS represents late (Aug.–Sep.) growing season.

4.2 Temperature increase leads to higher C losses

The important role played by temperature controlling C exchange has been extensively found in alpine marshland across the QTP (Qi et al., 2021). For example, Zhao et al. (2010) and Zhao et al. (2005) show that Re follows the exponential variation of soil temperature. Zhu et al. (2020) also suggested that soil temperature plays the most important role in the change of monthly Re in the alpine wetland at Luanhaizi, northeastern Qinghai-Tibetan Plateau. We therefore explored another comparison between the late growing season of 2014 and 2018 (Fig. 7(a), (b); Table S2) when phenology, radiation, and SWC were almost identical at both periods but temperature differed. Compared to 2014, a 25% increase in Ta in the late growing season of 2018 led to joint larger GPP and Re fluxes (Fig. 7a, b; Table S2). Although both GPP and Re increased, the intensification in Re was greater than GPP, indicating that warmer

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temperatures had a stronger impact on Re, resulting in a decrease of the net C uptake (Fig. 7(b); Table S2). To evaluate if this finding is also consistent at an annual scale, we further analyzed annual aggregated data. An annual comparison was made between 2014, 2017, and 2018 when SWC were found insignificantly different while temperatures in 2017 and 2018 were 44.4% higher than in 2014 (Table S4). Again, this 44.4% increase in Ta in 2017 and 2018 both led to stronger GPP and Re (Table S4). Although both GPP and Re increased, the intensity in Re was greater than GPP, indicating that warmer temperatures have a stronger impact on Re at this site, resulting in an approximately 50% decrease of the net C uptake (Table S4).

This comparison suggests that future warming could weaken the overall C sink strength in this alpine swamp meadow ecosystem. Similar climate sensitivities have also been found in recent studies. For example, a study performed by Niu et al. (2017) in an alpine swamp meadow on the central Tibetan Plateau suggests Re was more sensitive to increased temperature than GPP. This suggests that global warming may exacerbate future C releases in the alpine wetlands of the QTP (Gao et al., 2019; Niu et al., 2017; Zhu et al., 2020). Liu et al. (2018) concluded that warming has a significant inhibitory effect on GPP and minor effect on Re, resulting in a weaker carbon sequestration capacity of their studied alpine wetland ecosystem. However, other researchers have also reached different conclusions. For instance, Qi et al. (2021) found that GPP is consistently more sensitive than Re to changes of temperature at daily, seasonal, and annual scales, suggesting that cold condition can act as strong constraint on C uptake in alpine marshlands. Wei et al. (2021) also found that the uptake of C by plants will exceed the amount of C release under warmer and wetter climate conditions based on manipulative experiments and model simulations for the Tibetan Plateau. Their study is based on a longer-term trend while our study only covers 4-years of year-round observations thus site-specific differences in time and space scales may explain this variability. These inconsistent ecosystem responses suggest that there are still large uncertainties regulating the responses of C fluxes to temperature variation and further work is still crucial.

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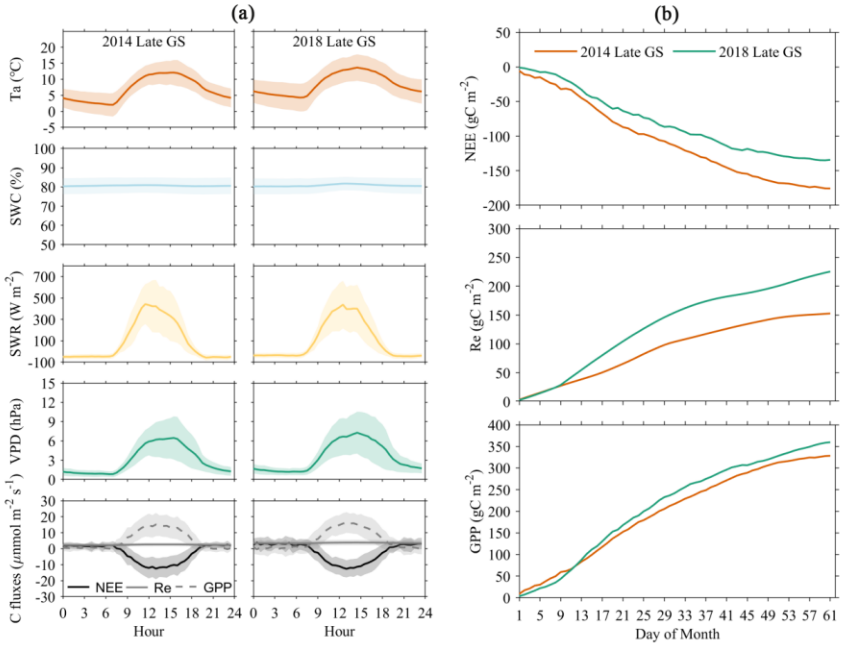

Figure 7. (a) Comparisons of the diurnal variations of environmental drivers (Ta, SWC, Rn, and VPD) and C fluxes (NEE, Re, and GPP) between the late growing season of 2014 and 2018. The shading represents the mean ± standard deviation of the presented variables. (b) Comparisons of the daily accumulated C fluxes (NEE, Re, and GPP) between the late growing season of 2014 and 2018. Note: late GS represents late (Aug.–Sep.) growing season.

4.3 Combined effects of temperature and soil moisture on C exchange dynamics

The QTP experienced a higher rate of temperature increase than that of the Northern Hemisphere average (Zhang et al., 2013). The effects triggered by climate-induced warming over NEE in this area have been argued to either increase or decrease the net C balance NEE, or even have no effect whatsoever (Ganjurjav et al., 2018; Li et al., 2020; Wu et al., 2011; Zhu et al., 2017). These inconsistent responses could be due to water limitations offsetting the C balance or even reversing the effect of elevated temperatures, which change the decomposition and photosynthetic processes (Wu et al., 2011; Yu et al., 2013; Zhao et al., 2019a). Alpine swamp meadows of the QTP have recently attracted much attention because they hold 5.9% (~ 1.98 Pg C) of the total grassland soil organic C (~ 33.52 Pg C). Such ecosystems have the highest organic C density (~ 50 kg C m^{-2}) and play an important role in the global

C cycle (Niu et al., 2017). To test whether the observed SWC effects in this study were representative of other sites on the QTP and put it into a broader perspective, we examined the temperature and precipitation (as a proxy for SWC) impacts on NEE (Liu et al., 2016).

The NEE observations from this study were within the NEE ranges of previous studies in similar ecosystems located across the QTP (-255.5 – 173.2 g C m^{-2} y^{-1}) (Table 2). According to Wei et al. (2021), there are six observational studies about C flux around our study site, three of them are focused on alpine swamp meadows. Among them, one study had one-year dataset (Zhang et al., 2008), and the other two characterized the same location (Zhao et al., 2005, 2010). The three studies were reported as a net C source, while our 4-year dataset revealed that this alpine swamp meadow functioned as a net C sink of -168.0 ± 62.5 g C m^{-2} y^{-1} at a 3571 m asl.. The different directions of C exchange suggest that there are still uncertainties in our understanding of C exchange in alpine swamp meadows, and further efforts are still needed to improve our projection of C balance change of this ecosystem under changing climate.

In addition, the NEE estimates of this alpine swamp meadow show a stronger C sink strength than those from alpine meadows (-161.3 – 85.4 g C m^{-2} y^{-1}) (Chai et al., 2017; Wang et al., 2017; Wu et al., 2020), alpine steppes (-30 – 21.8 g C m^{-2} y^{-1}) (Wang et al., 2018; Wang et al., 2020a; Wang et al., 2020b; Wu et al., 2010), and alpine shrublands (-14 – -67 g C m^{-2} y^{-1}) (Zhao et al., 2005, 2006). This is likely a result of the inhibiting effects of the nearly-saturated soil condition over soil respiration (Sun et al., 2021). In permanently or seasonally inundated swamp meadows, high SWC may have triggered lower C loss rates and further benefited C preservation. At our site, the higher C sink strength was likely attributed to higher precipitation (and therefore higher SWC) and lower temperature, which created colder and more humid conditions than other sites (Table 2). It has been demonstrated that cold and humid conditions favour stronger C sinks in alpine meadow ecosystems (Fu et al., 2009).

The interannual comparison of the sites presented in Table 2 shows that under low annual precipitation conditions (~ 300 mm), the joint effects of warming and reduced precipitation weakened the net C uptake at Damxung (Niu et al., 2017), and even turned the C sink of Xiaobo Lake wetland into a C source when comparing 2015 with 2012 and 2013 (Cao et al., 2017; Wu et al., 2018). Under relatively high annual precipitation (~ 500 mm), the joint effects of warming and increased precipitation enhanced C release in Haibei^{a} site when comparing 2006 to 2004 and 2005 (Zhao et al., 2010). This indicates that net C uptake under warming conditions can be weakened even under high annual precipitation rates.

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Table 2 Comparison of annual NEE (g C m^{-2} y^{-1}) at different sites in the QTP.

Site	Altitude (m)	Ecosystem	Year	Ta (°C)	P (mm)	Annual NEE	Reference
Haibei^{a} (37º35′N, 101º20′E)	3200	AWM	2004	2.3	493.5	101.1	Zhao et al., 2010
			2005	2.2	475.2	44.0	
			2006	3.6	562.4	173.2	
Xiaopo Lake (36°42′N, 100°46′E)	3228	AWM	2015	2.8	304.3	54.6	Wu et al., 2018
			2012	1.2	357.0	-225.6	Cao et al., 2017
			2013	1.2	357.0	-255.5	
Damxung (30°28′N, 91°4′E)	4285	ASM	2009	3.4	208.9	-148.5	Niu et al., 2017
			2011	2.6	393.3	-190.8	
Haibei^{b} (37º35′N, 100º00′E)	3571	ASM	2014	-0.9	662.8	-240.3	This study
			2015	-0.6	521.4	-200.1	
			2017	-0.5	661.2	-118.1	
			2018	-0.3	624.3	-113.4	

Note: P denotes precipitation, AWM denotes Alpine Wetland Meadow and ASM represents Alpine Swamp Meadow, Haibei^{a} and Haibei^{b} denotes different sites.

5. Conclusions

The alpine swamp meadow from the QTP presented in this study has been found to act as a consistent and strong sink of CO$_2$ (-168.0 ± 62.5 g C m^{-2} y^{-1}). The results from a novel machine learning technique revealed that air temperature is the most important variable driving NEE and GPP on a diurnal scale, while net radiation has a stronger importance controlling the seasonal variability of the same fluxes. Soil moisture, however, has the largest influence over Re variability on diurnal and seasonal scales, suggesting that SWC is a key control on Re. In addition, air temperature played a less important role in regulating Re. This study reveals that both drying and warming can suppress net C uptake in water-saturated alpine swamp meadow ecosystems by enhancing Re. The response of net C uptake to climate warming further indicates that the forecasted warming in the QTP will not always increase the net C sink strength. Our results not only highlight the contributions of soil moisture in regulating C sequestration

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under high water conditions but also support future process-based modelling initiatives focusing on alpine swamp meadow ecosystem C dynamics.

Data availability. Post-processed data and scripts used in this paper are available from the authors upon request (xyli@bnu.edu.cn).

Author contribution

JQ, XL, LL, TRC, XW, and ELB designed the research. JQ, LL, and ELB processed the data and performed the analyses. YJ and HY helped collect the data. JQ and ELB created the visualization of the outputs. JQ, XL, and ELB prepared the manuscript with contributions (writing, review, and edition) from LL, TRC, and ZJ.

Competing interests. The authors declare that they have no conflict of interest.

Acknowledgements

The study was financially supported by the National Natural Science Foundation of China (NSFC 41730854 & 41971029), the second Tibetan Plateau Scientific Expedition and Research Program (STEP 2019QZKK0306), the Strategic Priority Research Program of Chinese Academy of Sciences (XDA20100102), and projects from the state Key Laboratory of Earth Surface Processes and Resource Ecology. We also gratefully acknowledge the financial support from the China Scholarship Council (No. 201906040130) and the Faculty of Technical Science from Aarhus University. Additionally, ELB was funded by the Greenland Research Council, grant number 80.35, financed by the “Danish Program for Arctic Research.

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